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AN EARLY TRIASSIC VERTEBRATE ASSEMBLAGE FROM KARST DEPOSITS AT CZATKOWICE, POLAND

(WCZESNOTRIASOWY ZESPÓŁ KRĘGOWCÓW Z UTWORÓW KRASOWYCH
STANOWISKA CZATKOWICE, POLSKA)

EDITED BY

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(WITH 194 TEXT-FIGURES)

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PREFACE

The Early Triassic (early Late Olenekian) fauna of small vertebrates presented in this volume comes from karst deposits developed in Early Carboniferous (Turnaisian to Mid Visean) limestone at the Czatkowice quarry near Kraków (Southern Poland). All the material comes from a single exposure, referred to as Czatkowice 1.

In Czatkowice quarry the bone-bearing breccia was first collected from waste-heaps, but was eventually discovered *in situ* by a team from the Institute of Geological Sciences of Jagiellonian University, Kraków (Paszkowski and Wieczorek 1982). Unfortunately, the geology of the site was only briefly studied, because of the rapid exploitation of the quarry. The original description of the geological setting is that of Paszkowski and Wieczorek (1982).

Through the kindness of colleagues from the Jagiellonian University (and notably Ryszard Gradziński), the material was transferred to Teresa Maryańska and Halszka Osmólska (Museum of the Earth and Institute of Paleobiology of the Polish Academy of Sciences, Warsaw, respectively), who took part in the exploration of the site and performed a preliminary paleontological examination.

The bone-bearing breccia was subjected to chemical preparation in acetic acid in the Museum of the Earth and the Institute of Paleobiology, Polish Academy of Sciences. However, more effective preparation started only in the 1990's and has now terminated. Around this time, Halszka Osmólska and Teresa Maryańska, both fully engaged in dinosaur studies, kindly offered the Czatkowice 1 material to one of us (MBB). A more detailed study then began in collaboration with Susan Evans from University College London, first under the British/Polish Joint Collaboration Programme funded by the British Council and Polish State Committee for Scientific Research (1993–1996), then only under the latter organization (2000–2003; 6 P04D 072).

We were later joined by colleagues who contributed to the study of particular groups. Michail Shishkin, a fossil amphibian expert from the Paleontological Institute of the Russian Academy of Sciences (Moscow), took over the temnospondyl material in collaboration with Tomasz Sulej (Institute of Paleobiology); Andriej Sennikov from the Paleontological Institute of the Russian Academy of Sciences (Moscow) contributed to the work on archosauriforms; and Mariusz Lubka, a PhD student from Wrocław University, contributed to the procolophonian paper.

This long and detailed project would not have been possible without the help and support of many people, especially the technical staff of the Institute of Paleobiology and Museum of the Earth who completed the time-consuming chemical preparation of the matrix and the recovery of bone fragments. We are particularly indebted to Ewa Hara for her exquisite preparation work, to Cyprian Kulicki for SEM micrographs, to Marian Dziewiński for photography, and to Aleksandra Hołda-Michalska for most of computer illustration work. In total, several hundred kilograms of Czatkowice 1 breccia were processed, yielding around 1500 catalogued specimens and many thousands of valuable unnumbered specimens.

Early Triassic tetrapod faunas are of particular interest in documenting the biotic changeover that took place on land at the Permo-Triassic boundary (Ochev 1993). In terms of Scythian paleogeography, these faunas are best known from the temperate latitudes of southern Gondwana (primarily in South Africa, Australia and Antarctica) and, in the northern hemisphere, from the areas adjacent to the circum-equatorial xeric belt (such as Eastern Europe and Greenland). The belt represented a vast arid/semiarid zone which included, in particular, most of Central and Western Europe (Lozowsky 1993). It was inhabited by impoverished tetrapod communities largely concentrated within and around freshwater basins. Accordingly, their fossil record is usually dominated by aquatic temnospondyl amphibians (Shishkin and Ochev 1993).

In this context, the Early Triassic tetrapod assemblage from Southern Poland, surveyed for the first time in its entirety in the present volume, deserves special attention. Although it came from the xeric belt, its structure differs notably from that of other assemblages from elsewhere in the same climatic zone (mostly in Central Europe and North American southwest). In contrast to them, the Polish fauna is dominated by a terrestrial component, with abundant archosauriform reptiles, while the bones of aquatic amphibians are much rarer. This "reversed" pattern of faunal preservation unquestionably resulted from the specific environmental setting and unusual mode of burial of the Czatkowice vertebrates (Shishkin and Sulej 2009). Their remains were accumulated in karst fissures developed within the upland relief rather than in the lowland floodplain deposits that typically host vertebrate fossils. As a result, unlike most other localities, there was no preferential burial of aquatic or subaquatic animals.

The unusual conditions under which the Czatkowice 1 locality developed were probably responsible for the presence of a number of exceptionally rare forms, such as stem-frogs, small lepidosauromorphs, and the earliest euparkeriid archosaurs, all hitherto unknown from the Early Triassic of Laurasia. On the other hand, the Czatkowice temnospondyl amphibians have been found to be readily comparable at generic level with those of East Europe, where they provide a basis for high resolution subdivision of the regional Triassic faunal succession (Shishkin and Ochev 1993; Shishkin *et al.* 2000). This correspondence is regarded as a decisive factor in dating the Polish assemblage. In summary, these new records and the often exquisite preservation of the material from which they are described, make a significant contribution to our current knowledge of early Mesozoic land vertebrates.

The Editors

THE EARLY TRIASSIC KARST OF CZATKOWICE 1, SOUTHERN POLAND

MARIUSZ PASZKOWSKI

Paszkowski, M. 2009. The Early Triassic karst of Czatkowice 1, southern Poland. *Palaeontologia Polonica* **65**, 7–16.

The Czatkowice 1 locality, that yielded a rich fossil assemblage of small tetrapods, is situated in the Dębnik area near Kraków as one of a number of karst forms developed within the Paleozoic Moravia-Małopolska carbonate platform. The fossiliferous deposits occurred in a funnel-shaped structure, about 4 m in width, and 6 m in depth, tapering downwards and passing into several subhorizontal corridors in the basal part. It probably represented a system of collapsed and coalescent paleodolines. The upper part of the main sinkhole was filled with a few meter thick sequence of yellow sands and silts, whereas the lower part contained green-brownish and variegated cave loams with gypsum intercalation and calcite concretions (hollow septarians) as well as calcite flowstones. The deepest 0.7 m of the cave was filled with fine cross-bedded calcareous sandstone as well as by spar-cemented layers and discrete lenses of bone breccia. The fallen blocks of early Permian rocks indicate a post-Autunian, probably early Triassic age for the breccia. Biostratigraphic evidence suggests the early Late Olenekian age of Czatkowice 1 bone bearing deposits. They underlie the cave loams with gypsum and stromatolites that may have been deposited under marine inundation of the late Late Olenekian Röt transgression.

Key words: Karst, Early Triassic, Czatkowice.

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INTRODUCTION

The karst deposits developed in host limestones of the Early Carboniferous (late Tournaisian to mid Viséan) at the Czatkowice quarry (Kraków Upland, southern Poland) are the source of the Early Triassic fauna of small vertebrates, which is a focus of the present volume. The quarry is located some 20 km to the WNW of Kraków in the area of Paleozoic exposures bordered by the young tectonic depression, the Krzeszowice Graben, to the south, by the Upper Silesian Coal Basin to the west, and by a large area of Kraków Jura to the east and north (Fig. 1). The Krzeszowice Graben extends nearly east-west and is filled with Miocene sediments.

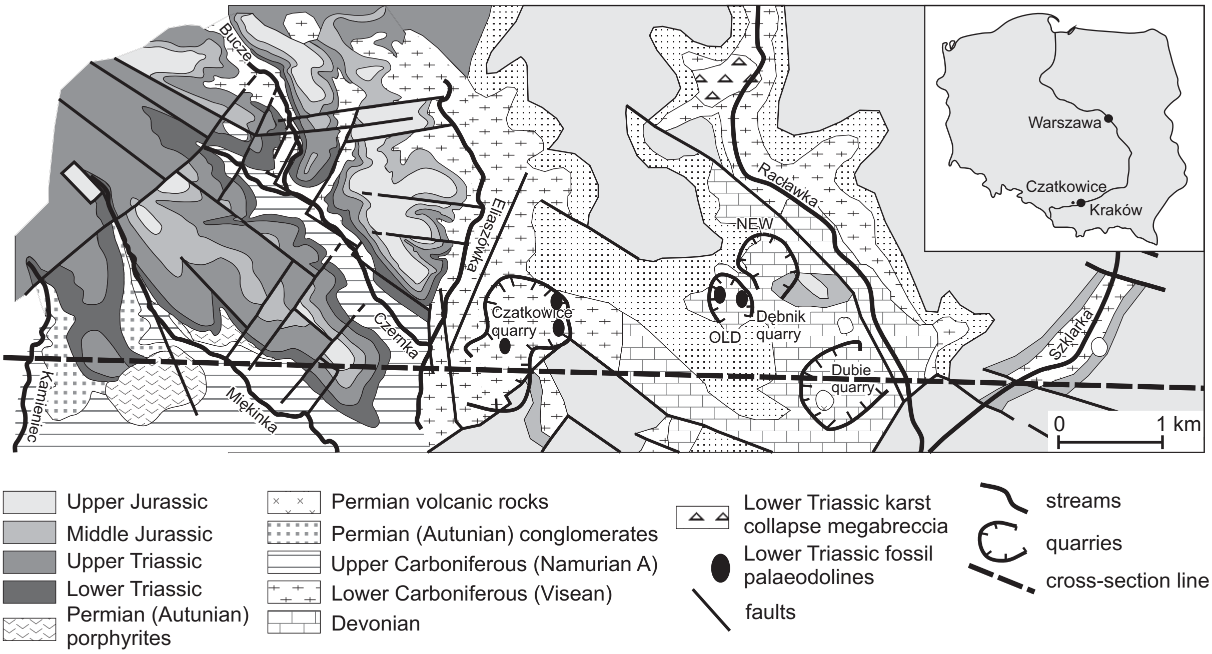

Fig. 1. Geological map of the Dębnik Anticline area (north of Krzeszowice town).

All the material described in the present volume comes from one of the numerous karst forms, of different ages, developed in the Czatkowice quarry (Paszkowski and Wieczorek 1982). This funnel-shaped megabreccia (Fig. 2B), referred to as the Czatkowice 1 locality, was discovered in late 1970's. It was briefly studied by Paszkowski and Wieczorek (1982) and then quarried out. The objective of this paper is to present a geological setting for the locality at Czatkowice 1, and to discuss the paleoenvironment of the Czatkowice 1 site.

The dating of the Czatkowice 1 deposits is based upon biostratigraphical criteria worked out for the East European (Cis-Uralian) Triassic tetrapod succession (Shishkin *et al*. 2000). This succession has been shown to include subsequent faunal groupings spanning the entire range of the Triassic (Ochev and Shishkin 1989; Shishkin and Ochev 1993). It was calibrated against the standard marine scale owing to marine intercalations with stratigraphically diagnostic fossils, such as *Parotosuchus*, which occurred in both continental Yarenskian deposits of Moscow syneclise and the marine Upper Olenekian sediments of Bogdo Mountain and Mangyshlak, Tethyan Province (Lozovsky 1993). The Czatkowice 1 assemblage correlates with the lower *Parotosuchus* faunal grouping of this scale (Fig. 5), and on this basis, the age determination of these deposits is early Late Olenekian (Shishkin and Sulej 2009). Attempts to extract spore/pollen material (S.E. Evans, unpublished data) gave no result, and no conchostracan remains have been found.

Karstification was a multiple process (polyphase karst) (Lis and Wójcik 1973; Paszkowski and Wieczorek 1982; Paszkowski 2000) that occurred several times in the basement of the Kraków–Silesia Laramide monocline, mainly in the host platform of Devonian and Carboniferous carbonates. The existence of the Permian–Triassic paleokarst has also been documented in the Holy Cross Mountains (*e.g.*, Głazek 1989;

Urban 2007). The best review of paleokarst investigation in the whole of Poland has been done by Głazek (1989 and references therein).

Outside of Poland, the Mesozoic paleokarst is best known from South Britain (Robinson 1957; Ford 1966; Fraser 1985; Fraser 1994; Wall and Jenkyns 2004; Whiteside and Marshall 2008), but is no older than the Late Triassic. The early Triassic karst is practically unknown except from unconformity-related early Triassic karst discovered in the Devonian carbonate host rocks of the Barrandian area in Bohemia (Bosák 1997; Žak *et al.* 2007).

Acknowledgments. — I am indebted to all the colleagues, who discussed with me the problems related to the topic of this account, for their valuable criticism and comments. Thanks are also due to Artur Kędzior (Institute of Geological Sciences, Polish Academy of Sciences, Kraków) and to Aleksandra Hołda-Michalska (Institute of Paleobiology, Polish Academy of Sciences, Warsaw) for preparing figures to this paper.

GEOLOGICAL SETTING OF CZATKOWICE 1 LOCALITY

The Czatkowice quarry (Fig. 2A) is a large active quarry of the Early Carboniferous limestones located in the western limb of the Variscan Dębnik Anticline (Kraków Upland, southern Poland), north of Krzeszowice area. The central part of the Dębnik Anticline is composed of dolomites and limestones of Givetian to Famenian age that pass into late Tournaisian to mid Viséan sediments towards the western limb of the anticline, where Czatkowice quarry is situated (Fig. 3). The whole complex of Devonian and Early Carboniferous limestones, up to 1600 m in thickness, belongs to the wide Moravia-Małopolska carbonate platform (corresponding to Bohemian–Vindelician Massif plus Pre-Carpatian Massif; Fig. 6).

To the west of Krzeszówka (Fig. 3B) and Eliaszówka faults the Carboniferous (Mississippian and lower part of the Pennsylvanian) rocks are continuously covered with continental or marine Triassic and Jurassic deposits (Fig. 3B). Further to the west, Carboniferous rocks are covered by an Early Permian succession of continental deposits, up to 600 m thick. The most characteristic deposits of the Permian complex in the described area are various volcanogenic rocks. Red clasts of these Permian rocks are found redeposited in some coarse grained Mesozoic karst infillings (*e.g.*, at the Czatkowice 1 site). In contrast, to the east of the Krzeszówka and Eliaszówka faults (Fig. 3B) there is no continuous cover of Permian and Triassic deposits,

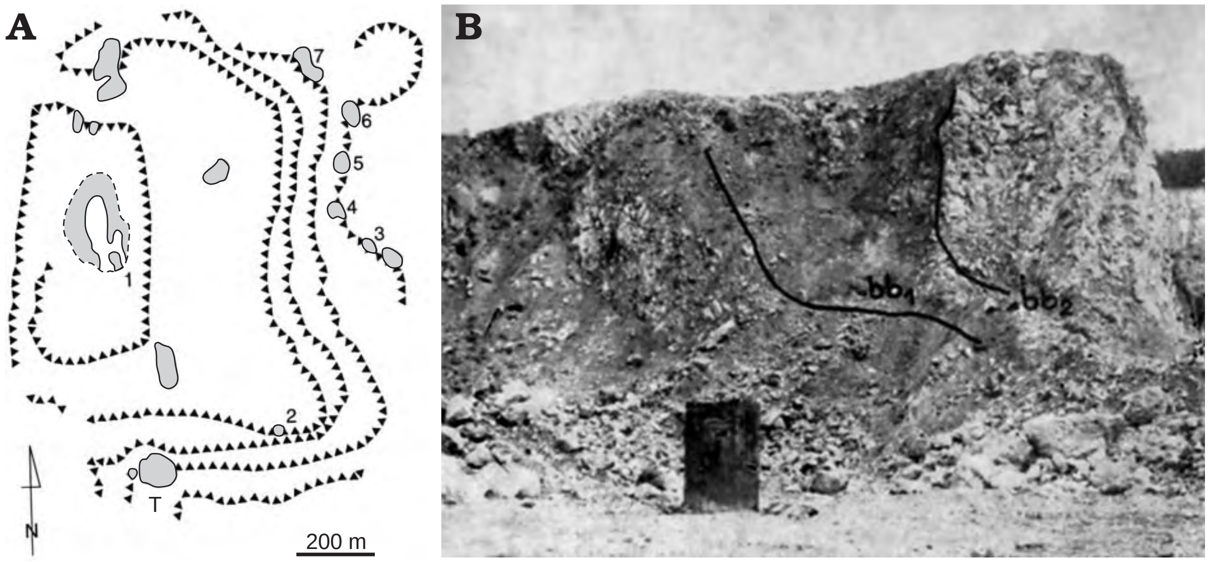

Fig. 2. **A**. Sketch map of Czatkowice quarry (in 1979) showing localizations of karst forms (1–7 and T after Paszkowski and Wieczorek 1982). **B**. View of the Czatkowice 1 karst form at the north wall of the Czatkowice quarry (level 310) according to original picture taken by J. Wieczorek in 1979 (after Paszkowski and Wieczorek 1982, phot. 1). The funnel-shaped outline of a preserved fragment of the cave with bone breccia in the lower part – bb1; a fragment of subhorizontal corridor covered by rubble heap – bb2.

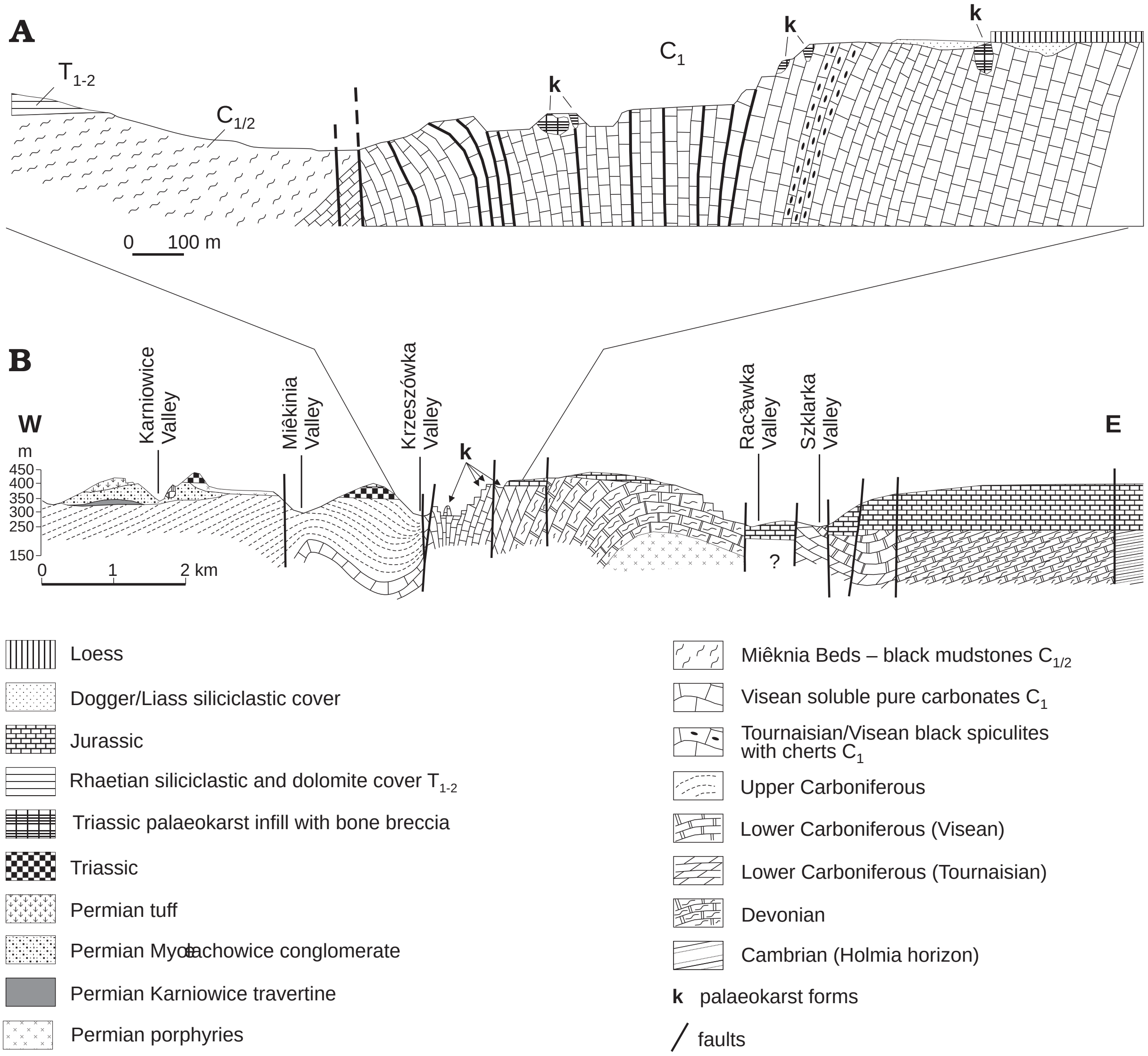

Fig. 3. **A**. WE cross-section of the Dębnik Anticline, crossing Czatkowice quarry. **B**. Regional geological WE cross-section of the Dębnik Plateau karstified area.

the older Paleozoic rocks (Cambrian to Early Carboniferous) being directly covered by Mid Jurassic deposits. The Early Permian, Early Triassic, Late Triassic and Jurassic pre-Callovian deposits occur as only local fillings of paleokarstic depressions in this region (Fig. 3A), including those in Czatkowice quarry (Paszkowski and Wieczorek 1982).

In the Czatkowice part of the Dębnik Anticline, the Carboniferous rocks display a very steep inclination, the dip changing from 50°–60° in the eastern part to about 90° in the central part of the quarry and then dipping to the east in the western part of the quarry (Fig. 3A). Resulting from Variscan tectonics, this subvertical bedding enhanced the development of very deep karst forms of different age beginning with the Late Paleozoic and continuing until the advance of the Callovian sea with an interruption during the Muschelkalk transgression (Paszkowski and Wieczorek 1982).

Several forms of a supposed Late Permian to Early Triassic karst have been discovered in the Dębnik anticline area. The main object of these studies, the Czatkowice 1 karst form, was preserved as a funnel-shaped structure (Fig. 2B), about 4 m in width, and 6 m in depth, tapering downwards and passing into several subhorizontal corridors in the basal part. It probably represents a system of collapsed and coalescent paleodolines (uvala). It was developed in the steeply oriented, light-colored Viséan thick-bedded limestone and was preserved, as a remnant left intact during the exploitation process, on the bottom of the quarry, at the

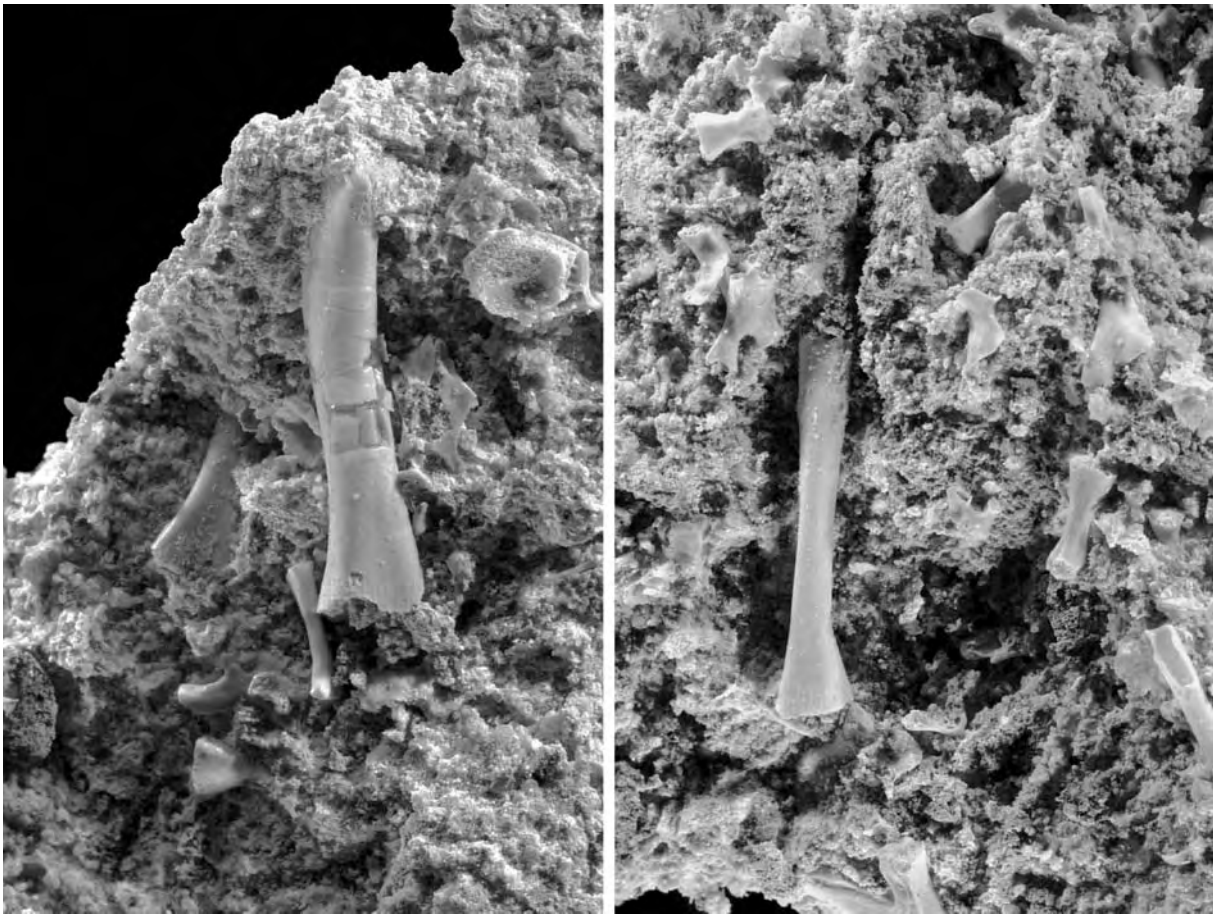

Fig. 4. Pieces of Czatkowice 1 bone-bearing breccia with bones exposed after treatment with dilute acetic acid.

altitude 310–330 m. Until the late 1970's, it still existed in the middle of the quarry floor (Fig. 2A), but was later completely quarried out.

The walls and especially the roof of the cave were covered in some places by coarse crystalline, brown and pink calcite flowstones, from 20–30 cm up to 1 m thick, strongly resembling and probably interconnected with the Early Permian hydrothermal onyx vein system of the neighborhood. The upper part of the main sinkhole was filled with a few meter thick sequence of yellow sands and silts, whereas the lower part contained green-brownish and variegated cave loams with gypsum intercalation and calcite concretions (hollow septarians) as well as calcite flowstones. An important constituent of this megabreccia, despite of host Mississipian limstones, are fallen blocks of Early Permian hydrothermal endokarst speleothems: red crystaloclastic carbonates with flowstones and red endostromatolite-bearing calcite-veins.

The bone breccia occupied only the deepest 0.7 m of the cave infill. This part of the cave was filled with fine cross-bedded calcareous sandstone as well as by spar-cemented layers and discrete lenses of bone breccia. The breccia was vertically cracked and the cracks were filled by cave loams. The bone breccia layers demonstrated a distinctive grading, and flute marks on the bottom surfaces. In some places they formed elongated gutter casts with bowl-shaped cross section.

Both in the calcite-cemented bone breccia, and calcareous sandstone above it, minor constituents are well-rounded quartz grains (0.2 mm in average diameter, reaching up to 1 mm), most probably recycled from adjacent Carboniferous and Permian deposits.

Layers and lenses of brittle sandstone and breccia may possibly have been broken into blocks by mass movements or earlier by compaction or liquefaction of karst loam and telescoping karstification. The edges of separated blocks of breccia were slightly rounded. Smaller fragments have fallen and slid into deeper parts of the cave. This supports a supposition that the Czatkowice 1 megabreccia represents a collapsed and coalescent paleodoline (uvala). This is also true of some other karst forms of Czatkowice quarry, as *e.g.*, the locality

T (Fig. 2A) filled mainly with Permian tuffites (Paszkowski and Wieczorek 1982, phot. 3) that bears traces of roof collapse.

The bone material collected from the Czatkowice 1 breccia (Fig. 4) was disarticulated and damaged, usually broken into pieces, but the fragments were generally finely, three-dimensionally preserved, with relatively little abrasion and polishing. Usually there is no stratification bedding or parallel orientation of the long bones.

STRATIGRAPHIC CORRELATION OF CZATKOWICE 1 BRECCIA

The fallen blocks of early Permian age rocks present in the karst form at Czatkowice 1, provide reliable evidence of a post-Autunian, probably early Triassic age for the breccia (Paszkowski and Wieczorek 1982). As the direct correlation of the Czatkowice 1 karst deposits with the transgression/regression cycles of the Buntsandstein is impossible, the dating of these deposits is based on biostratigraphic criteria of the east European faunal succession (Shishkin and Ochev 1985; Shishkin *et al.* 1995, 2000).

The Early Triassic age of the Czatkowice 1 karst fillings is supported by the studies of the included fauna, with a slight suggestion of a Late Olenekian age, mainly on the basis of the procolophonids (Borsuk-Białynicka *et al.* 1999). The diapsid taxa of the assemblage are less conclusive in this regard. Czatkowice 1 procolophonids display a mosaic morphology, their unicuspid, possibly paedomorphic (Borsuk-Białynicka and Lubka 2009) teeth being combined with a derived heterodonty and reduced tooth count, most compatible with the Olenekian. The rare teeth of *Gnathorhiza*, which is a dipnoan fish ranging up to the early Late Olenekian (Fig. 5), and the lack of *Ceratodus*, another dipnoan fish that already appeared and coexisted with *Gnathorhiza* in the early Late Olenekian (Minikh 2000), suggest an Early Olenekian age of the assemblage (Borsuk-Białynicka *et al.* 2003). However, the cooccurence of *Gnathorhiza* with temnospondyl index taxa of the Late Olenekian (*Parotosuchus* and *Batrachosuchoides*; Shishkin and Sulej 2009) allows still more exact dating of the Czatkowice 1 assemblage. An earliest Late Olenekian age thus seems most probable for the Czatkowice 1 bone bearing deposits.

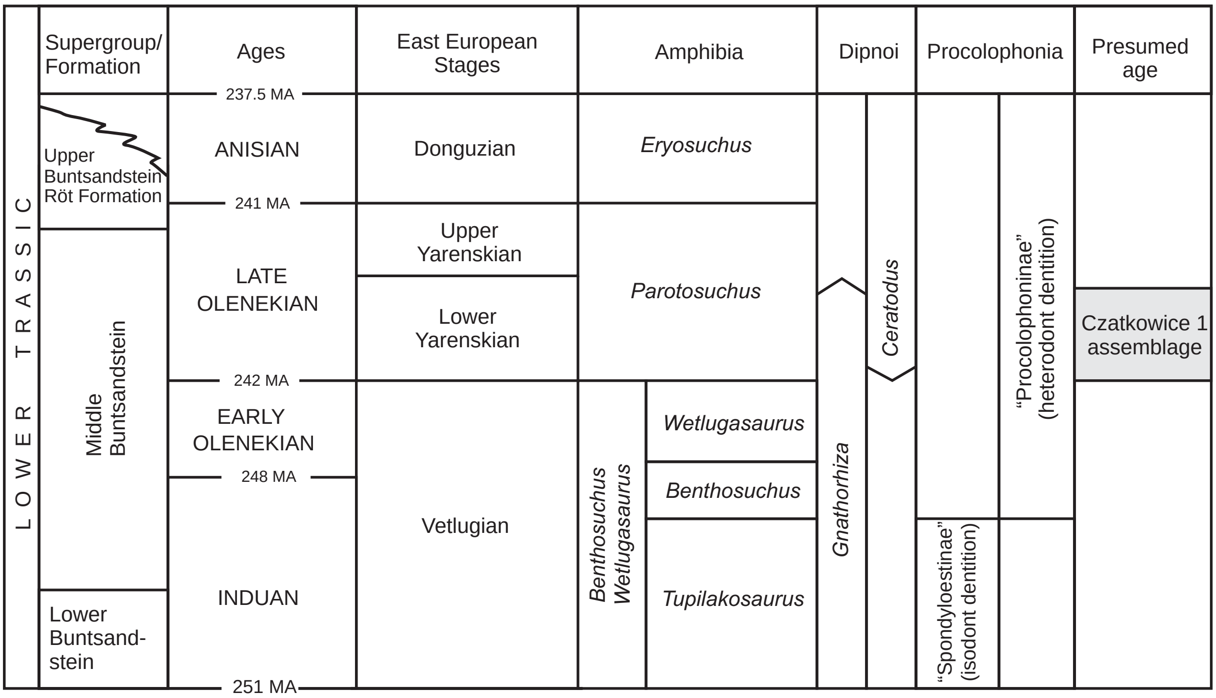

Fig. 5. Biostratigraphy of the Early Triassic of Eastern Europe mainly after Lepper and Röhling (1998) and Shishkin *et al.* (2000). Absolute ages compiled after Gradsten *et al.* (1995) and Becker *et al.* (2008).

DISCUSSION

In the early Triassic, the Dębnik area was situated in the SE part of the central European Buntsandstein or German Basin (Fig. 6) — a post-Variscan epicontinental depression, which extended from England to Poland and from the North Sea to southern Germany (Bachmann 1998). In the Triassic it was affected by syndepositional tectonism (Feist-Burkhardt *et al*. 2008), and by a transgression/regression cyclicity (Bachmann 1998). The seaways opened and closed at different times *via* hypothetical East Carpathian and Silesian-Moravian Gates (Lepper and Röhling 1998), first at the very beginning of the Middle Buntsandstein sedimentation (Szyperko-Teller *et al*. 1997), then at the advent of Röt trangression. The basin was surrounded by the Fennoscandic Baltic Massif to the north to northeast, by the Ardennian–Gallian Massif to the west, and the Bohemian–Vindelician Massif and Pre-Carpathian Massif (including the Dębnik Massif) to the south (Fig. 6). The elevated areas, and mainly those affected by the Variscan and post-Variscan tectonics (Paszkowski 1988), were subjected to karstification. The process occurred several times in a host platform of Paleozoic rocks of the Pre-Carpatian Massif, and particularly in the Devonian through Carboniferous Dębnik Anticline (Paszkowski and Wieczorek 1982; Paszkowski 2000), and notably in the Czatkowice part of the Anticline.

Two main phases of karstification have been recognized in Czatkowice and Dębnik quarries (Paszkowski and Wieczorek 1982). The first one occurred during one of synsedimentary Devonian or Early Carboniferous short emersions (Fig. 2A; locality T of Paszkowski and Wieczorek 1982) and continued through the Early Triassic (*i.e.*, around 243 Ma: Gradsten *et al*. 1995; Becker *et al.* 2008), under continental conditions after Variscan deformations and Late Carboniferous siliciclastic cover removal. It is the Early Triassic section of this phase that is represented by the karst form at Czatkowice 1 (Paszkowski and Wieczorek 1982). The second, distinctive Mesozoic phase began in the Late Triassic and ended in the Mid Jurassic, before the Callovian transgression. The locality Czatkowice 2 (Fig. 2A) and a waste-heap designated as Czatkowice H

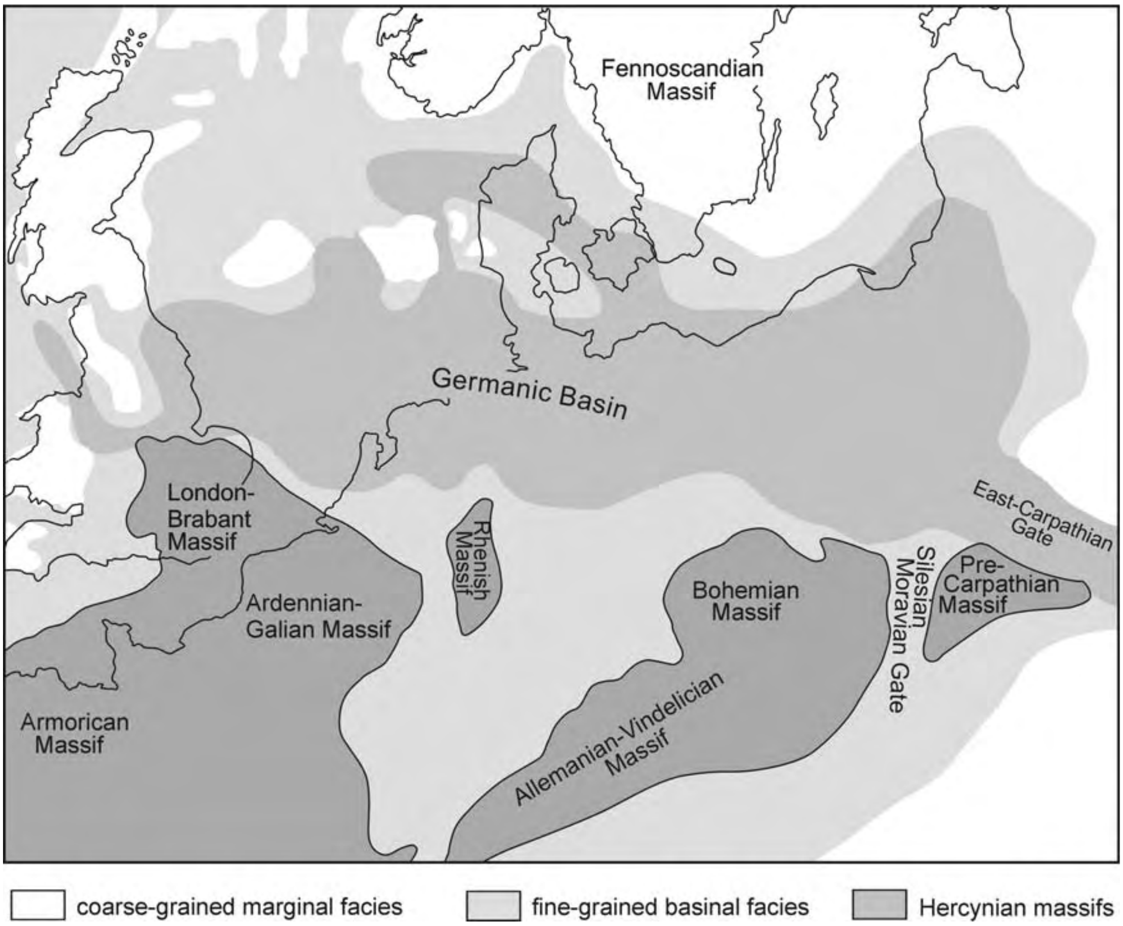

Fig. 6. Late Early Triassic (Röt) palaeogeography of Europe based on Lepper and Röhling (1998).

(Paszkowski and Wieczorek 1982), that yielded the early and middle Jurassic dipnoan fish *Ceratodus phillipsi*, represent this phase.

The Buntsandstein Basin was located within the subtropical zone of northern Pangea, under dry climatic conditions (Feist-Burkhardt *et al.* 2008), and was characterized by a predominantly continental sedimentation in a fluvio-lacustrine environment with restricted marine (two small transgressions prior to the Röt one, the first one coming from the boreal zone: Szyperko-Teller *et al.*1997), and local aeolian influences and a high rate of evaporation. This kind of sedimentation definitely ended with the Röt transgression which corresponds to the late Late Olenekian age (Lepper and Röhling 1998) of the Early Triassic. The transgressing sea, which entered the German Basin, came over the eroded surface of the Dębnik Massif and, most probably, ended the karstification process (Paszkowski and Wieczorek 1982). Apart from this premise, no other suggestion concerning the dating of Czatkowice 1 karst deposits can be deduced from the transgression-regression cyclicity that affected the early Triassic. Whether the process could have continued on partially submerged erosion resistant mogot/inselbergs and horsts, which formed an archipelago until the late Muschelkalk, is not definitely known.

Recent equivalents of the Triassic paleokarst environment of Dębnik area are known from different parts of the world, and notably from Serbia (Miroc Mountains), Spain, Albania, and western-central Anatolia, all of them situated in a classic region of Alpine lateral escape tectonics resulting from Arabian plate collision with Eurasia. They include tectonically uplifted, karstified plateaux penetrated by several sinkholes (dolines), some of them filled with impermeable *terra rossa* clay and fresh water ephemeral water reservoirs (Canik and Corekcioglu 1986), surrounded by alluvial plains, with fauna of small amphibians and fish. Grabens filled up with ephemeral salt lakes and playas contribute to this landscape. In contrast, the shallow marine-flooded Ha Long Bay karst area in northern Vietnam is an archipelago of partially submerged mogot/inselbergs of resistant rocks, and the host of extensive karstification processes. The drowned dolinas are filled with marine water, and include small biostromes and stromatolites.

In Czatkowice 1, the presence of gypsum (as indicator of marine waters evaporation) and stromatolites with coarse calcite crystal fan (pseudomorphs after aragonite), elsewhere known from shallow marine, both carbonate and siliciclastic Permian–Triassic passage sections (Peryt 1975; Szulc 2007), are suggestive of occasional invasions of marine waters on the karstified Dębnik plateau. Discrimination between the marine and fresh-water stromatolites is problematic (Peryt 1975; Paul and Peryt 2000), but the very low level of karstified Dębnik plateau in the Early Triassic, both relative and above sea level altitude (about 200 m above sea level), makes the invasions of highly sediment-charged, turbid flood waters or marine waters quite probable. The main question to be answered is whether the accumulation of the bone-bearing deposits at Czatkowice 1 occurred on an island surrounded and occasionally invaded by the Röt sea or did it occur prior to the Röt transgression?

The following premises support the second option:

The early Late Olenekian age determined for the Czatkowice 1 vertebrate assemblage provides evidence that it existed before the onset of the Röt transgression.

The bone-bearing deposits at Czatkowice 1 underlie, and are thus older than, the several meter thick sequence of cave deposits, such as sands, silts and cave loams with gypsum and stromatolites that may have been deposited under occasional marine inundations of the approaching Röt transgression (Fig. 5).

The vertebrate assemblage of Czatkowice 1 includes definitely terrestrial and fresh-water vertebrates, and no marine elements which would indicate sea shore proximity. In the early Late Olenekian, the region was situated in a low upland and probably well inland.

CONCLUSIONS

The Late Permian/Early Triassic fossil karst forms that occur in the Paleozoic Dębnik massif, are considered remnants of sinkholes (paleodolines). Czatkowice 1 megabreccia probably represents a collapsed paleodoline (uvala).

Variscan and post-Variscan strike-slip tectonics is considered an important agent behind the polyphase karstification of the Dębnik area.

The data inferable from the transgression/regression cyclicity of the Late Paleozoic–Mesozoic sedimentation in the Germanic Basin support the suggestion that the Czatkowice 1 karst deposits belong to the Early Triassic. Similarly, the presence of fallen blocks of Early Permian rocks in the karst form at the Czatkowice 1 locality provides evidence of post-Autunian, probably Early Triassic age of the deposits. This is consistent with the age determination of the Czatkowice 1 breccia as early Late Olenekian (Shishkin and Sulej 2009) based on a correlation with the Early Triassic tetrapod succession worked out for the Eastern Europe (Cis-Uralian) (Shishkin *et al.* 2000). According to this dating, the breccia was deposited prior to Röt transgression.

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TAPHONOMY AND GEOCHEMISTRY OF A VERTEBRATE MICROREMAINS ASSEMBLAGE FROM THE EARLY TRIASSIC FISSURE DEPOSITS AT CZATKOWICE 1, SOUTHERN POLAND

ELIZABETH COOK and CLIVE TRUEMAN

Cook, E. and Trueman, C. 2009. Taphonomy and geochemistry of a vertebrate microremains assemblage from the Early Triassic karst deposits at Czatkowice 1, southern Poland. *Palaeontologia Polonica* **65**, 17–30.

Surface morphology and trace element geochemistry of the bone assemblage from the Early Triassic fissure deposits of the Czatkowice 1 locality near Kraków, Poland, suggest that bones were reworked (probably from ephemeral water bodies) and transported into the nearby cave systems *post mortem*. Geochemical analyses indicate the influence of aeolian conditions during concentration of the Czatkowice assemblage, and show that the assemblage is relatively mixed (averaged) when compared to similar Triassic cave deposits.

Key words: Taphonomy, Triassic, karst deposits, microvertebrates, Rare Earth Elements (REE), geochemistry.

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INTRODUCTION

The processes that contribute to the formation of fossil assemblages are complex. Detailed sedimentological and taphonomic analyses are often needed to determine the extent of time averaging and mixing suffered during the formation of a faunal assemblage, and therefore its ecological significance. Historical archived collections are the main primary source for palaeontological investigations, but these collections consist of bones that have already been excavated and curated, in some cases without full recognition of the importance of detailed taphonomic and sedimentological analysis. Site practicalities may make detailed contextural investigations impossible. In such circumstances it is necessary to develop techniques that may be applied to isolated bones, in the absence of coherent sedimentological data.

Techniques that relate the surface morphology of bones to their *post mortem* history are well established (see for example Behrensmeyer, 1975, 1978, 1982; Fiorillo 1988). Recently these techniques have been augmented by methods based on the geochemical composition of fossil bones. As these characters are intrinsic to the bones themselves, they may be investigated after excavation and curation. The primary aim of this study is to construct a taphonomic history for a microvertebrate assemblage from karst deposits of southern Poland, where primary sedimentological data are missing, using a combination of "classical" physical taphonomic indices and geochemical techniques.

Paszkowski and Wieczorek (1982) report ten fissures (Fig. 1) discovered in the Carboniferous limestone at Czatkowice quarry, near Krzeszowice, Kraków Uplands in 1978. The fissures contain Mesozoic sediments of various ages, some of which preserve vertebrate material. The most important of these fissure fillings is Czatkowice 1, a funnel-shaped karst form, that yielded a diverse Early Triassic microvertebrate assemblage (Paszkowski and Wieczorek 1982; Paszkowski 2009). The vertebrate remains were extracted from the bone-bearing breccias using acetic acid. Most of the bone material is housed in the Institute of Paleobiology, Polish Academy of Sciences, Warsaw, and in the Museum of the Earth, Polish Academy of Sciences, Warsaw.

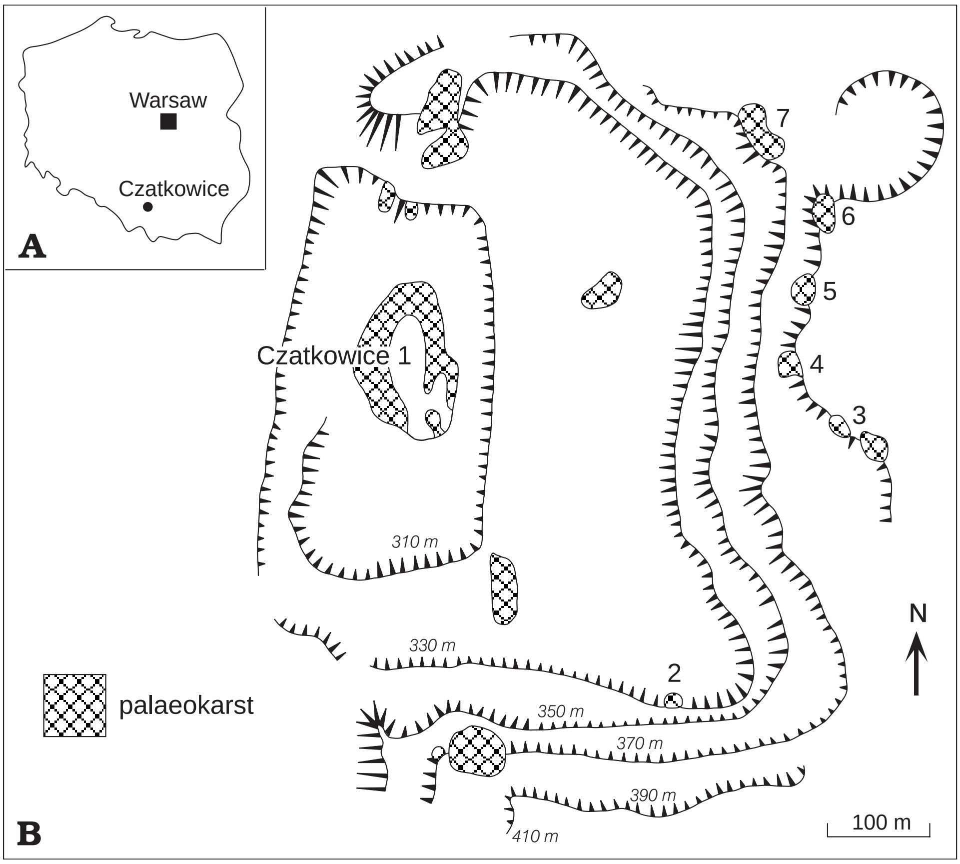

Fig. 1. **A**. Location of the Czatkowice quarry in Poland. **B**. Mesozoic fissures in the Czatkowice quarry (modified from Paszkowski and Wieczorek 1982); numbers refer to fossil karst lacalities.

The Czatkowice 1 fauna (Borsuk-Białynicka *et al.* 1999) is dominated by a small (approximately 1 m long) archosauriform predatory reptile *Osmolskina czatkowicensis* (Borsuk-Białynicka and Evans 2003, 2009a; Borsuk-Białynicka and Sennikov 2009). Other taxa include a prolacertiform grade reptile (Borsuk-Białynicka and Evans 2009b), lepidosauromorphs (Evans and Borsuk-Białynicka 2009a; Evans 2009), procolophonids (Borsuk-Białynicka and Lubka 2009) and temnospondyl amphibians (Shishkin and Sulej 2009) as well as rare fish and an extremely rare salientian *Czatkobatrachus polonicus* (Evans and Borsuk-Białynicka 1998; Evans and Borsuk-Białynicka 2009b). These animals are considered to have inhabited an area of arid or semi-arid desert with shallow ephemeral water bodies (Gradziński *et al.* 1979; Gradziński 1992; Gradziński and Uchman 1994; Paszkowski 2009).

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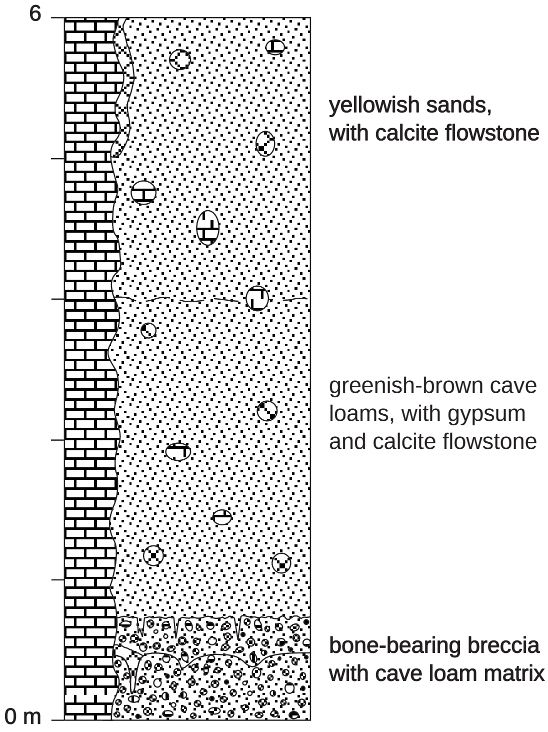

Fig. 2. Sketch of the sediment infilling the Czatkowice 1 fissure (information taken from Paszkowski and Wieczorek 1982).

GEOLOGICAL SETTING

Czatkowice 1 is the largest of several karst fissures cut into the Early Carboniferous (Tournaisian to Mid Viséan) limestone (Paszkowski and Wieczorek 1982; Paszkowski 2009) of the Dębnik Massif (southern Poland). Sedimentary data relating to Czatkowice 1 are scanty (Paszkowski and Wieczorek 1982; Paszkowski 2009). The karst form described was a small fragment of a cave, approximately 6 m in depth (exact dimensions not given), the upper part of the walls and the roof of which were decribed as "pockmarked", and supported a 0.2 to 0.3 m thick flowstone deposit. The cave sediments were divided into two (Fig. 2). The lower sediments reached a thickness of 4 m, were coloured green-brown and contained intercalations of gypsum and calcite flowstones; fragments of limestone and calcite were present throughout the sediments. These were overlain by approximately 2 m of yellow sandy sediments (Paszkowski and Wieczorek 1982; Paszkowski 2009).

A variety of fragments of the bone-bearing sediments from Czatkowice 1 have been studied in hand specimen, polished section and thin section. The sediments are yellowish, creamy-yellow, or dark ochre in colour. According to Paszkowski and Wieczorek (1982, p. 35), the lowest part of the cave was filled with bone breccia layers. Most of the specimens examined show no evidence of sedimentary structures; the sediments tend to be poorly sorted with large clasts of bone, lithics and nodules, and often contain large patches of crystalline calcite cement (Table 1).

Table 1. Summary of the physical characteristics of the hand specimens of Czatkowice 1 fissure-fill sediments.

Sample	Colour	Grain size	Matrix/Cement	Texture	Clast types
Cz 1	creamy-yellow, darker grey when fresh, dendritic magnetite on surface		clay-grade matrix and crystalline calcite cement	subangular grains	quartz; rare opaques
Cz 2	mottled pale creamy-brown and pale creamy-white with patches of ochreous material	fine sand to coarse sand	well-cemented with crystalline calcite	poorly-sorted	quartz, bones; rare opaques and mica
Cz 5	pale creamy-white, surfaces darker yellow	fine sand	crystalline calcite cements (possibly two phases)		quartz; rare opaques, mica and bones
Cz 7	ochreous with dark speckles on surface (magnetite?)	very fine sand or silt		possible parallel orientation of the bones, matrix supported, sediment poorly sorted	bones, quartz, lithics
Cz 18	pale creamy-yellow, with darker grey clasts, giving a speckled appearance	very fine sand with rare larger clasts	calcite cement	poorly sorted	quartz, lithics, bone
Cz 19	pale cream, ochreous when weathered	very fine sand, with clasts up to 15 mm diameter	very fine-grained matrix and crystalline calcite cement	very poorly-sorted, graded and parallel bedding, possible geopetal structure, possible parallel orientation of the bones, veins of calcite	quartz, lithics, bones; rare mica and opaques
Cz 23	pale creamy-yellow, with small patches of ocreous sediment	coarse sand and larger clasts	very well cemented by crystalline calcite	bones randomly scattered throughout the sediment, moderately well-sorted	quartz, bones, lithics
Cz 24	dark ochre, with brownish sediment adhering to the surface	coarse sand	silty matrix, with crystalline calcite cement	possible weak parallel bedding	very little bone, ? quartz

Recent studies have tied the Czatkowice 1 vertebrate assemblage into the terrestrial vertebrate sequence for Eastern Europe (Shishkin *et al*. 2000). The presence of tooth plates of the dipnoan *Gnathorhiza* and the characteristics of the teeth of the procolophonids suggests that the assemblage should be placed within the early to late Olenekian time frame (Borsuk-Białynicka *et al*. 2003). The temnospondyl remains from Czatkowice 1 deposits support an earliest Late Olenekian age (Shishkin and Sulej 2009).

METHODS

PHYSICAL TAPHONOMY

Behrensmeyer (1978) designed a classification scheme for the weathering of mammal bones in the tropical grassland environments of Africa. Following this work, Fiorillo (1988) adapted Behrensmeyer's (1978) scheme for use with fossil material (simplifying the classification to take into account the loss of resolution seen in fossil material when compared to recent bones) and produced a similar scheme for the classification of abraded bones (Table 2). Cook (1995a, b) further modified the schemes to take into account the extreme levels of abrasion frequently observed in the fossil record.

Additional information may be gained from an analysis of the nature of the fractures (Table 3) and breakage surfaces of the bone:

Spiral fractures: Bones that break relatively soon *post mortem*, while the collagen is still intact, break with a characteristic spiral or jagged fracture. In this case the growth of the fracture is controlled by the tensile strength of the collagen fibres. Such fractures are caused by predation, scavenging and trampling (especially associated with large animals), but are rarely caused during transport (Cook 1995b).

Parallel fractures: Fractures running parallel to the length of the bone are commonly associated with weathering damage (such as changes in relative humidity and temperature) to bone before permineralisation (Behrenesmeyer 1978).

Table 2. Taphonomic parameters used to describe the vertebrate material preserved at Czatkowice 1 (Fiorillo 1988; Cook 1995a, b).

Abrasion stage	Characteristics
Stage 0	Very angular: the bone is fresh and unabraded. Processes and bone edges are well-defined.
Stage 1	Subangular: the bone edges and processes are slightly abraded and polished.
Stage 2	Subrounded: the bone edges are well-rounded, processes are still recognisable. Moderate abrasion.
Stage 3	Rounded: edges show a high degree of rounding. Processes are remnant or absent. Heavily abraded.
Stage 4	Extremely rounded: bones often show a high degree of sphericity. Extremely abraded.

Transverse fractures: After collagen has degraded, the bone loses its tensile strength and typically breaks with a clean fracture, perpendicular to the length of the bone.

Conchoidal fractures: After significant mineralisation, the bone loses most of the internal porosity and conchoidal fractures may develop (Fiorillo 1988).

It is also productive to consider vertebrate fossils as sedimentary particles. Grain size and grain shape analysis of bone fragments can help to shed light on the sedimentary regime, and particularly on the energy levels of the transport agent (Martin 1999). Voorhies (1969) classified bones according to their susceptibility to transport in fluvial environments (simulated in a flume tank).

Voorhies Group I: Bones that are easily removed by currents by processes of flotation and saltation, for example ribs and vertebrae.

Voorhies Group II: Bones that move more slowly, moving by traction along the river bed, comprise long bones and metapodials.

Voorhies Group III: Includes the skull and mandible: bones which move very slowly.

Certain bones appear in more than one Voorhies Group, for example the ulna and scapula appear in both Groups I and II. It has been suggested that Group I bones can be moved by normal flow rates, and that Groups II and III material can only be moved during flood events (Behrensmeyer 1975).

At the time of acid preparation the blocks of sediment were numbered consecutively; these numbers bear no relation to the sedimentological context of the blocks. One sample from the Czatkowice 1 fissure infill, designated Cz 24, was analysed before the identifiable and well-preserved bones had been removed, and may be regarded as an unbiased cross-section of the remains preserved in sediment block Cz 24.

Most of the Czatkowice 1 samples have been sorted into various taxonomic groups, therefore it was not possible to complete an unbiased quantitative analysis of the complete collection. Small blocks of unprepared sediment were used to provide an unbiased bone sample: any bones visible on the surface of the blocks were also categorised according to their taphonomic characteristics.

However, it should be kept in mind that the Czatkowice 1 samples differ from the reference material used to construct the various “classic” taphonomic classification schemes which were based on the degradation behaviour of large (>50 kg) mammalian carcasses. The Polish fossils described here are mostly reptilian microremains.

GEOCHEMICAL TAPHONOMY

During fossilisation bone mineral changes from carbonate hydroxyapatite (dahllite), to carbonate fluorapatite (francolite). Many trace elements are taken up from pore waters by the bone during recrystallisation, and are incorporated into the apatite lattice via adsorptive substitution for Ca^{2+} ions. Consequently, a fossil bone contains a record of the trace element composition of the pore waters at the site of burial (Trueman and Tuross 2002). After early diagenetic recrystallisation the trace element signal is essentially stable. Further ionic exchange must occur by solid-state diffusion, which is a very slow process at low temperatures. The trace element content of fossil bone may therefore be used to reconstruct some aspects of the burial environment and *post mortem* history of a single bone.

The variation in trace element compositions of bones within a single accumulation is a function of the variation in original burial environments and the rate of introduction of bones into the deposit (Trueman 1999). Therefore, the amount of trace element variation seen in fossil bones from two assemblages can be

Table 3. Results of the physical taphonomy analysis of the Czatkowice 1 fissure-fill vertebrate samples. P, present; VC, very common; C, common. * vertebrate samples consisting of well-preserved, identifiable remains.

Sample	Sample type	Abrasion Index		Grain size (mm)			Grain shape							Fractures							
		Range	Most common	Max.	Min.	Average	Conical (teeth)	Blade	Rod	Disc	Cuboid	Flattened cone	Misc	Straight, fresh	Oblique, fresh	Parallel, fresh	Jagged, fresh	Straight, abraded	Oblique, abraded	Parallel, abraded	Jagged, abraded
Cz 1	Sorted sample	0-1 to 3	1-2 to 2	12	1	5 to 6	–	–	–	–	–	–	–	VC	–	–	–	C	–	–	–
Cz 2	Hand specimen	0-1 to 1-2	0-1	9	4	5.5	0	1	4	0	1	0	0	2	0	1	0	1	0	0	0
Cz 2	Sorted sample	0-1 to 3	1-2 to 2	19	1	7 to 8	–	–	–	–	–	–	–	VC	–	–	–	–	–	–	–
Cz 3	Sorted sample	–	1-2	–	–	–	–	–	–	–	–	–	–	VC	–	P	P	–	P	P	P
Cz 4	Hand specimen	1 to 2	1-2	18	1.5	6.99	0	6	17	0	5	0	6	22	0	1	1	8	0	3	3
Cz 4	Sorted sample	1 to 2	1-2	15	1	5 to 10	–	–	–	–	–	–	–	VC	–	–	–	C	–	–	–
Cz 5	Sorted sample	0-1 to 1-2	1 to 1-2	25	3	5 to 10	–	–	–	–	–	–	–	VC	–	–	–	–	–	–	–
Cz 6-7	Sorted sample	1 to 2	1-2	10	1	5	P	–	–	–	–	–	–	VC	–	P	P	–	P	P	P
Cz 7	Sorted sample	1 to 2-3	1-2	18	1	4	–	–	–	–	–	–	–	VC	P	–	P	P	P	–	P
Cz 7*	Sorted sample	0-1 to 1-2	0-1	6.5	2	4.3	–	–	–	–	–	–	–	5	0	0	0	0	0	0	2
Cz 7b	Hand specimen	0-1 to 2	1-2	15	1.5	5.57	0	17	18	0	1	0	1	17	0	3	11	3	0	0	0
Cz 11	Sorted sample	–	1-2	20	1	4 to 6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cz 12	Sorted sample	0-1 to 3	1-2	17	1	4 to 5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cz 13	Sorted sample	0-1 to 3	1-2	10	1	4 to 6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cz 14*	Sorted sample	0-1 to 2	0-1 to 1-2	–	–	–	P	–	–	–	–	–	P	–	–	–	–	–	–	–	–
Cz 14	Sorted sample	–	1-2	17	1	~ 5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cz 16	Sorted sample	1 to 2	–	14	1	~ 5	–	–	–	–	–	–	–	VC	–	–	–	C	–	–	–
Cz 17	Sorted sample	0-1 to 1-2	1 to 1-2	20	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cz 18	Hand specimen	0 to 1	0-1	26	6	13	–	2	4	–	1	–	–	–	–	–	–	–	–	–	–
Cz 18	Sorted sample	0 to 2	1-2 to 2	15	1	~ 7	–	–	–	–	–	–	–	VC	–	–	–	C	–	–	–
Cz 19	Hand specimen	1 to 2-3	2	4	1.5	7.92	0	16	25	0	0	0	2	13	3	1	0	20	2	1	1
Cz 19	Sorted sample	1 to 3-4	1-2 to 2	10	1	~ 5	–	–	–	–	–	–	–	VC	–	–	–	C	–	–	–
Cz 24	Hand specimen	0-1 to 2	0-1 & 2	9	2	4.5	0	4	2	0	0	0	0	3	0	1	0	0	0	0	0
Cz 24	Unbiased sample	0 to 2-3	1-2	10	1.2	4.41	19	38	45	0	34	82	69	155	5	15	13	45	20	15	35
Cz 26	Sorted sample	0-1 to 2	1-2	10	1.5	4.5	1	6	14	0	3	0	2	28	3	6	4	4	3	4	7

used as a proxy for the relative amounts of time and space averaging suffered by those assemblages, provided that they are matched in terms of their general sedimentary setting (Trueman *et al*. 2003).

Previous work (Trueman and Benton 1997; Trueman 1999; Staron *et al*. 2001; Patrick *et al*. 2002; Trueman *et al*. 2003) has shown that the rare earth elements (REE) are ideal for geochemical taphonomic studies as they are present in low concentrations in life, but are rapidly incorporated into bone after death. Fossil bone commonly contains concentrations of REE more than four orders of magnitude greater than those found in fresh bone (Wright *et al.* 1984; Chenery *et al*. 1996; Trueman and Tuross 2002). The REE are fractionated from one another during weathering and sedimentary transport, and thus the relative abundances of REE found in natural waters and minerals are potentially sensitive to small changes in depositional environment or recrystallisation behaviour (Dupré *et al*. 1996; Sholkovitz *et al.* 1990; Denys *et al*. 1996). The REE composition of fossil bones is therefore governed by the REE composition of the pore waters at the site of burial, and can be used as a natural tag indicating the early depositional locality. All bones from a single depositional locality will share a common REE signal (Trueman and Tuross 2002; Trueman *et al*. 2003).

REE concentrations in eleven bones from the Czatkowice 1 locality were determined by ICP-MS analysis (Table 4). Values were obtained on a VG Plasmaquad II ICP-MS at the University of Bristol, Department of Earth Sciences. A detailed description of the procedure for sample preparation and methods are given in Trueman (1999). Briefly, the samples were washed and any adhering sediment was removed. The cleaned bones were crushed to a powder in an agate pestle and mortar and dried overnight. Approximately 0.1 g of sample was accurately weighed and digested on a hot plate with HNO_3. Solutions were evaporated to dryness and redissolved in 1% HNO_3. Final solutions were made up to 100 ml (resulting in a total dilution of 1000 times) together with an internal standard of 100 ppb Re and Ru. Analytical precision and accuracy were monitored with reference to international standards, errors (2s) were within 10% of certified values. Analytical detection limited (3* blank standard deviation) were less than 0.5 ppb.

RESULTS

PHYSICAL TAPHONOMY

All of the bones from the Czatkowice 1 fissure sediments are disarticulated, and most (approximately 99% of the sample) are incomplete. Most of the bone fragments recovered from the cave sediments are white, pale yellow or orange in colour, with occasional dark coloured heavily abraded shark teeth reworked from the Carboniferous Limestones enclosing the Mesozoic fissure-fill. Similar reworked teeth are found in the Triassic cave sediments of the Cromhall fissures, south west England.

Shape analysis: The bone fragments are typically small with a maximum length of approximately 30 mm, but most are considerably smaller: between 5 and 7 mm long. All of the main categories of bone fragment shape (based in part on the sediment particle classification scheme of Zingg 1935), except disc, are present within the Czatkowice 1 collection. In samples Cz 24 and Cz 26 the most commonly occurring vertebrate clast shapes are rods, blades, flattened cones and “miscellaneous” (bones with an irregular shape which does not really fit into the other categories).

Fractures: Few bones show longitudinal cracks (cracks orientated parallel to the major axis of the bone or to the principle direction of collagen fibres), but some of the archosaur tooth crowns have such cracks running from the tooth tip to the root. The most commonly occurring breaks preserved in the samples are transverse or straight fractures. Jagged and parallel fractures are present, but uncommon. The vast majority of the skeletal elements have been broken at some point in their *post mortem* history. From observations of the acid digestion process it is clear that most (at least 60%) of the breakage (but not the disarticulation) is produced during preparation. Many bones show evidence of multiple breakage events. Such bones have been broken and then abraded, producing smoothed or rounded breakage surfaces, and broken again at a later stage, producing sharp, fresh surfaces.

Weathering: A few bones show signs of *in situ* weathering (producing cracks parallel to the bone fibres), including the archosaur teeth described above.

Abrasion: The abrasion (degree of rounding) of the bones is low; most have abrasion damage characteristic of stage 1 to 2 (Fiorillo1988; Cook 1995a, b), although a few specimens show more extreme abrasion.

There is little or no difference between the taphonomic characteristics of the indeterminate and identified material. Analysis of an unsorted unbiased sample (Cz 24) confirms the observations of the biased samples (samples where the identifiable material has been isolated). A total of 268 fragments of bone from Cz 24 were described. None of the specimens show any definite evidence for weathering. The bone fragments display a range of abrasion states, ranging from stage 0 (fresh bones with no sign of abrasion) to stage 2–3 (moderate levels of abrasion). Most of the bones (54.5% of the sample) show abrasion-related modifications characteristic of stage 1–2 (slight abrasion). Several types of fracture were identified from bones of the Cz 24 sample. Of these, the most common were fresh (unabraded) straight fractures. Such damage is typified by a very smooth breakage surface, which generally (but not always) cuts across the long axis of the bone tissue at an angle of 90°. Less common, but still occurring in significant numbers, are abraded straight fractures. Parallel (or longitudinal) fractures and jagged breakages are present in small numbers, and have both fresh and abraded surfaces. In many cases a bone will show more than one kind of fracture.

There does not appear to be any difference in the preservational characteristics of the different taxa. Only terrestrial taxa have been identified from Cz 24 (procolophonids, archosaurs and small reptiles); the aquatic and semiaquatic creatures (fish, temnospondyls, and protofrogs) known from other samples in the Czatkowice 1 fissure are absent from the Cz 24 sample.

GEOCHEMICAL TAPHONOMY

Total rare earth elements (REE) concentrations range from 600 to 7 000 ppm (Table 4). These are a function of both the REE concentrations in the bone, and the relative amounts of apatite and other authigenic minerals in the sample. As REE are concentrated strongly in the apatite, other authigenic minerals do not significantly alter the relative concentrations of the REE in the sample, but effectively dilute the REE concentrations overall. However, the total REE concentrations measured in these bones are similar to those recorded in fossil bone samples from other terrestrial environments (*e.g.*, Denys *et al*. 1996; Hubert *et al*. 1996; Trueman 1999; Samoilov and Benjamini 2001).

REE data from sedimentary rocks and natural waters are commonly reported relative to an average shale value, which approximates the average REE composition in the crust. Several shale composite values are used, and in this study all REE values are reported normalised to Post Archean Average Shale (PAAS) values (Taylor and MacClennan 1985). The shale-normalised REE concentrations in fossil bones from Czatkowice show distinct convex-upward patterns, with relatively high concentrations of intermediate or middle REEs, and higher concentrations of the light REE compared to the heavy REE. These patterns are generally expressed as inter-element ratios (*e.g.*, Sm/La, Dy/Yb, La/Yb). Bones from Czatkowice 1 all yield Sm/La,

Table 4. REE, U and Th concentrations (ppm) in bones from the Czatkowice assemblage.

	CZ 6-7L	CZ 6-7LC	CZ 17 LC	CZ 33	CZ 2VB	CZ 23 LB	CZ 23 LC	CZ 2 (13) L	CZ 6-7LB	CZ 17	CZ 2V
La	285.69	226.65	257.65	436.74	98.29	429.07	137.37	116.89	773.97	517.62	117.51
Ce	924.15	965.15	1078.20	1415.54	247.95	1909.23	541.96	456.87	3186.46	1609.76	469.33
Pr	115.34	112.75	121.35	150.62	30.14	205.49	59.27	51.19	367.50	183.31	48.50
Nd	465.91	453.43	473.46	574.67	115.98	783.70	227.43	197.29	1521.93	699.84	190.27
Sm	100.43	101.95	110.10	133.12	26.79	176.87	51.52	45.76	335.67	160.06	45.64
Eu	21.54	20.56	19.39	22.09	4.48	31.60	9.34	8.02	67.60	26.33	7.41
Gd	114.79	106.66	104.09	136.02	30.85	178.09	53.45	44.82	347.22	163.33	46.07
Tb	14.31	13.25	13.14	16.84	4.08	23.20	6.92	5.71	41.99	19.61	5.78
Dy	78.80	69.47	72.19	92.89	24.77	122.93	37.16	30.68	218.85	103.88	30.25
Ho	13.44	10.85	11.82	16.25	4.80	19.33	6.10	4.87	34.47	16.50	4.82
Er	32.08	23.89	28.26	39.72	13.17	47.09	15.17	11.48	77.41	40.46	11.14
Tm	3.74	2.36	3.20	4.77	1.73	5.14	1.74	1.28	7.91	4.49	1.17
Yb	18.09	10.36	14.14	21.15	8.38	21.15	7.56	5.92	33.32	19.74	5.10
Lu	2.62	1.30	2.09	3.21	1.25	3.02	1.08	0.76	4.57	2.94	0.69
Th	8.87	6.61	8.33	9.31	9.51	28.27	14.66	10.21	19.22	17.54	14.43
U	33.57	30.88	31.30	37.59	5.04	57.71	10.75	10.95	115.16	52.55	11.33

Dy/Yb, and La/Yb ratios >1. Uniquely amongst the REE, Ce may be present as a tetravalent ion in oxidising conditions. As Ce^{4+} behaves rather differently to Ce^{3+}, Ce anomalies are frequently developed in oxidising environments. The Ce anomaly is simply the ratio between the measured value of Ce and the expected value derived from either linear interpolation between Ce and Pr, or by linear extrapolation from Nd and Pr. All samples from Czatkowice 1 display a positive Ce anomaly, although the size of this anomaly varies within the sample tested. In addition to the REE, concentrations of U and Th were also determined in bones from Czatkowice 1. In the Czatkowice 1 sample, U/Th ratios range from 0.5 to 6.

INTERPRETATION

PHYSICAL TAPHONOMY

The taphonomic characteristics of the various Czatkowice 1 samples (biased and unbiased) provide limited evidence for the depositional history of the Czatkowice 1 cave accumulation. The scarcity of weathering damage (parallel cracks or splintering of the surface of the bones) suggests several possible histories: (1) that the bones were not subjected to any prolonged episodes of subaerial exposure and were rapidly buried or transported into the cave system before any surface modification could take place; (2) that complete carcasses were washed into the cave systems. The second option is less probable, because of the lack of articulated elements within the assemblage. The longitudinal cracks seen in some archosaur teeth may be a product of mechanisms other than weathering (*e.g.*, damage during life, chemical changes during diagenesis, or damage caused by the processes of fossil recovery, extraction and preparation).

The wide range of abrasion states displayed by the Czatkowice 1 fossils are typical of an assemblage that has accumulated over an extended period of time. Accumulations that are a product of catastrophic process tend to have a limited range of abrasion states as all the bones have a virtually identical taphonomic history. The assemblage preserved in the Czatkowice 1 fissure typically displays slight abrasion, most likely reflecting low levels of fluvial transport. In an arid or semi-arid environment with ephemeral water bodies wave action is unlikely to have played a significant part in the modification of the vertebrate debris. Multiple phases of reworking of terrestrial and lacustrine sediments during flash floods is to be expected. However, in such an arid environment it is reasonable to expect that bones could also have been abraded by air-borne sand.

The presence of several types of fracture hints at a complex taphonomic pathway. The presence of straight fractures suggests that a portion of the bone sample underwent some degree of diagenetic alteration, involving the loss of collagen and/or recrystallisation, and was then broken and transported or reworked before final deposition. The proportion of the biased and unbiased samples showing evidence for permineralisation and subsequent abrasion is similar (33% of bones in the biased samples compared with 37.8% of the bones from the unbiased sample). In the case of the Czatkowice 1 material, the parallel fractures were probably caused during the acid preparation of the sediment blocks, as there is no other evidence of the *in situ* weathering of the material. The Cz 24 sample has examples of fresh and abraded spiral or jagged fractures, suggesting that bones in the assemblage were broken by predators and/or scavengers before diagenesis.

The generally small size of the vertebrate fossils preserved in the Czatkowice 1 assemblage suggests that the bones were transported and deposited in a relatively low-energy environment. The limited size range of the bones indicates winnowing or hydrodynamic sorting. The bones described as blades, rods, cuboids and flattened cones are all classified as Voorhies Group I skeletal elements (Voorhies1969). Flume tank experiments with a range of mammalian skeletal elements (Voorhies 1969; Korth 1979) indicate that these bones are rapidly and easily moved by river currents. It is likely that reptilian bones displaying similar shapes would also be easily transported.

The evidence from the physical taphonomic characteristics of the Czatkowice 1 assemblage suggests that the material was either incorporated into the sediment or transported into the ephemeral water bodies or cave system soon after death, thus protecting the bones from *in situ* weathering damage. The generally low levels of abrasion suggest that the assemblage was not subject to transport over any great distance, although aeolian processes may have been important. However, abrasion experiments (Cook 1995b) imply that the degree of abrasion observed on a bone cannot be related directly to the distance travelled. Very large transport distances are required to produce mild levels of abrasion on fresh bones, whereas bone that had previously been buried for approximately 100 years was rapidly abraded. Therefore it is likely that the majority of abrasion seen on bone is a result of reworking and static abrasion. This suggests that many of the Czatkowice 1 bones were subject to at least one phase of reworking. It is difficult to calculate the relative timing of these events. The fact that some of the bones have abraded fractures associated with post-mineralisation breakage would suggest that reworking, at least for part of the assemblage, took place after diagenesis. Other bones display features consistent with breakage of unmineralised tissue, followed by transport and/or reworking.

GEOCHEMICAL TAPHONOMY

The relative abundances of the rare earth elements (REE) developed in fossil bones are principally controlled by the distribution of REE in pore waters, which are in turn controlled by REE weathering and transport mechanisms. Broadly speaking, in environments where the bulk of the REE are transported into sediments associated with particle surfaces, fossil bones will inherit a shale normalised REE pattern characterised by La/Yb ratios >1, and commonly middle REE enrichment. This pattern is most frequently seen in bones from estuarine and coastal marine environments where light REE are scavenged from solution during particle flocculation and settling. In most terrestrial settings the heavy REE apparently form more stable dissolved complexes than the light REE, and consequently the light REE may be more effectively immobilised through adsorption onto particle surfaces. This process results in pore waters with a relatively high proportion of exchangeable heavy REEs with respect to the initial REE source. Bones from most terrestrial settings are consequently characterised by shale normalised La/Yb ratios <1. Bones recovered from soils typically have slightly higher La/Yb ratios than bones from associated fluvial sediments (Trueman 1999). Bones from the Czatkowice 1 assemblage plot in the field of REE space characterized by bones from coastal marine and estuarine environments (Fig. 3). This is evidently inconsistent with their true palaeogeographic setting. However, the Czatkowice 1 assemblage shares its position in REE space with bones recovered from the Cretaceous Djadhokta Formation (Samoilov *et al.* 2001), an environment characterised by extensive local dune fields. This association points strongly to the influence of particle-surface associated transport of REE in aeolian settings, and therefore confirms a significant role for wind-blown dust in the Czatkowice palaeoenvironment.

As discussed earlier, the comparative behaviour of Ce and the adjacent REE can potentially indicate redox conditions during fossilisation. All bones from the Czatkowice assemblage display positive Ce anomalies, suggesting that Ce was present in oxidised form, and was preferentially incorporated into the apatite lattice compared to other trivalent light REE. Ce^{4+} is a smaller ion than Ce^{3+}, similar to the heavy REE. Thus, increasing positive Ce anomalies should correlate with increasing heavy REE enrichment. In fact, the Ce anomaly shows no significant relationship with either La/Yb ratios, or Dy/Yb values. This suggests that the development of Ce anomalies cannot be explained simply by considerations of ion radius (although charge considerations may be important), and thus variations in the extent of the Ce anomaly within the Czatkowice assemblage may reflect real differences in the transport chemistry of Ce^{4+} compared to trivalent REEs in the environment, and therefore derivation of bones from different burial settings.

The variation in trace element chemistry of fossil bones from a single assemblage can also be used as a taphonomic characteristic for a particular assemblage. Bone samples from the Czatkowice assemblage show considerable variation in their REE patterns, particularly in terms of the relative abundance of light REE (*e.g.*, La), and heavy REEs (*e.g.*, Yb). To test the significance of this variation, the assemblage must be compared to another assemblage from a similar sedimentary setting, preferably using similar bones, with a contrasting taphonomic history. We compared the geochemistry of the Czatkowice 1 assemblage to bones from Cromhall Quarry, a Triassic fissure-fill deposit from the south-west of England containing an abundant and diverse small reptile fauna (Fraser and Walken 1983; Fraser 1994; Blessed 1998). The geological setting for the Cromhall deposit is broadly similar to that proposed for Czatkowice 1 (*i.e.*, fissure fills developed in Carboniferous limestone proximal to extensive aeolian Triassic red bed sedimentation). The fissure system at Cromhall, however, was developed in a coastal setting, presumably with some influence of marine waters. The vertebrate-bearing Triassic sediments within the Cromhall fissures are capped by Rhaetic sediments containing abundant marine fossils. REE concentrations in bones from a several blocks of sediment from the

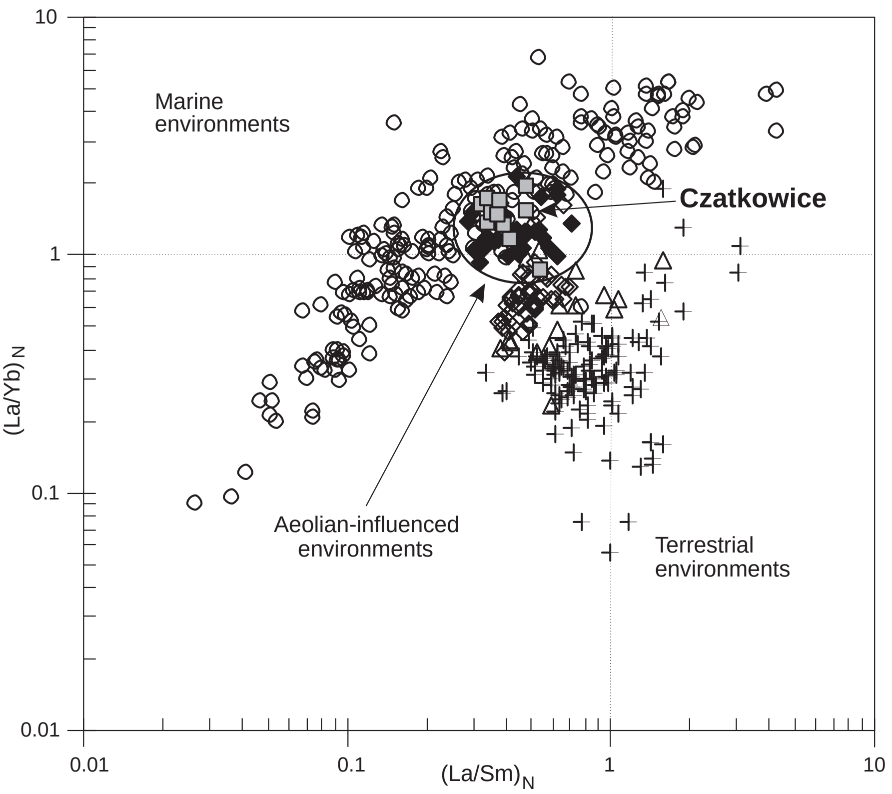

Fig. 3. Shale-normalised ratios of REE concentrations in bones from a variety of depositional settings. Open circles, coastal shelf marine environments (6 localities); open triangles, deep marine environments (4 localities); open diamonds, single estuarine setting; crosses, terrestrial fluvial settings (22 localities); closed symbols, bones from terrestrial localities with aeolian influence (3 localities). Note that broad environmental settings are well-separated in REE-space, and that aeolian influenced localities are distinct from other terrestrial settings. Bones from Czatkowice (filled squares) have similar REE compositions to bones from other aeolian influenced localities. Data taken from Blessed (1998); Elderfield and Pagett (1986); Girard and Albarède (1996); Grandjean-Lécuyer *et al*. (1993); Laenen *et al* (1997); Samoilov *et al*. (2001); Trueman, 1997; and Wright *et al.* (1984).

Cromhall fissure-fill were determined at the University of Bristol using the same analytical equipment and methods (Blessed 1998).

The variation in shale normalised La/Yb ratios in both assemblages was compared using an F-Test (the values were first transformed using common logarithms to ensure normal distributions and thus validate parametric statistical testing methods). Using the F-Test, the variance of REE patterns in bones from the Czatkowice 1 assemblage is not significantly different from the Cromhall Triassic assemblage (as long as the assumption of equivalence in geochemical environments is correct). However, the Cromhall assemblage is mixed, including reworked Carboniferous shark teeth, and stratigraphically younger Rhaetian shark teeth. If these allochthonous elements are removed, then the Cromhall assemblage is significantly less varied than the Czatkowice assemblage. Variation in La/Sm ratios accounts for almost all difference between the two populations (ANOVA (La/Sm values) F = 4.66, p = 0.04).

The relatively high levels of variation in geochemical composition of bones from Czatkowice 1 suggests that this assemblage contains bones from a range of local depositional environments. Furthermore, these bones must have remained in these separate horizons long enough to inherit distinct geochemical signals before being reworked and introduced into the cave deposit. The absolute time required to produce these separate geochemical signals is linked to the rate of bone recrystallisation, which is poorly known and varies with the depositional environment. However, recent attempts at modelling rates of recrystallisation of bone suggest that fossil bones are recrystallised within 103–104 years (Trueman and Tuross 2002). Therefore, this suggests time averaging over at least 100 year time scale in the Czatkowice 1 deposit. It should be noted, however, that it is possible that trace metals are adsorbed rapidly onto bone crystal surfaces or associated organics, and are introduced into the apatite lattice from this adsorbed reservoir. If so, the amount of time needed to develop the varied trace element signals seen in bones from the Czatkowice assemblage (and thus the minimum time averaging) would be much less. These interpretations are consistent with the relatively complex behaviour of the Ce anomaly discussed above.

Based on the inter-element REE ratios, Ce anomalies, and U/Th ratios, three bones can be identified as distinctly different from the main sample, Cz 33, Cz 17, and particularly, Cz 2 VB. This suggests that these bones were derived from distinctly different depositional environments, compared to the rest of the bones. As all the bones analysed were indeterminate fragments, no palaeoecological inferences may be drawn from this geochemical evidence.

CONCLUSIONS

The excavation and sampling techniques necessarily employed at Czatkowice 1 have led to the loss of almost all detailed sedimentological and stratigraphic information, and preparation and curation has further resulted in a taxonomically and taphonomically biased assemblage — both situations are common to many important historical vertebrate collections. Such loss of information places significant constraints on the palaeobiological and palaeoenvironmental inferences that can be obtained from the collection.

Some sedimentological and taphonomic information can, however, be derived retrospectively through physical and chemical characterisation of the curated bone assemblage. The physical characteristics of bones from the Czatkowice 1 cave suggest an attritional, winnowed assemblage that experienced limited fluvial-lacustrine transport and multiple cycles of reworking. The absence of cracking and flaking of the outer layers of the bone tissue suggests that the bulk of the material was buried rapidly, either in the aeolian-lacustrine sediments or within the cave complex. The presence of abraded post-mineralisation fractures, however, suggests that some bones were mobilised after significant periods of burial. After burial the bones were subjected to chemical changes and associated mineral deposition, for example the bone cavities are frequently infilled with crystalline calcite and dendritic manganese growths cover many bone surfaces.

The geochemical characteristics of the bones support these observations, suggesting a significant aeolian influence on the early diagenetic environment, and derivation of bone remains from a variety of different early burial settings. It is likely that the vertebrate remains were sourced from a small-scale depocentre, possibly an ephemeral water body or channel bank. In addition, interpretations concerning the relative degree of time and space averaging represented in the Czatkowice fissure deposit can be made through comparison of the chemical variation of bones from the Czatkowice 1 cave with other, similar fissure deposits. These studies suggest that the Czatkowice 1 deposits represent relatively large spans of time and/or varied depositional settings.

Inevitably, the strength of such interpretations is limited by the lack of sedimentological and stratigraphic information available, however the combination of independent sources of taphonomic information adds some weight to the reliability of the interpretations. Similar techniques could be applied to historical collections where supporting palaeoenvironmental data are missing, and localities are inaccessible or lost.

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EARLY TRIASSIC TEMNOSPONDYLS OF THE CZATKOWICE 1 TETRAPOD ASSEMBLAGE

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Shishkin, M.A. and Sulej, T. 2009. The Early Triassic temnospondyls of the Czatkowice 1 tetrapod assemblage. *Palaeontologia Polonica* **65**, 31–77.

Examination of dissociated Early Triassic vertebrate microfossils from the fissure infillings of the Czatkowice quarry in southern Poland (locality Czatkowice 1) allowed recognition of the two taxa of temnospondyl amphibians, the capitosaurid *Parotosuchus* (*Parotosuchus speleus* sp. n.) and brachyopid *Batrachosuchoides* (*Batrachosuchoides* sp.). Both are represented almost entirely by remains of the young, obviously metamorphosed, juveniles. Based on comparison with the Cis-Uralian Triassic faunal succession, these taxa enable us to refine previous dating of the Czatkowice 1 vertebrate assemblage as early Late Olenekian. The overall composition of this assemblage is believed to provide evidence of its development outside the lowland biotopes. An analysis of structural patterns and growth changes of elements of the palate, occipital arch and jaws demonstrated by the local temnospondyls revealed in them a number of peculiar or surprisingly archaic juvenile characters, mostly unrecorded hitherto in Triassic capitosauroids or in the late Temnospondyli in general. These primarily include: the ectopterygoid dentition strongly dominated by tusks; the ectopterygoid contributing to formation of the provisional palatal vault; the mandibular symphyseal plate broadly sutured with the precoronoid (as in basal tetrapods) and presumably incompletely integrated with the dentary; the palatal elements articulated with the maxilla-premaxillary complex mostly dorsally or ventrally rather than laterally; and the subotic process of the exoccipital shaped as a vertical plate. As these features were largely found both in capitosaurid and brachyopid juveniles, they can be suggested to characterize some generalized pattern of provisional cranial morphology in the development of advanced temnospondyls.

Key words: Triassic, Poland, karst, Amphibia, Temnospondyli.

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INTRODUCTION

Early Triassic karst deposits of the locality Czatkowice 1 (Czatkowice quarry near Kraków, Poland, Paszkowski and Wieczorek 1982) yielded a rich vertebrate assemblage (Borsuk-Białynicka *et. al*. 1999) that is a subject of the present volume.

Among the tetrapods of Czatkowice 1 the amphibians are rare. Their recognized remains include about two hundred bones overall, in contrast to several thousand known for associated reptiles. This ratio is exactly the reverse of that known for most other Early Triassic tetrapod burials in Euramerica; normally they demonstrate overwhelming predominance of amphibian bones that pertain to the aquatic Temnospondyli (*cf.* Shishkin *et al.* 2000, 2006).

Previous examinations (Evans and Borsuk-Białynicka 1998; Borsuk-Białynicka *et al.* 1999) recognized members of two amphibian groups, a new stem-frog *Czatkobatrachus* and some undiagnosed temnospondyls at the locality. The frog material was the subject of two earlier accounts (Evans and Borsuk-Białynicka 1998; Borsuk-Białynicka and Evans 2002), whereas the temnospondyls remained unstudied until now.

The objective of the present paper is to give an account on the temnospondyl material from Czatkowice 1. It is represented by isolated bones and almost entirely belongs to the juvenile growth stages. With respect to its taxonomic recognition, of primary importance is that it contains numerous fragments of jaw bones with antero-posteriorly compressed tooth bases. This indicates that the temnospondyl assemblage was dominated by the capitosaurids and, possibly, their trematosauroid (benthosuchid-trematosaurid) derivatives which are here referred to, altogether, as the Scythian “stereospondyls”. The design of some cranial bones indicates that they belong to the capitosaurid *Parotosuchus*, a typical member of the terminal Scythian (Late Olenekian) tetrapod assemblages of Eastern Europe and Germanic Basin (Ochev and Shishkin 1989; Shishkin *et al.* 2000 and 2006). *Parotosuchus* from Czatkowice 1 is distinguished as a new species. Among the rest of the material most specimens also conform to the capitosaurid pattern, although their generic attribution may sometimes be open to question. No trematosauroid bones have been identified with confidence.

The temnospondyl material under study also includes a few brachyopid remains. These belong to *Batrachosuchoides*, a genus known hitherto from the Late Olenekian (Yarenskian Superhorizon) of Eastern Europe. It is the only member of the Brachyopidae recorded in the Early Triassic of Euramerica. The Polish brachyopid remains show some distinctions from the Russian form, but their taxonomic value remains uncertain in view of the rarity and immaturity of the available fossils. The taxon is referred to as *Batrachosuchoides* sp.

Our assumption that the Czatkowice 1 “stereospondyls” were dominated by, or even limited to, a single capitosaurid genus, is not in contrast with data on coeval tetrapod communities of Eastern Europe. As a rule, in the each tetrapod biozone discernible for the Scythian of Eastern Europe the amphibian component known for particular areas includes a single abundantly represented temnospondyl genus, usually associated with one or two more scarce forms.

Specifically, the Induan time span in the southeast of the Eastern European Platform is characterized by the wide occurrence of archaic species of the capitosaurid *Wetlugasaurus*, with other “stereospondyls” being virtually absent. In a number of geographically different assemblages of the basal Early Olenekian (Rybinskian Horizon), there is an overwhelming predominance of one or the two benthosuchid genera, *Benthosuchus* or *Thoosuchus*, whereas *Wetlugasaurus* is extremely rare. Conversely, in the late Early Olenekian (Sludkian Horizon) the “stereospondyls” are typically represented by *Wetlugasaurus*, with a minor role played by the advanced benthosuchids.

More variable proportions in abundance of the capitosaurids and other “stereospondyls” are observed in the Late Olenekian biozones of Eastern Europe, the older of which, the Fedorovskian Horizon, corresponds in age to the Czatkowice 1 fauna (*cf.* p. 73). The capitosaurid *Parotosuchus*, a guide fossil for the Late Olenekian, is recorded everywhere in the region, but its role in the local amphibian communities may vary (in terms of abundance) from nearly 100% to 50%. The trend towards the last value, reflecting a commensurate increase in the role of the accompanying trematosaurs, is typical for the areas adjacent to brackish water or lagoonal environments. The absence or negligible role of trematosaurs in the Czatkowice 1 locality support a terrestrial depositional setting suggested for this locality.

The share of the brachyopid component of the Czatkowice 1 assemblage, represented by *Batrachosuchoides*, in the total amount of collected temnospondyl fossils is close to 8–10%. This value is not far from that recorded for the same genus in the Late Olenekian tetrapod localities of Eastern Europe.

To sum up, although the role of amphibians in the Czatkowice 1 assemblage is strongly reduced in comparison with its age equivalents in Eastern Europe, the suite of contained temnospondyl genera and their relative abundance in both cases do not seem to be very different.

Brief comments are needed on the use of group names followed in this paper. The term Capitosauroidea is accepted to unite the bulk of the Triassic taxa placed by most authors in the Capitosauroidea or Mastodonsauroidea (Schoch and Milner 2000; Yates and Warren 2000; Damiani 2001) with the rhinesuchids and lydekkerinids, thus basically following Shishkin (1964), Ochev (1966), and Shishkin *et al*. (1996, 2004). The inclusion of the heylerosaurids in this unit is not supported. The content of the Capitosauridae is accepted according to Shishkin *et al*. (2004, p. 134). The Trematosauroidea is presumed to embrace the benthosuchids, thoosuchines and trematosaurids (Shishkin 1980). The extension of this group to include the metoposaurids and almasaurids (Schoch and Milner 2000) or the placement of them together in a common clade with the Rhytidosteidae and Brachyopidae (Warren and Black 1985; Yates and Warren 2000) is rejected (*cf.* Shishkin 1967, 1973, 1991; Sulej 2007).

Institutional abbreviations. — BMNH, Natural History Museum, London, UK; BPI, Bernard Price Institute for Palaeontological Research, University of Witwatersrand, Johannesburg, South Africa; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland. In some references to the collection numbers made in succeeding sections of this paper the abbreviation ZPAL Ab is omitted.

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GEOLOGICAL SETTING

The bone material surveyed in this study comes from the infillings of a single fissure exposure (Czatkowice 1) that belongs to the karst systems developed in the Lower Carboniferous limestone of the Kraków region (Paszkowski and Wieczorek 1982; Paszkowski 2009). The bone-bearing sediments are of a fine grained sandy limestone with occasional clasts. On geological evidence, the age of sediments was defined as not younger than the latest Scythian (Paszkowski and Wieczorek 1982). Succeeding analysis of the contained vertebrate assemblage showed it to be the Early Olenekian–early Late Olenekian in age (Borsuk-Białynicka *et al.* 2003). Based on the amphibian component of the assemblage, this dating is now refined as the early Late Olenekian (this paper).

MATERIAL

The identified temnospondyl material comprises about 90 bones (including poorly diagnosable fragments) extracted from fine grained sandy limestone that forms the basal part of karst fissure infilling. The bones are completely disarticulated and may show various degrees of damage. As a rule, they do not exceed 8–10 mm in length. Heavily reworked specimens are rare; most fossils underwent little, if any, abrasion and in most cases are perfectly preserved. This indicates a low energy depositional setting, with only limited and short-term water transport of sediments (*cf.* Borsuk-Białynicka *et al.* 1999; Cook and Trueman 2009).

The dissociated state of the bones, combined with largely fine preservation, suggests that the dismembering of amphibian skeletons proceeded in shallow standing water. Most likely, they were laid down in the coastal zone of a small lake that covered the area of the karst fissure. The transport of the bones to the final burial (in the fissure) obviously followed soon after dissociation in the shallows. This could have occurred at times of seasonal rain when temporary flows washed out and displaced the coastal deposits.

The small size of temnospondyl remains from Czatkowice 1 partially reflects the low energy sedimentation. On the other hand, it is notable that the bulk of skeletal elements pertain to small juveniles with skull length not exceeding 4–4.5 cm. This may correspond to the total body length of about 30 cm, which is 3 to 5 times less than the normal value expected for adult individuals of the Early Triassic temnospondyl genera. Based on that, one can assume that the coastal shallows served as a natural life space for young metamorphosed animals. An occasional death of such individuals probably provided the main source for gradual accumulation of the temnospondyl bones in the karst sediments.

SYSTEMATIC PALEONTOLOGY

Order **Temnospondyli** Zittel, 1890

Family **Capitosauridae** Watson, 1919

Genus ***Parotosuchus*** Ochev *et* Shishkin, 1968

Type species: *Parotosuchus nasutus* (Meyer, 1858).

Referred species. — *Parotosuchus helgolandiae* (Schroeder, 1913), *P. orenburgensis* (Konzhukova, 1965), *P. orientalis* (Ochev, 1966), *P. panteleevi* (Ochev, 1966), *P. sequester* Shishkin, 1974, *P. komiensis* Novikov, 1986. The taxa from latest Early and Mid Triassic of Gondwana described as members of *Parotosuchus* (Chernin and Cosgriff 1975; Mukherjee and Sengupta 1998; Damiani 2001) are considered to be generically distinct.

Distribution. — Late Early Triassic (Late Olenekian) of Europe and North America.

Comment. — The assignment of the Czatkowice 1 capitosaurid to *Parotosuchus* is mainly based on the structure of its palate. The latter demonstrates the slit-like choanae with the estimated width/length ratio of about 0.28–0.30 (roughly corresponding to that in adult *Parotosuchus*) and the pattern of vomerine dentition much advanced over the level of primitive, *Wetlugasaurus*-grade, Early Triassic capitosaurids (*cf.* Diagnosis and Comments on *P. speleus*).

Parotosuchus speleus sp. n.

(Figs 1–6, 8C, 9–21, 22A, B, 23–31)

Holotype: ZPAL AbIV/105, left vomer.

Etymology: Species name from the Greek *spelaion*, cave, in reference to discovery of the new amphibian in rock infillings of the karst cavities.

Type locality: Czatkowice 1, southern Poland (Kraków region).

Type horizon: Bone-bearing breccia of the earliest Late Olenekian. For the refinement of previous dating (Borsuk-Białynicka *et al.* 2003), see p. 73.

Referred material. — A series of isolated bones and bone fragments from the type locality, all belonging to collection ZPAL AbIV. The specimens include: postfrontal 43; postorbital 151; vomers 37, 38, 58, 59, 65–67, and 73; palatine 97; ectopterygoids 46, 50, and 107; exoccipitals 33 and 104; premaxillae 62 and 92; maxillae 31,106,116,118, and 153; maxillae or dentaries (poorly identifiable fragments) 47, 51, 52, 57, 60, 64, 74, 91, and 93; dentaries 32, 34, 35, 82, and 119; angular 63; surangular 68; clavicles 75 and 87; interclavicle 102; neural arches 158–160; scapulae (?) 88 and 103; humeri 84 and 86; radius (?) 96; ribs 85 and 99.

Diagnosis. — A new species distinguished from all other members of *Parotosuchus* by a combination of the following character states: (1) adjacent portions of interchoanal and parachoanal palatal tooth rows are nearly aligned instead of forming a right angle, (2) assuming the retention in *P. speleus* of the standard capitosauroid outline of the snout, the presence of character 1 implies anterior convexity of the interchoanal row, in contrast to straight transverse alignment or gentle concavity of this row in other species.

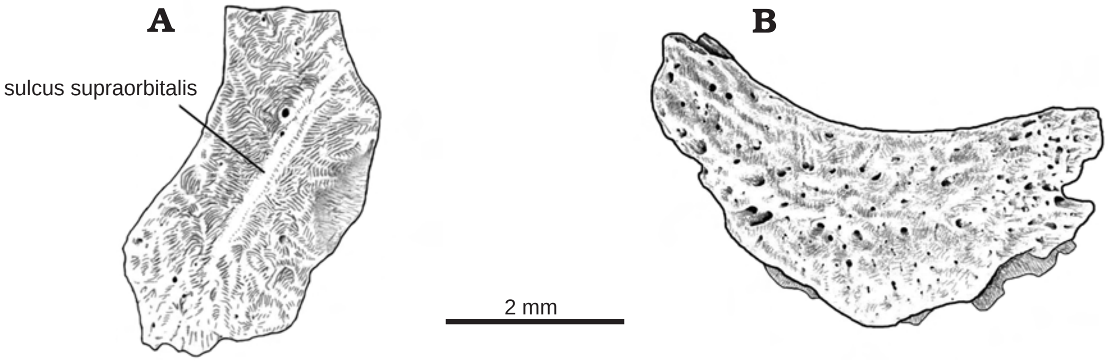

Fig. 1. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Bones of skull roof in dorsal view. **A**. Left postfrontal ZPAL AbIV/43. **B**. Right postorbital ZPAL AbIV/151.

Comments. — Diagnostic value of the above-listed characters 1 and 2 cannot be invalidated by ascribing them to the juvenile condition of the holotype. The early growth stages and paedomorphic morphotypes known in the other Capitosauroidea (*sensu* Shishkin, 1964) show a concave or wedge-shaped interchoanal tooth row forming an acute angle with the parachoanal row (Shishkin *et al.* 1996; Shishkin and Rubidge 2000; Steyer 2003). For this reason, diagnostic characters of *P. speleus* are regarded as apomorphic with respect to dentition patterns known in both the other *Parotosuchus* species and the more primitive *Wetlugasaurus*-grade capitosaurids (with adult dentition retaining or approaching the juvenile type).

On the other hand, many of the unusual characters displayed by *P. speleus* are presumed to reflect immaturity of available cranial material. With respect to some of the characters such an explanation is proved by a growth series demonstrating a trend towards the standard capitosauroid condition with age (*e.g.*, the ectopterygoid dentition combining a tusk pair with highly reduced number of regular teeth; the presence on the ectopterygoid of the medial wall and the dorsally exposed *facies maxillo-jugalis*, see pp. 44–46). Immaturity of other revealed characters is substantiated by parallels with larval or paedomorphic morphotypes known in Paleozoic forms (the vomer with step-like demarcation between dentiferous division and medial plate). In other cases the same conclusion is based on similarity with remote ancestral patterns (symphyseal plate of dentary broadly sutured with flattened precoronoid). Lastly, some unique traits detected in the juveniles of *P. speleus* are attributed to early developmental features conventionally, in view of the lack of comparable data on the ontogeny of other temnospondyls. This relates, in particular, to the plate-shaped design of the subotic process of the exoccipital.

Among the juvenile traits revealed in *P. speleus* some additional diagnostic value may be supposed for the pattern of ectopterygoid dentition showing a tusk pair and just a few regular teeth. This pattern is basically retained even in semi-grown individuals, in contrast to normal condition in other *Parotosuchus* species that display only long row of regular teeth.

Family **Brachyopidae** Lydekker, 1885

Genus ***Batrachosuchoides*** Shishkin, 1966

Type species: *Batrachosuchoides lacer* Shishkin, 1966.

Distribution. — Late Early Triassic (Late Olenekian) of Eastern and Central Europe.

Batrachosuchoides sp.

(Figs 32, 33, 34B, 35, 36, 37B, 38–41, 43, 45)

Locality: Czatkowice 1, southern Poland (Kraków region).

Horizon: Bone-bearing breccia of the earliest Late Olenekian.

Material. — A series of incomplete isolated bones, collection ZPAL AbIV: postparietal 101; ectopterygoids 36, 53; exoccipitals 48, 120, 152; surangular 69; clavicle 61.

Comment. — The typical brachyopid characters displayed by the above-listed specimens are surveyed in the next section (pp. 61–71). In most characters essential for comparison, especially in those displayed by the

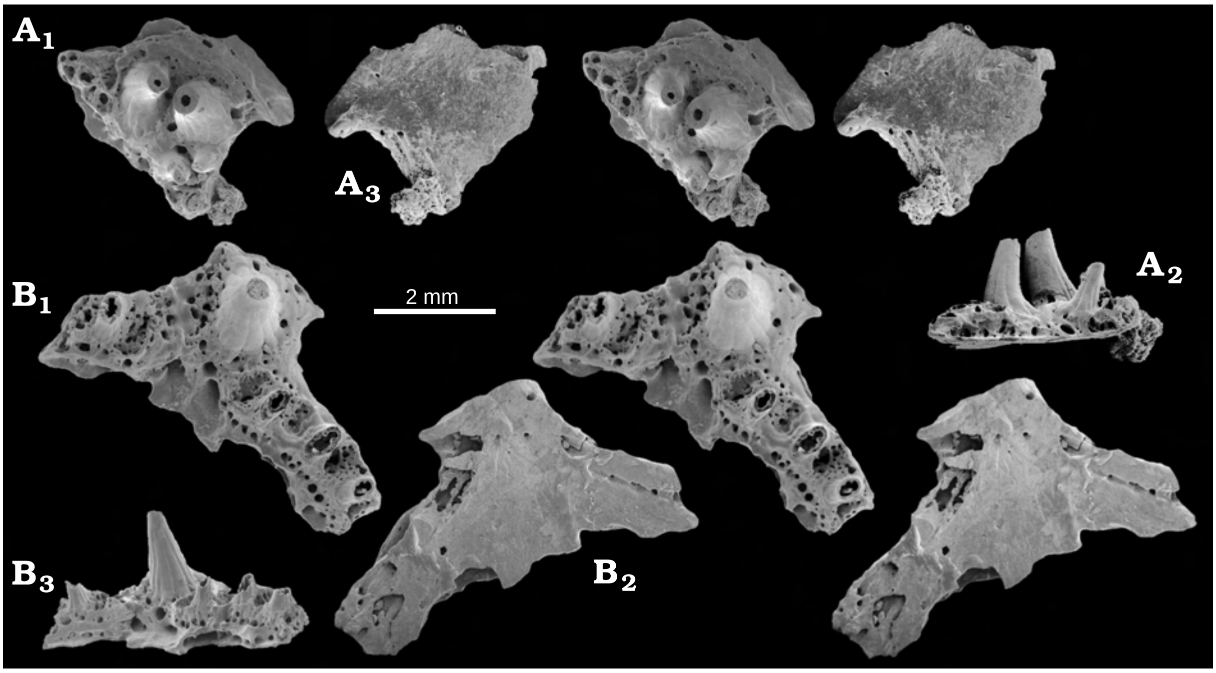

Fig. 2. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Vomers: ZPAL AbIV/65 (**A**) and ZPAL AbIV/105 (**B**, holotype), in ventral (A_1, B_1), dorsal (A_2, B_2), and medial (A_3, B_3) views. SEM micrographs; all but A_3, B_3 stereo-pairs.

exoccipital and surangular, the Czatkowice 1 brachyopid conforms to *Batrachosuchoides* from the late Early Triassic of Eastern Europe. Consistent with such generic attribution is also the trend to incomplete or retarded closure of the vagus foramen of the exoccipital, a character known to be a common variation in *Batrachosuchoides*. The attribution to this genus may be further indirectly supported by the fact that it is the only brachyopid recorded in the Triassic of Europe. The scarcity of available material of the Polish form precludes us from a decision about its species status.

MORPHOLOGY OF *PAROTOSUCHUS SPELEUS* SP. N.

SKULL ROOF

Postfrontal (Figs 1A, 9A). — In contrast to palatal and jaw bones, which are the most common in the collection, only a very few skull roof remains have been recognized. The specimen ZPAL AbIV/43, tentatively identified as the left postfrontal is over 4 mm long, with an extensive anterolateral concavity marking the medial orbital margin. The broken anterior end is thick in a cross section, suggesting that the bone continued farther forward. It is not clear whether it reached the prefrontal or whether they were separated by the intervening frontal. For most of its extent, the dorsal surface of the postfrontal (Figs 1A, $9A_1$) bears a dermal ornamentation. A very shallow supraorbital sensory groove passes forward along the orbital margin and evidently fades out anteriorly. On the ventral side of bone (Fig. $9A_2$) its plate-like medial zone bears indications of extensive flat contact with neighboring elements, evidently the parietal and frontal.

Postorbital (Figs 1B, 9C). — The right postorbital (ZPAL AbIV/151) is shaped as a narrow crescent extending transversely around the posterior margin of the orbit. Although attribution of the bone to a capitosaurid cannot be proved with confidence, it seems most plausible. From its proportions it is very similar to that in the youngest growth stages of the Australian capitosaurid *Rewanobatrachus* (“*Parotosuchus*”) (Warren and Hutchinson 1988a, figs 9B, 10A; *cf.* Schoch and Milner 2000). The lateral side of the bone that sutured with the jugal is wider than the tapered medial end, directed toward the postfrontal. The dorsal surface (Figs 1B, $9C_1$) bears smoothed ornament and faint indications of the postorbital sensory groove bending around the orbital rim.

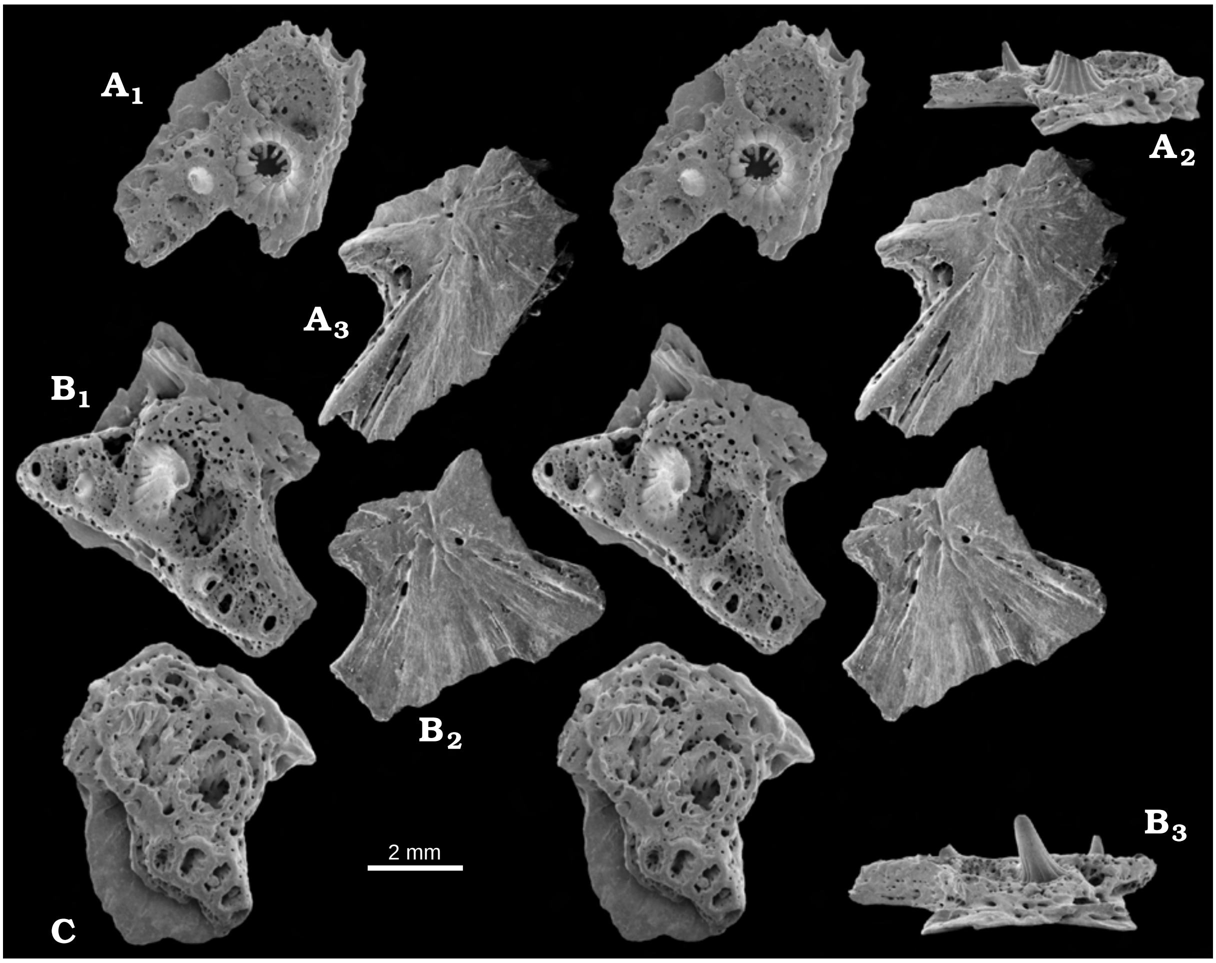

Fig. 3. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Vomers: ZPAL AbIV/38 (**A**), ZPAL AbIV/37 (**B**), and ZPAL AbIV/66 (**C**), in ventral (A_1, B_1, C), dorsal (A_2, B_2), and medial (A_3, B_3) views. SEM micrographs; all but A_3, B_3 stereo-pairs.

PALATAL COMPLEX

Vomer (Figs 2–6, 8C, 14). — The bone is best exemplified by incomplete specimens ZPAL AbIV/105 (holotype) and ZPAL AbIV/37, with some additional details shown by more fragmentary ZPAL AbIV/38, 65, and 66. Most specimens fall into two size classes (ZPAL AbIV/65, 105 against ZPAL AbIV/37, 38) with the minimum prechoanal length value (measured along the tusk pair) close to 2.1–2.3 mm and 3.6–3.8 mm respectively; somewhat bigger is a reworked fragment IV/66 with a value about 4.2 mm. Only a very few characters, such as the pattern of parachoanal dentition, show directed change with growth; otherwise there is no clear correlation between the individual size and variability.

As in many temnospondyls, the vomer can be subdivided in two parts: a thickened marginal tooth-bearing area (the zone of initial ossification) and a flattened medial plate that normally forms a median contact with its counterpart. In contrast to the standard capitosauroid pattern, all the specimens show a clear-cut demarcation between these parts, such that in the palatal aspect the tooth-bearing area is markedly elevated above the medial plate (Figs 2A_1, A_3, B_1, B_3, 3A_1, A_3, B_1, B_3, C, 4B, D, and 5). Their boundary forms a vertical step usually incised by a trough along its extent. A similar condition is known in a number of Permian temnospondyls, primarily the paedomorphic trimerorhachoid (dvinosaurid) *Dvinosaurus* (Shishkin 1973, pl. 1: 4; pl. 4: 1) and, to lesser extent, in many branchiosaurs and juveniles of eryopoid or eryopoid-related taxa, such as *Onchiodon* and *Sclerocephalus* (Boy 1986, figs 3b, 5; 1990, fig. 3A; Schoch 2001, fig. 3; 2003, p.1061, fig. 3A, B; Boy 2002, fig. 2A). The presence in *Parotosuchus speleus* of such demarcation between the tooth-bearing part and medial plate suggests that the vomers under study represent the early growth stages. The above character is well expressed even in the largest member of sample (ZPAL AbIV/66).

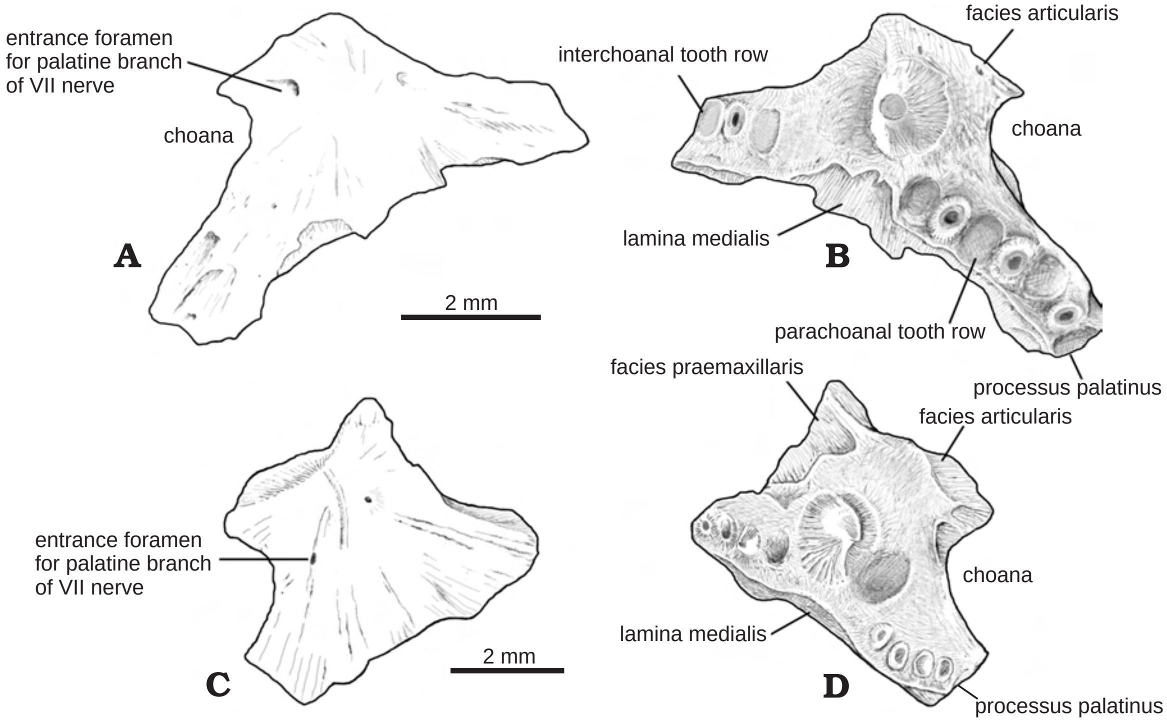

Fig. 4. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Vomers: ZPAL AbIV/105, holotype (**A**, **B**) and ZPAL AbIV/37 (**C**, **D**), in dorsal (A, C) and ventral (B, D) views.

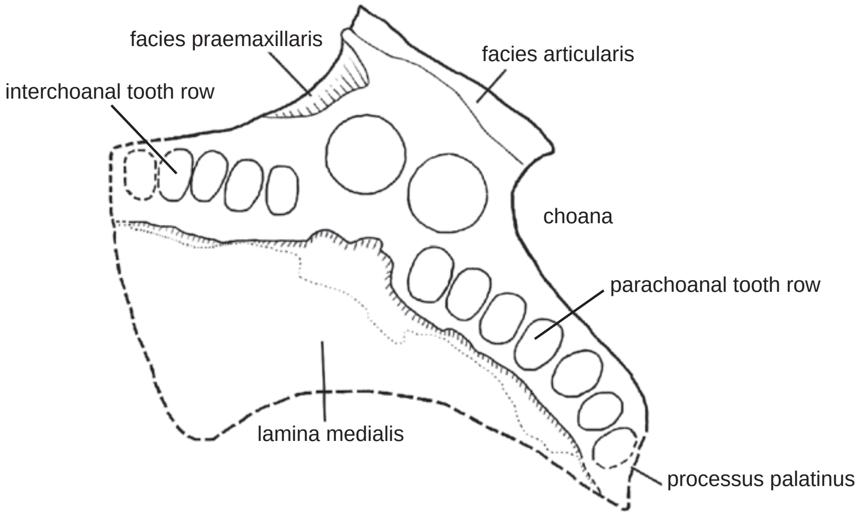

Fig. 5. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Left vomer of juvenile individual in ventral view (diagram): attempted reconstruction based on ZPAL AbIV/37 and ZPAL AbIV/105. Not to scale.

The anterolateral edge of the vomer bordering the tooth-bearing area includes three subdivisions referred to as the anterior, jaw-supporting, and choanal margins. The anterior margin extends more or less transversely. Its lateral part contacted the posterior palatal projection of the premaxilla; the rest of the margin might have contributed to the rim of the anterior palatal vacuity. Actual interrelations of the vomer with these structures are not quite clear and undergo individual variation. In the palatal aspects of ZPAL AbIV/37, 38, and possibly 65, the entire preserved portion of the anterior margin is occupied by a depressed ridged surface (*facies praemaxillaris*) that formed a flat contact with underlying palatal projection of the premaxilla (Figs $2A_1$, $3A_1$, B_1, 4D, 5). By contrast, on small specimen ZPAL AbIV/105 showing the anterior margin preserved for most of its extent, it is uniformly concave and devoid of surface for contact with the premaxilla (Figs $2B_1$, 4B).

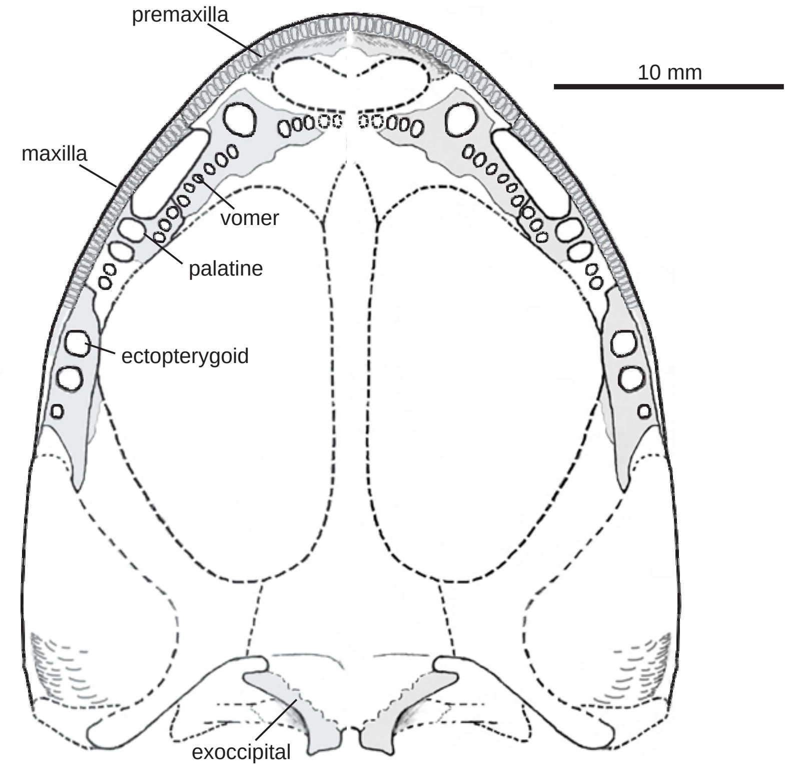

Fig. 6. Skull of early juvenile of *Parotosuchus speleus*, Early Triassic of Czatkowice 1, Poland. Reconstruction of palate showing the pattern of palatal dentition. Based mainly on the vomer ZPAL AbIV/105, palatine ZPAL AbIV/97, ectopterygoid ZPAL AbIV/50, exoccipital ZPAL AbIV/33, and premaxilla ZPAL AbIV/92.

The jaw-supporting margin of the vomer is gently convex in younger individuals ZPAL AbIV/65, 105 and straighter in others. In adult capitosaurids it was bordered by adjacent parts of the maxilla and premaxilla. Distinct from the standard condition in temnospondyls, on the specimens under study this margin is blade-like rather than forming a steep wall to contact the upper jaw bones. The area of this contact is mostly limited to the palatal surface of the vomer and forms the depressed marginal shelf (*facies articularis*) lateral to the tusk pair (Figs 2A$_1$, 3A$_1$, B$_1$, 4B, D, 5). Hence, in the early juveniles of *Parotosuchus speleus* the tooth-bearing portions of the premaxilla and maxilla(?) partially underlay the lateral margin of the vomer. With growth, as evidenced by the fragment ZPAL AbIV/66, the marginal shelf tends to face more ventrolaterally and develops sutural ridges. It is not clear whether the vomer contacted the maxilla in the juveniles. Judging from the structure of their maxilla (Fig. 20D), it seems likely that the latter did not extend anterior to the choana, as is the case in many branchiosaurs (Fig. 6; *cf.* Schoch 1992, figs 14, 19, 24–26).

The choanal margin of the vomer is best preserved on the holotype ZPAL AbIV/105 (Figs 2B$_1$, B$_2$, 4A, B, 6). Here it is straight for most of its length and terminates anteriorly as a narrow embayment. The extent and outline of the choanal margin suggest that the choana was rather long and compressed, with the estimated width/length proportions about 0.28–0.30. In all these respects it was very similar to the slit-like choanae of adult *Parotosuchus*, in which the corresponding value is usually close to 0.25–0.28 (MAS personal observations). Hence, at least in some individuals of the Polish species the advanced capitosaurid condition was well expressed already in the early juvenile stages, without showing transformation from the more elliptical choanal pattern. The latter is typical for the more primitive *Wetlugasaurus*-grade capitosauroids and shows the width/length proportions about 0.35–0.45. The state of preservation of the vomers ZPAL AbIV/37 and 38 does not allow for an unambigous conclusion about the shape of the choana.

A tooth-bearing area forming the main body of the vomerine ossification shows a standard capitosauroid dentition, *i.e.*, a pair of prechoanal tusks combined with the interchoanal and parachoanal tooth rows. It seems evident that the interchoanal row, formed by the two adjacent vomers, was at least slightly convex anteriorly. Judging from condition on ZPAL AbIV/65 (Fig. 2A$_1$), in the early growth stages the tooth row rudiments were irregular clusters of denticles set close to the tusk pair. With growth, these tiny teeth became or-

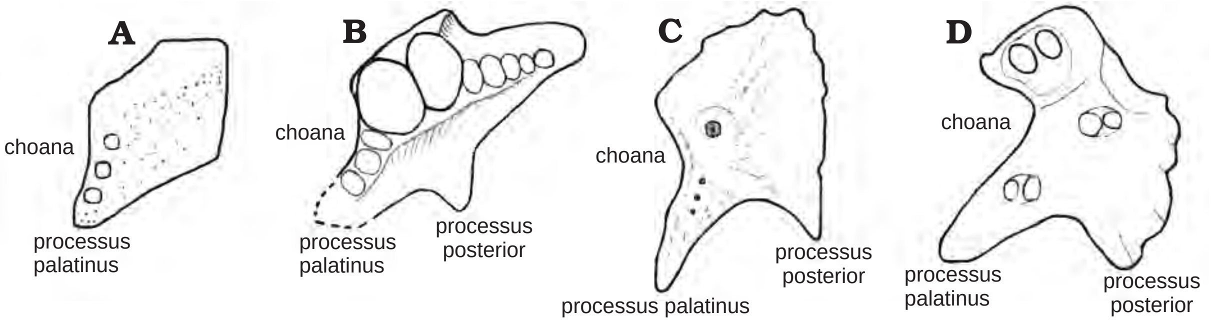

Fig. 7. Patterns of vomer in paedomorphic temnospondyls as exemplified by some dissorophoids (**A**, **C**, **D**) and trimerorhachoids (**B**). **A**. *Apateon* ("*Branchiosaurus*"). **B**. *Dvinosaurus*. **C**. *Branchierpeton*. **D**. *Micropholis*. After Boy (1972), Shishkin (1973), Werneburg (1988), and Schoch and Rubidge (2005). Not to scale.

dered in a row and later suffered moderate anteroposterior compression at their bases. In a sample of the vomers under study, the maximum tooth count seen (as preserved) on ZPAL AbIV/105 is 3–4 for the interchoanal row, and 7 for the parachoanal row. The shape of the latter varies from straight on ZPAL AbIV/38 to notably curved on ZPAL AbIV/37.

Among the features shown by the vomer of the Czatkowice 1 capitosaurid, of special importance is the relative position of the parachoanal and interchoanal tooth rows. The neighbouring parts of these rows are nearly aligned, forming an angle from ca. 140° on specimen ZPAL AbIV/105 to 160°–170°on ZPAL AbIV/37 (Figs $2B_1$, $3B_1$, 4B, D). This character seems decisive both for the species discrimination and for assessment of life position of the vomers within the assembled palate. This position cannot be directly inferred from the specimens' shape as in none of the vomers is the zone of median contact with its counterpart preserved.

Generally, in *Parotosuchus*-grade capitosaurids, which normally possess a straight (or slightly concave anteriorly) interchoanal tooth row, the angle between it and the parachoanal row is close to 90° or slightly exceeds this value. The exceptions showing a smooth bend between the rows are known mostly in senile individuals (such as the type of "*Capitosaurus*" *haughtoni*: Broili and Schroeder 1937, figs 1b, 9; *cf.* Shishkin *et al.* 2004, fig. 1b). Similar gradual transition is known in Permian rhinesuchids showing a marked anterior convexity of the interchoanal row (Watson 1962, and personal observations of MAS on the BPI collection) and in a few Middle Triassic forms (Watson 1958, fig. 1). On the other hand, in primitive *Wetlugasaurus*-grade capitosaurids, whose interchoanal row tends to be shaped as a rounded wedge or an arch with anterior concavity, it forms an acute angle with the parachoanal row. This pattern seems to be typical for juveniles of various early capitosauroids, judging from data on rhinesuchids (Shishkin and Rubidge 2000, fig. 5B), *Wetlugasaurus*-grade taxon *Edingerella* ("*Watsonisuchus*") *madagascarensis*: Warren and Hutchinson 1988b, fig. 2; Steyer 2003, *cf.* figs 1C, 2C) and lydekkerinids (Shishkin *et al.* 1996, *cf.* figs 6, 7b). This warrants the conclusion that in early capitosauroids the interchoanal tooth row typically appeared in ontogeny as a sickle-shaped or wedge-shaped structure projecting backward.

The above condition was clearly not the case in the ontogeny of the Polish capitosaurid. Based on tooth arrangement in a small individual ZPAL AbIV/105, any attempt to restore its palate with the anteriorly concave interchoanal tooth row would result in enormously broad outlines of the snout, comparable with those in plagiosaurs. For the much larger individual ZPAL AbIV/37 the same result would be attained even if one assumes that the interchoanal row was straight. All this leads to the following conclusions: (1) in *Parotosuchus speleus* and, not unlikely, in *Parotosuchus* overall, the interchoanal teeth were arranged transversely starting from the earliest stages of their development, without recapitulation of the *Wetlugasaurus*-grade pattern; (2) at the more advanced growth stages of the Polish species the interchoanal row attained some degree of anterior convexity, which brought the lateral ends of the row nearly into alignment with the parachoanal rows (Figs 6, 14).

The shape and extent of the medial vomerine division (medial plate) are uncertain (*cf.* Fig. 5). It is preserved as a narrow irregularly shaped strip of bone extending alongside the tooth-bearing elevation (Fig. 4B, D). The strip is positioned far away from the median axis of the skull, *i.e.*, from the zone of presumed intervomerine suture. It is unclear whether this condition shows the true extent of ossification of the medial plate in the juveniles, or is caused by incomplete preservation. Although some of the specimens can be abraded, most show no clear indication of break or damage along the edge of the medial plate. This makes it

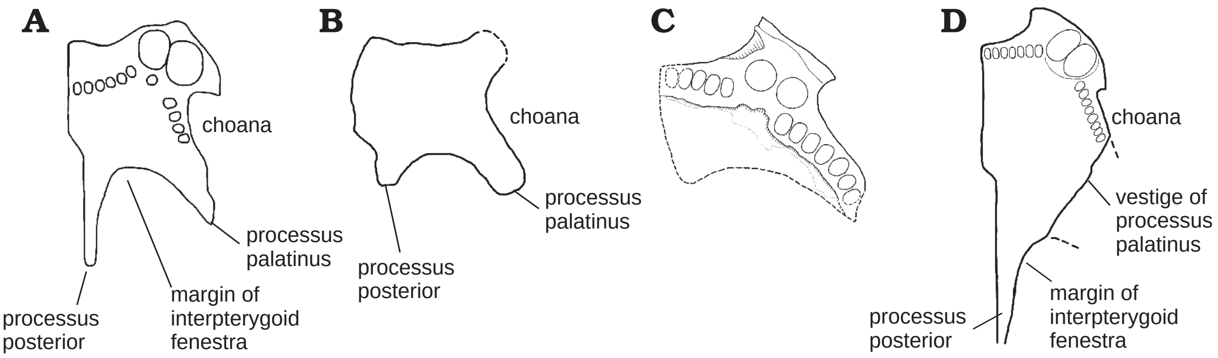

Fig. 8. Modifications of vomerine processes in capitosauroids. **A**. Rhinesuchid *Muchocephalus* (*M. muchos*). **B**. Juvenile of early capitosaurid *Rewanobatrachus* (*R. aliciae*). **C**. Juvenile of capitosaurid *Parotosuchus* (*P. speleus*). **D**. Adult *Parotosuchus* (*P. orenburgensis*). A after BPI 213 (mirror image; MAS personal observation); B after Warren and Hutchinson (1988a); C attempted reconstruction based on ZPAL AbIV/37 and 105; D based on PIN 951/42. Not to scale.

possible that at the stages under study the ossification of the plate was still in progress, such that ossified portions of the vomers remained broadly separated for most of their extent. A similar pattern is known for the larval and/or early metamorphic stages of many urodeles (Lebedkina 1979). In any case, it seems evident that the first portion of the vomer to have ossified in temnospondyls was the thickened lateral area adjacent to the upper jaw and choana, as was shown for the branchiosaur growth series (Schoch 1992, fig. 1).

Predominance of the tooth-bearing portion of the vomer over the medial plate seen in the Polish juvenile capitosaurid is most closely paralleled by the condition in the paedomorphic dvinosaurid taxa *Dvinosaurus primus* (Fig. 7B; *cf.* Shishkin 1973, fig. 4, pl. 1: 4) and *Hadrokkosaurus* (“*Vigilius*”) *bradyi* (Welles and Estes 1969, fig. 26b; *cf.* Warren and Marsicano 2000). However, in these forms the reduction and wide separation of the medial plates are combined with expanded palatal exposure of the cultriform process of the parasphenoid.

Of the two caudal vomerine processes bordering the interpterygoid fenestra, *i.e.*, the *processus posterius* and *p. palatinus*, the examined specimens, as preserved, show only the *p. palatinus*, extending towards the palatine. As in many paedomorphic forms including *Dvinosaurus* (Fig. 7B; cf. Shishkin 1973, pl. 1: 4), *Trimerorhachis* (Holmes 2000, fig. 17B), *Micropholis* (Fig. 7D; Schoch and Rubidge 2005, fig. 1D) and various branchiosaurs (Fig. 7A, C; *cf.* Boy 1972, figs 31, 32; 1978, figs 6, 7, 20b; 1986, figs 3, 5, 14, 18; 2002, figs 2A, 4G; Werneburg 1989, figs 6, 7), the *p. palatinus* is strong and formed from the thickened lateral vomerine division, with only limited, if any, contribution from the medial plate. A more or less similar condition is known in the juveniles of early capitosaurids (Fig. 8B; *cf.* Steyer 2003, fig. 1C; Warren and Hutchinson 1988a, figs 8D, 10B) and in adult rhinesuchids (Fig. 8A). By contrast, in all adult capitosaurids including *Parotosuchus*, the *p. palatinus* is barely expressed and much widened at the cost of the medial plate, tending to be entirely incorporated in the latter (Fig. 8D). All this suggests that the pattern of the vomerine palatine process demonstrated by the Czatkowice 1 sample may have corresponded to a primitive state, still retained by the early growth stages of *Parotosuchus*.

On the evidence from examined specimens, nothing can be concluded about the presence of the posterior vomerine process that spreads in the adults along the cultriform process of the parasphenoid. As seen from the branchiosaur growth series (Boy 1972, figs 31–36; 1986, fig. 3; Schoch 1992, figs 11, 12), the posterior process, when present (Fig. 7C), developed in temnospondyl ontogeny much later than the *p. palatinus* and appeared as an outgrowth of the vomerine medial plate. The same was evidently the case in development of capitosauroids that had in the adult the long, spine-like posterior processes (Fig. 8A, D). Based on the incomplete vomers of the Polish capitosaurid, it seems most likely that their semi-grown stages resembled the type known in the juveniles of the Australian *Rewanobatrachus aliciae* (*cf.* Figs 5, 8B, C). The latter shows a well-developed *p. palatinus* which seems to be combined with rudimentary *p. posterior*.

The dorsal surface of the vomer of *P. speleus* is flattened and bears the entrance foramen for the *nervus palatinus* VII leading anteromedially (Figs 2B$_2$, 3A$_2$, B$_2$, 4A, C). As in many temnospondyls, it is situated close to the anterior portion of the choanal embayment. In front of the choana, the lateral margin of the surface shows a narrow triangular depression. It could have served as a dorsal attachment area for the premaxilla.

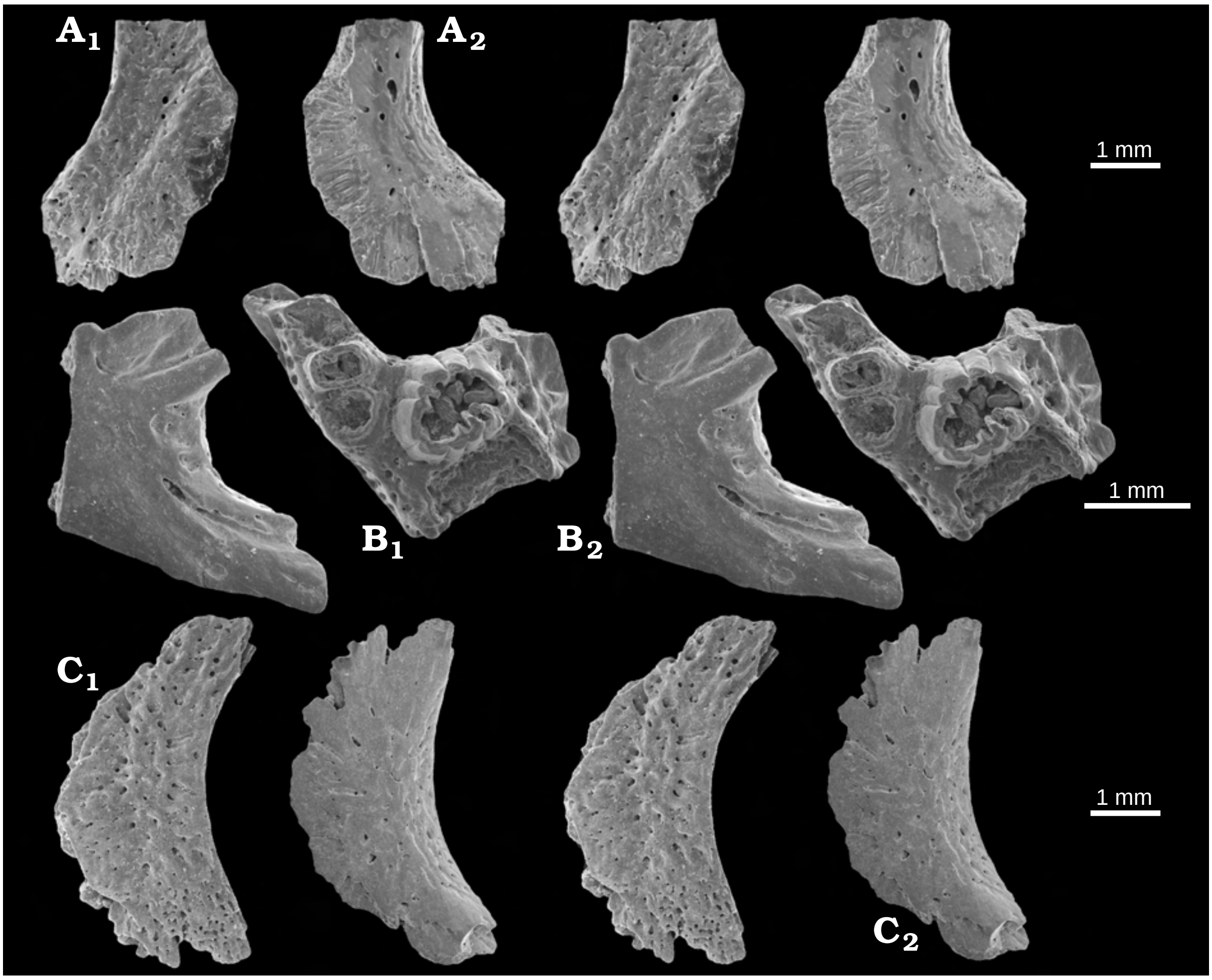

Fig. 9. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Cranial bones: left postfrontal ZPAL AbIV/43 (**A**), fragment of left palatine ZPAL AbIV/97 (**B**), and right postorbital ZPAL AbIV/151 (**C**), in dorsal (A_1, B_2, C_1) and ventral (A_2, B_1, C_2) views. SEM stereo-pairs.

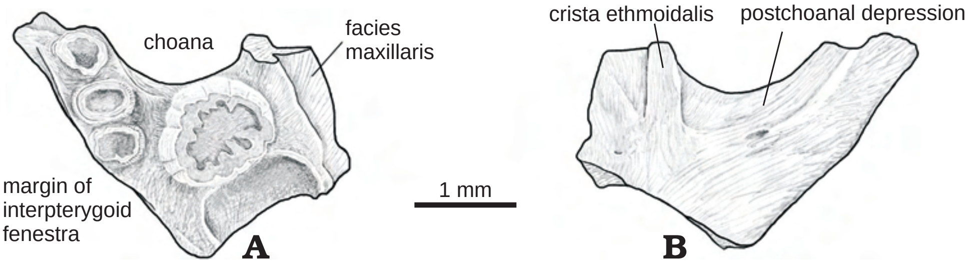

Fig. 10. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Anterior portion of left palatine ZPAL AbIV/97, in ventral (A) and dorsal (B) views.

Palatine (Figs 6, 9B, 10). — Except for a fragment ZPAL AbIV/97, none of the specimens available can be identified as the palatine. The above fragment represents an expanded postchoanal area bearing a tusk pair and three posterior parachoanal teeth aligned along the vomerine process of the bone (Figs $9B_1$, 10A). Compared to the same process in adult capitosaurids, it is much narrower, not expanded anteriorly, and extends farther forward. Lateral to the tusk pair, the ventral surface of bone bears a posterior continuation of the depressed marginal shelf noted above on the vomer and contacted by the upper jaw (*facies maxillaris*). As in the vomer, the lateral edge of the bone is thin and blade-like.

The structure of the dorsal surface of the palatine (Figs $9B_2$, 10B) somewhat departs from the typical pattern of adult Late Permian and Triassic temnospondyls. Peculiar to the latter is the presence of a cres-

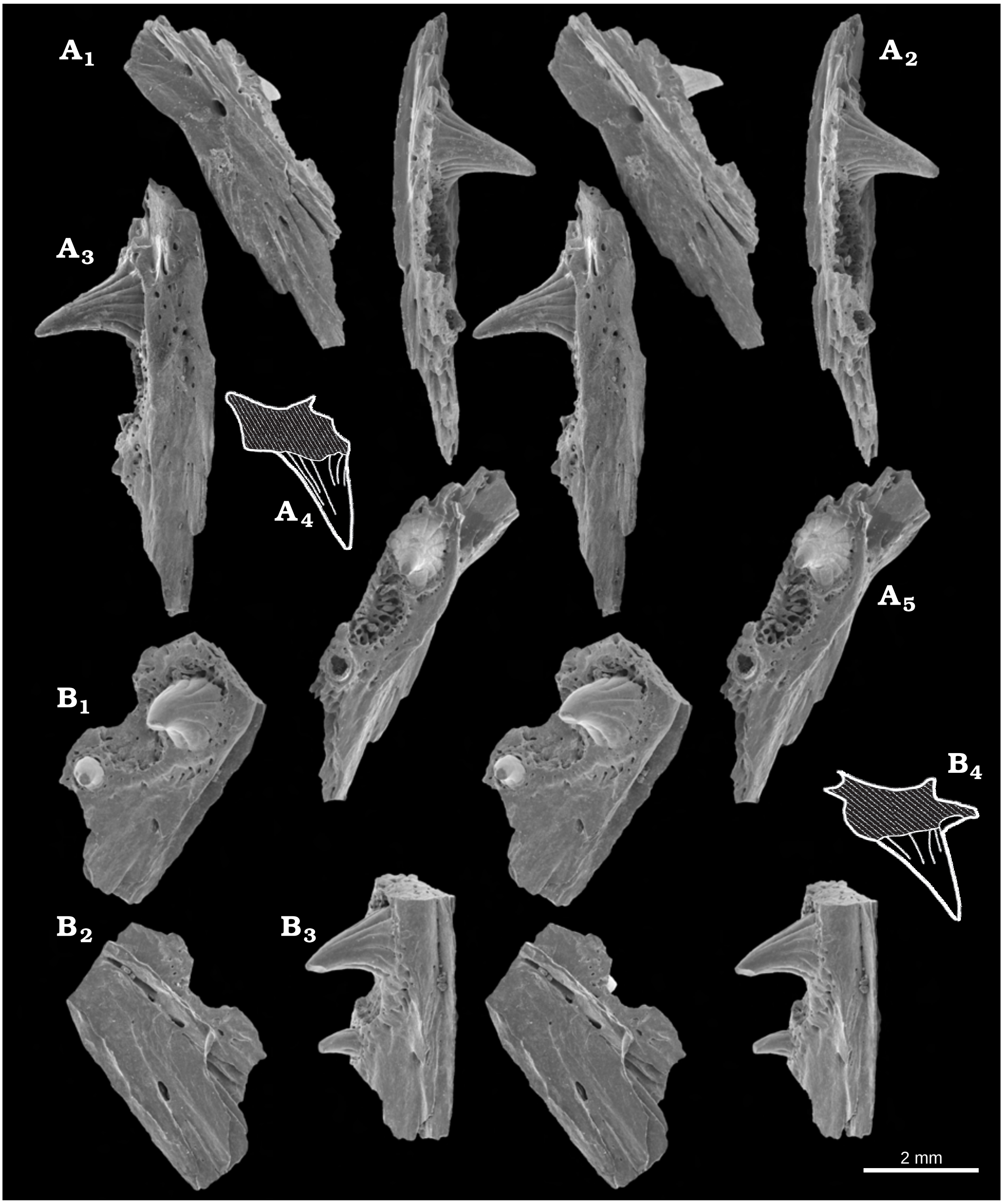

Fig. 11. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Right ectopterygoids: ZPAL AbIV/50 (**A**) and ZPAL AbIV/46 (**B**), in dorsal (A_1, B_2), lateral (A_2), medial (A_3, B_3), ventral (A_5, B_1) views, and cross sections (A_4, B_4). All but A_4 and B_4 SEM stereo-pairs.

cent-shaped or triangular postchoanal depression (*facies postchoanalis*: Shishkin 1973, figs 22, 30, 60b, 73, pl. 1: 3b, pl. 3: 6; Shishkin and Welman 1994, fig. 2A; *cf.* Säve-Söderbergh 1936, fig. 7, 8), which housed the posterolateral corner of the ethmoid capsule. Another character is the presence of a marginal ridge bordering the dorsal surface laterally and providing support to the maxilla. As can be inferred from the growth series of paedomorhic dissorophoids (branchiosaurs and related forms), the *f. postchoanalis* appeared in early growth stages and was succeeded by formation of the dorsal ridge (Boy 1972, figs 35–37; 1978, fig. 8a–c; 1986, figs

3a, 16a; Watson 1940, fig. 23). In the palatine fragment ZPAL AbIV/97 from Czatkowice 1 the subtriangular *facies postchoanalis* seems to be already distinguishable, along with the *crista ethmoidalis* (*cf.* Shishkin 1973) bordering this depression medially. On the other hand, the lateral zone of the dorsal surface is flat, with no trace of a marginal ridge.

Ectopterygoid (Figs 6, 11–14). — The ectopterygoids assigned to *P. speleus* include a small bone ZPAL AbIV/50 (7.9 mm long) and two more specimens belonging to larger individuals. These are a fragment ZPAL AbIV/46 and more mature ZPAL AbIV/107, which is nearly complete and attains 11 mm in length. Although they differ from the brachyopid ectopterygoids from the same locality (see below), it is remarkable that both types share a number of traits that are uncommon for adult Late Permian and Triassic temnospondyls (see pp. 61, 71).

The ectopterygoid ZPAL AbIV/50 (Figs 11A, 12A–D) is almost complete except for lack of some part of the anterior (palatine) process. The bone is elongate and narrow. Its posteromedial projection contacting the pterygoid and jugal is shaped as a narrow wedge. The lateral contour is gently convex, which is uncommon for "normal" adult temnospondyls with parabolic or triangular skulls. This suggests that at the growth stage represented by ZPAL AbIV/50 the skull was short (brachyopid-like) and had convex lateral outlines (*cf.* juvenile *Rewanobatrachus*: Warren and Hutchinson 1988a, figs 8–10).

Most of the ventral surface of the specimen (Figs 11A$_5$, 12A) is occupied by a tooth-bearing area which is tapered anteriorly and posteriorly and bordered medially by a flattened horizontal projection. Anteriorly, the area continues into the palatine process, and posteriorly, into the small terminal area that contacted the internal process of the jugal (*insula jugalis*). The palatine process overlapped the adjacent portion of the palatine and shows a flat sutural surface which abruptly wedges out posteromedially. In being much shortened, the process differs from that in adult capitosaurids, in which, judging by the shape of the posterior projection from the palatine, it formed a long narrow strip. The attachment area for the *insula jugalis* (Fig. 12A; *facies jugalis ventralis*) lies immediately behind the posterior ectopterygoid tooth. It bears short ridges and forms only a small part of the contact with the jugal, most of which lay on the dorsal side of the ectopterygoid.

The dentition in ZPAL AbIV/50 is completely preserved and consists of a pair of well-developed tusks with one regular tooth behind them. This condition, common for brachyopoids and many Paleozoic temnospondyls, is unique for both the capitosauroids and most of their derivatives (early benthosuchids, heylerosaurids), in which the ectopterygod dentition consists of but a row of regular palatal teeth. A tusk (single or paired), much reduced in size and combined with a tooth row, has been hitherto found in the juveniles of primitive capitosaurids, such as *Rewanobatrachus* and *Edingerella* ("*Watsonisuchus*") (Warren and Hutchinson 1988a, fig. 4; 1988b, fig. 2; Steyer 2003, fig. 2C), and, as an individual or geographic variation, in some adult lydekkerinids (Shishkin *et al.* 1996, fig. 7b), wetlugasaurines and benthosuchids (personal observations of MAS). The paedomorphic retention of a tusk pair is also known in benthosuchid descendants, the Trematosauridae. It seems evident that the primitive pattern demonstrated by the early growth stage of the Polish capitosaurid recapitulates the ancestral condition. As seen from comparison with larger individuals (Fig. 12E–H, see below), the ectopterygoid dentition in this form underwent a gradual growth change towards a more standard capitosauroid design, by developing a normal tooth row posterior to the tusks. On the other hand, even in the relatively large specimen ZPAL AbIV/46 the juvenile type of dentition is still retained (Fig. 11B$_1$).

An unusual feature seen in specimen ZPAL AbIV/50 is the presence of a steep medial wall (*planum mediale*), which formed the ventralmost portion of the palatal vault of the dermal skull (Figs 11A$_3$, A$_4$, 12C, D, 13A). The medial wall attains its maximum depth at the level of the tusk pair. Here it is deeply concave dorsoventrally and bordered at the palatal level by a projecting medial edge of the tooth-bearing shelf. The dorsal margin of the medial wall corresponds to the level of the pterygoid-ectopterygoid contact. Posteriorly the wall becomes shallower and faces ventromedially rather than medially. Overall, the described condition markedly departs from that in adult temnospondyls, where the medial margin of the ectopterygoid is flattened dorsoventrally. As seen from comparison of specimens ZPAL AbIV/50, 46, and 107, the flattening of the medial wall, initially detectable in its posterior part, gradually spreads with age over the entire extent of the wall until it transforms into the medial palatal shelf of the ectopterygoid (*cf.* Figs 11A$_4$, 12D, H, 13).

The dorsal surface of the juvenile ectopterygoid (Figs 11A$_1$, B$_2$, 12B, D) is subdivided by a nearly straight longitudinal ridge (*crista dorsalis*) into the main medial division and narrow lateral ledge. The latter (*facies maxillo-jugalis*) faces dorsolaterally and provided an attachment for the jugal and, more ventrally, the maxilla. The jugal contacted the lateral side of the *c. dorsalis*, while the maxilla covered most of the lateral

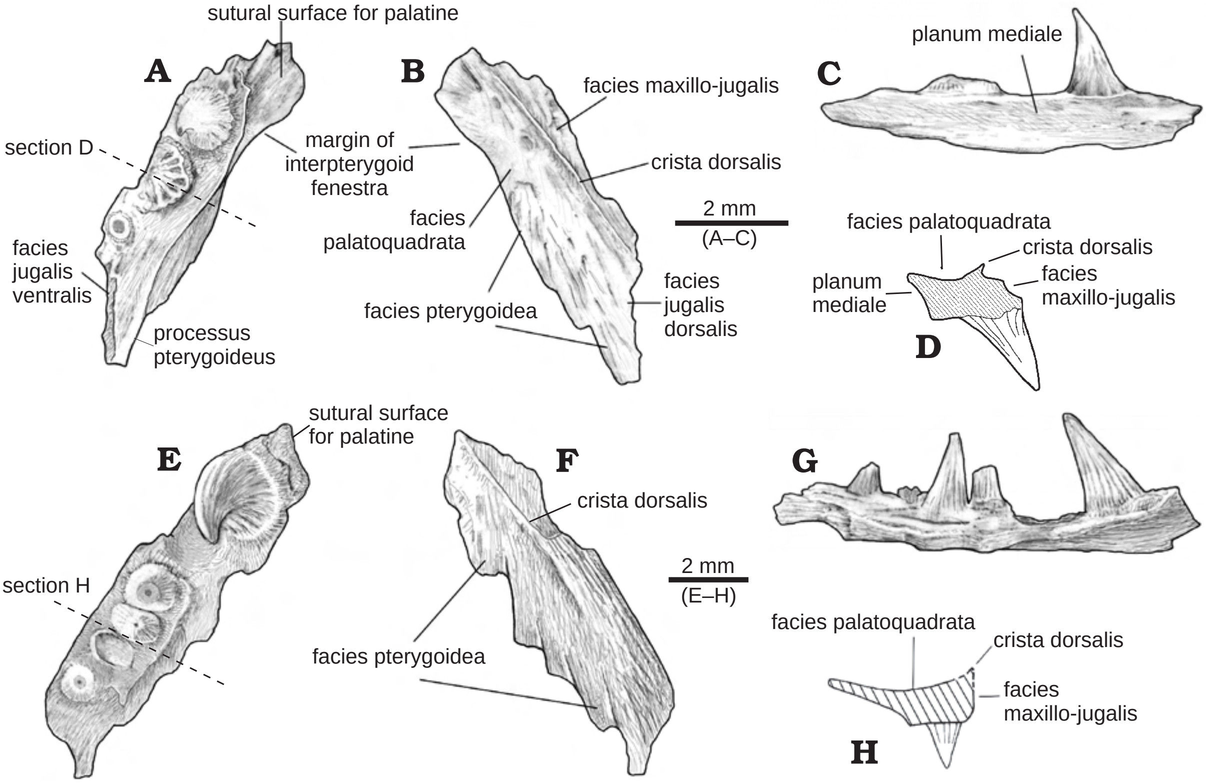

Fig. 12. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Right ectopterygoids ZPAL AbIV/50 (**A**–**D**) and ZPAL AbIV/107 (**E**–**H**), in ventral (A, E), dorsal (B, F), medial (C, G) views, and cross sections (D, H). Note the growth changes: increase in number of regular teeth, spreading forward from the sutural contact with the pterygoid (loss of free medial edge of ectopterygoid), reduction of the *planum mediale* and weakening of the *crista dorsalis*.

ledge. In overall position, the *facies maxillo-jugalis* notably differs from its homologue in adult temnospondyls. The latter forms a single vertical external wall of the bone, with its upper margin corresponding to the *crista dorsalis* of the young Czatkowice 1 specimens (*cf.* Figs 12D, H, 13).

The medial division of the ectopterygoid dorsal surface is preserved for most of its extent on ZPAL AbIV/50 (Figs $11A_1$, 12B). Its anterior portion is smooth and underplated the palatoquadrate cartilage. An expanded posterior portion projects backwards and slightly medially as a wedge-shaped pterygoid process (= *processus squamosus* of Bystrow and Efremov 1940). Most of it is occupied by a field of slightly radiating ridges which marks the zone of flat sutures with the palatal branch of the pterygoid (*facies pterygoidea*), and, more laterally, with the palatal process of the jugal (*facies jugalis dorsalis*). The lack of gap between these attachment areas shows that in the assembled skull the dorsal exposure of the ectopterygoid did not reach the subtemporal fossa. The *facies pterygoidea* narrows anteriorly and extends along the medial margin of the bone to the level of the posterior tusk or so. It seems almost certain that anterior to this level the ectopterygoid entered the interpterygoid fenestra, thus separating the pterygoid from the palatine. Among capitosaurids such a condition is uncommon and has been hitherto recorded only in juvenile skulls of *Rewanobatrachus* with midline length less than 40 mm (Warren and Hutchinson 1988a, p. 865, fig. 4B)

Along with growth changes of the ectopterygoid noted above, a few more can be inferred from comparison of ZPAL AbIV/50 with ZPAL AbIV/46. The latter (Fig. 11B) is a fragment 4.5 mm long, mostly limited to a tooth-bearing portion, and belonging to a somewhat larger individual than ZPAL AbIV/50. The dentition pattern and the structure of dorsal surface are close to that in ZPAL AbIV/50, but the *planum mediale* is notably shallower than in the latter specimen. Another change relates to sutural contact with the pterygoid. Judging from its impressions, the medial edge of the ectopterygoid was embraced by the pterygoid both dorsally and ventrally for the entire extent of the specimen ZPAL AbIV/46; *i.e.*, the suture continued ahead of the tusk pair. This suggests that the pterygoid could have reached the palatine in a standard capitosaurid fashion.

The later growth changes in the ectopterygoid structure are exemplified by specimen ZPAL AbIV/107, which tightly approaches the adult capitosaurid design (Figs 12E–H, 13B, 14). The tusk pair is followed here

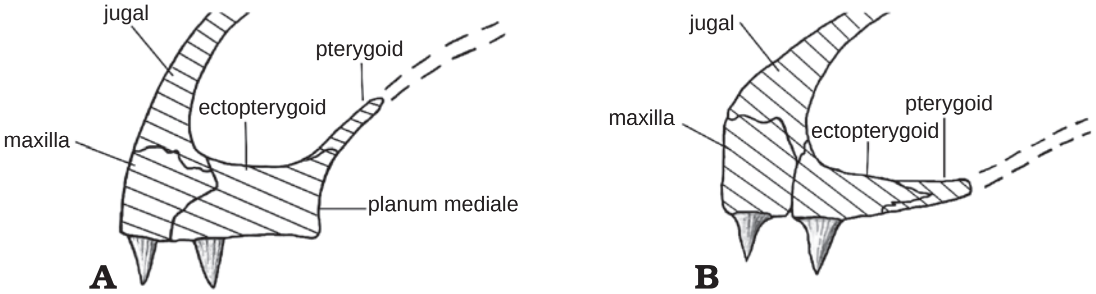

Fig. 13. Ontogenetic flattening of palatal vault in *Parotosuchus* as evidenced by three-dimensional growth changes of the ectopterygoid. Cross sections of cheek region of skull reconstructed for two generalised growth stages (diagram). **A**. Based on juvenile *Parotosuchus speleus* ZPAL AbIV/50. **B**. Based on more fully grown *Parotosuchus speleus* ZPAL AbIV/107, with some details from an adult skull of *Wetlugasaurus* sp. PIN 3583/22. Not to scale.

by a row of just four gently compressed regular teeth. The medial wall of the bone is not distinguishable any longer and transformed into the palatal shelf (*cf.* Figs 12D, H, 13). On the other hand, the gentle convexity of the lateral contour of the bone is still detectable. A zone of contact with the pterygoid is situated in the plane of the dentition, in contrast to its more dorsal position in younger individuals. In palatal view it extends over the entire medial edge of the ectopterygoid as a series of oblique sutural notches. The ventral surface for a contact with the palatine is still very short.

The dorsal and lateral sides of the specimen (Fig. 12F, H) are designed in a way comparable with that in adult capitosaurids. The differentiation of the *crista dorsalis* from the *facies maxillo-jugalis* is almost erased, such that both structures virtually form a single wall facing more or less laterally. A vestige of the *c. dorsalis*, shallow and rounded in cross section, is still discernible in the middle of the bone's extent. A posterolateral triangular area of the dorsal surface that served for a flat contact with the pterygoid and jugal is more elongate than in smaller specimens.

In summary, the most unusual characters of the ectopterygoid observed at the juvenile growth stages in the Czatkowice 1 capitosaurid are as follows: (1) archaic dentition strongly dominated by a tusk pair and supplemented by a very slowly increasing number of regular teeth; (2) the presence of the subvertical *planum mediale* that contributed to the palatal vault of skull and later became incorporated in the palatal surface of the bone (with shallowing of the vault; see Fig. 13); (3) differentiation and dorsolateral orientation of sutural surfaces for the jugal and maxilla, a condition succeeded by their unification into a single lateral wall; (4) inclusion of the ectopterygoid into the margin of the interpterygoid fenestra at the earliest growth stages.

Except for (4) and only partially (1), the above characters have never been recorded in capitosauroid juveniles. To this end, special attention should be paid to character 1 as it seems to afford some basis for comparison of developmental rates demonstrated by the ectopterygoid dentition in a some Early Triassic taxa. Judging from figures and/or restorations of juvenile skulls of the capitosauroid *Rewanobatrachus* and capitosauroid derivative *Benthosuchus* (Bystrow and Efremov 1940; Warren and Hutchinson 1988a), the proportions of the midline skull length to ectopterygoid length varied in them from 3.8 to 4.8. Based on these indices, the Czatkowice 1 juveniles represented by the available ectopterygoids could be expected to have shown a midline skull length from 31–39 mm in ZPAL AbIV/50 to 42–53 mm in ZPAL AbIV/46 and 107. The first of these ranges covers the value estimated for the juvenile skull of *Rewanobatrachus aliciae* (39 mm; see Warren and Hutchinson 1988a, p. 861, fig. 4), and much ex-

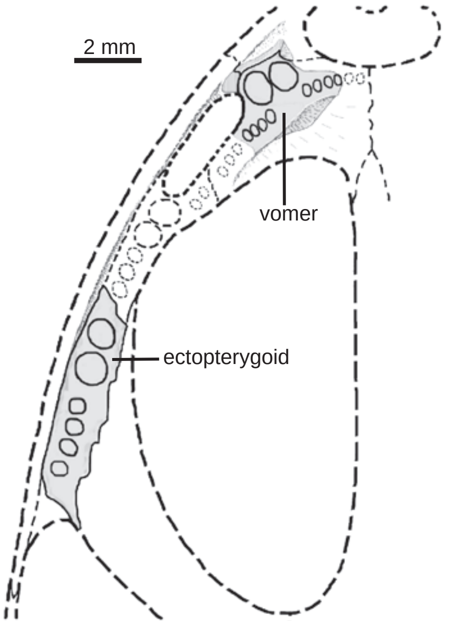

Fig. 14. Reconstruction of tooth-bearing portion of palate in advanced juvenile of *Parotosuchus speleus*. Based on the vomer ZPAL AbIV/37 and ectopterygoid ZPAL AbIV/107. In comparison with the earlier growth stage (Fig. 6), notable are the changes in design and dentition of the ectopterygoid combined with elongation of the pterygoid-ectopterygoid suture.

ceeds the value known for the juvenile *Benthosuchus sushkini* PIN 2252/4 (less then 27 mm, see Bystrow and Efremov 1940, p. 74, figs 56, 58). But, in spite of that, the Czatkowice 1 specimens demonstrate a much more primitive ectopterygoid dentition in comparison with the juveniles of *Rewanobatrachus* and *Benthosuchus* as the latter show a well developed regular tooth row combined with reduction or loss of tusk pair. One of possible explanations of this discrepancy is that the *Parotosuchus* juveniles of the same size as those of *Wetlugasaurus*-grade taxa in fact represent earlier developmental stages than the latter. This seems plausible taking into account the retardation of development progressed in capitosauroid evolution. As a consequence, in *Parotosuchus* the growth changes evidently proceeded at slower rate than in its Early Scythian forerunners.

OCCIPITAL ARCH

Exoccipital (Figs 15, 16). — The two left exoccipitals, ZPAL AbIV/33 and 104, are of similar shape and conform to capitosauroid type primarily in the following characters: (1) the occipital condyle is high and transversely compressed; (2) the bone is short anteroposteriorly and devoid of a well demarcated ventral surface; (3) in the dorsal view, the subotic process is strongly turned laterally.

The condylar surface (Figs 15B, 16C, E) is poorly ossified, stretched dorsolaterally in occipital view and forms the lateral border of a large irregular notochordal notch. Distinct from the condition in adult capitosauroids, the occipital surface above the condyle is not clearly demarcated from the lateral wall of the bone, such that they form a common posterolateral surface. Its medial edge forms a concavity marking the rim of the *foramen magnum*. Ventrally the edge continues into a medial projection (submedullar process), which spreads forward as a smooth hollowed submedullar ledge. The supracondylar (ascending) division of the exoccipital shows no trace of forking into the dorsal and paroccipital processes that most likely remained

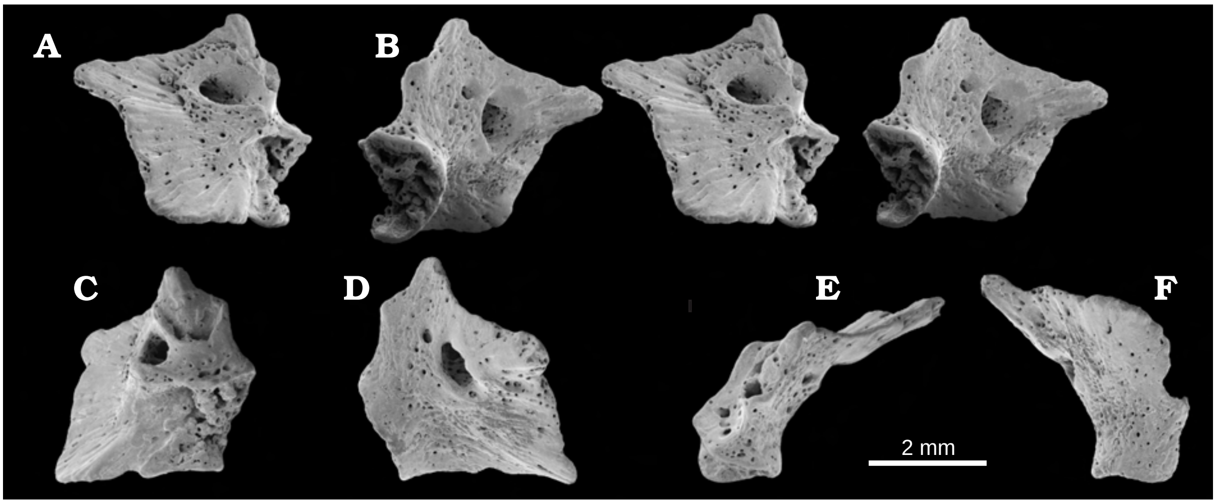

Fig. 15. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Right exoccipital ZPAL AbIV/33, in anteromedial (A), posterolateral (B), medial (C), lateral (D), dorsal (E), and ventral (F) views. SEM micrographs; A, B, stero-pairs.

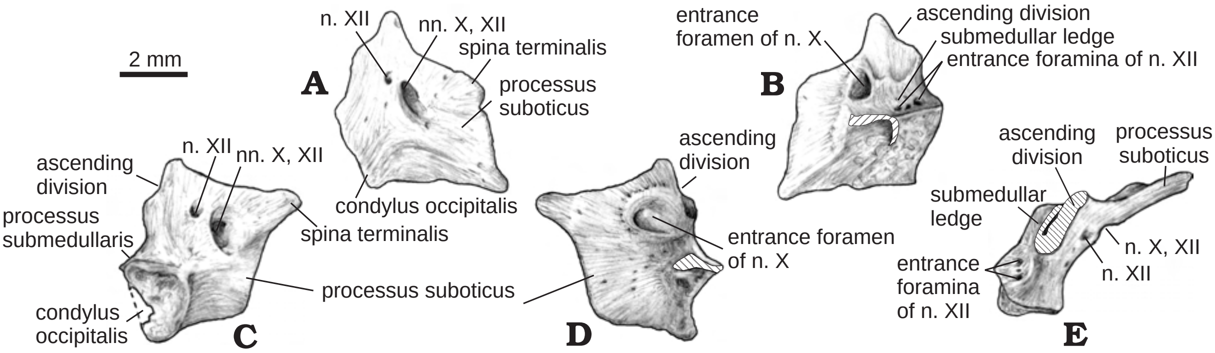

Fig. 16. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Right exoccipital ZPAL AbIV/33, in lateral (A), medial (B), posterolateral (C), anteromedial (D), and dorsal (E) views.

unossified at the stage under description. In contrast to the adult capitosauroid condition, the (morphologically) posterior surface of the supracondylar division faces laterally rather than backwards.

The lateral surface of the exoccipital (Figs 15B, D, 16A, C) is short and much flattened. It includes side exposure of the exoccipital body and, more anteriorly, the surface of the subotic process, which faces posterolaterally. Nearly half way along the free anterodorsal margin, the lateral surface bears a pointed projection (*spina terminalis*), which marks the dorsal limit of the plate-like subotic process. Most of the anterior edge of the process is nearly straight and subvertical in lateral view. Posterior to the *s. terminalis* there is located a large foramen of X nerve (*vagus foramen*). Most roots of the XII nerve also left the skull through this passage, as the separate hypoglossal exit foramina are either lacking (ZPAL AbIV/104) or represented by just a single tiny foramen (ZPAL AbIV/33). The ventral termination of the lateral periosteal surface shows only a very slight, if any, trend toward bending inward to a horizontal position. This suggests that the strictly ventral contact of the bone with the parasphenoid was effectively lacking. Such a condition is expectable in early capitosauroid ontogeny since even in adult *Parotosuchus*-grade capitosaurids the ventral (parasphenoid) sutural surface of the exoccipital remains rudimentary (MAS personal observation).

In dorsal aspect (Figs 15E, 16E), the lateral contour of the exoccipital shows a strong curvature from the condylar area toward the nearly transverse terminal portion of the subotic process, such that these divisions form an angle of about 100° (which is close to the condition in adult *Parotosuchus*). The subotic process in this aspect is straight and nearly vertical. The dorsal surface of the submedullar process (floor of the medullar cavity) appears as a narrow hollowed strip of periosteal bone extending from the condyle to the foramen of X nerve.

The medial surface of the exoccipital (Figs 15A, C, 16D) comprises three portions: the posteroventral (notochordal), posterodorsal (medullar) and anterior (subotic). The deep notochordal portion, limited dorsally by the floor of the medullar cavity, was formed by endochondral bony tissue, which seems only partially ossified at this stage; anteriorly it extends to the vertical level of the vagus foramen. The much shallower medullar portion has the same anterior limit and dorsally continues into ascending division of the bone. The base of the medullar portion bears a row of small entrance foramina for the roots of XII nerve. The entire anterior portion, lying ahead of the vagus foramen, forms a deep subvertical, plate-like subotic process.

Comparison of this structural pattern with that seen in adult capitosaurids (*Wetlugasaurus*, *Parotosuchus*) allows for some indirect conclusions about the order of changes that occurred in development of the capitosaurid exoccipital. The dorsoventral expansion of the condyles and strong lateral curvature of the subotic process had evidently already appeared in early growth stages. Some other typical features of the capitosaurid design seem to have shown more retarded development. These primarily include: (1) the appearance of the area for sutural contact with the parasphenoid; (2) differentiation of the supracondylar division into the dorsal and paroccipital processes; and (3) transformation of the juvenile plate-like subotic process into the adult structure.

UPPER JAW

Premaxilla (Figs 17A, 18). — The bone is best represented by the right element ZPAL AbIV/92. It is about 5.5 mm long and shows a nearly complete dentiferous margin. The tooth row is markedly curved in palatal aspect and includes about 17 compressed teeth (Fig. 17A_1, 18A); its posterior end is slightly damaged. The palatal shelf of the bone forms a median (symphyseal) expansion, most of which is broken off. A narrow posterolateral portion of the shelf underlay the marginal zone of the vomer. In front of the vomer, the middle portion of the palatal shelf forms a medial embayment presumably belonging to a lateral rim of the anterior palatal vacuity. The dorsal premaxillary division contributing to the skull roof (Fig. 17A_2, 18B) is preserved only at its base and shows faint traces of dermal ornamentation.

Another fragmentary specimen ZPAL AbIV/62 is 5.3 mm long and bears 10–11 moderately compressed teeth and tooth bases. The palatal shelf rises to the skull roof steeply and shows a distinct dorsoventral concavity. This indicates that the prevomerine palatal fossa housing the anterior palatal vacuity was rather deep. A partially preserved dorsal division of the bone seems to bear a narial notch and is separated from the palatal division by a slit-like cavity.

Maxilla (Figs 17B, 19A–D, 20). — The maxilla is best exemplified by similarly preserved juvenile specimens ZPAL AbIV/31, 106, 116, 118, 153, ranging in length from 5.6 to 6.4 mm. There are also a number of more uncertain tooth-bearing fragments (ZPAL AbIV/47, 51, 52, 57, 60, 64, 74, 91, 93), some of which may

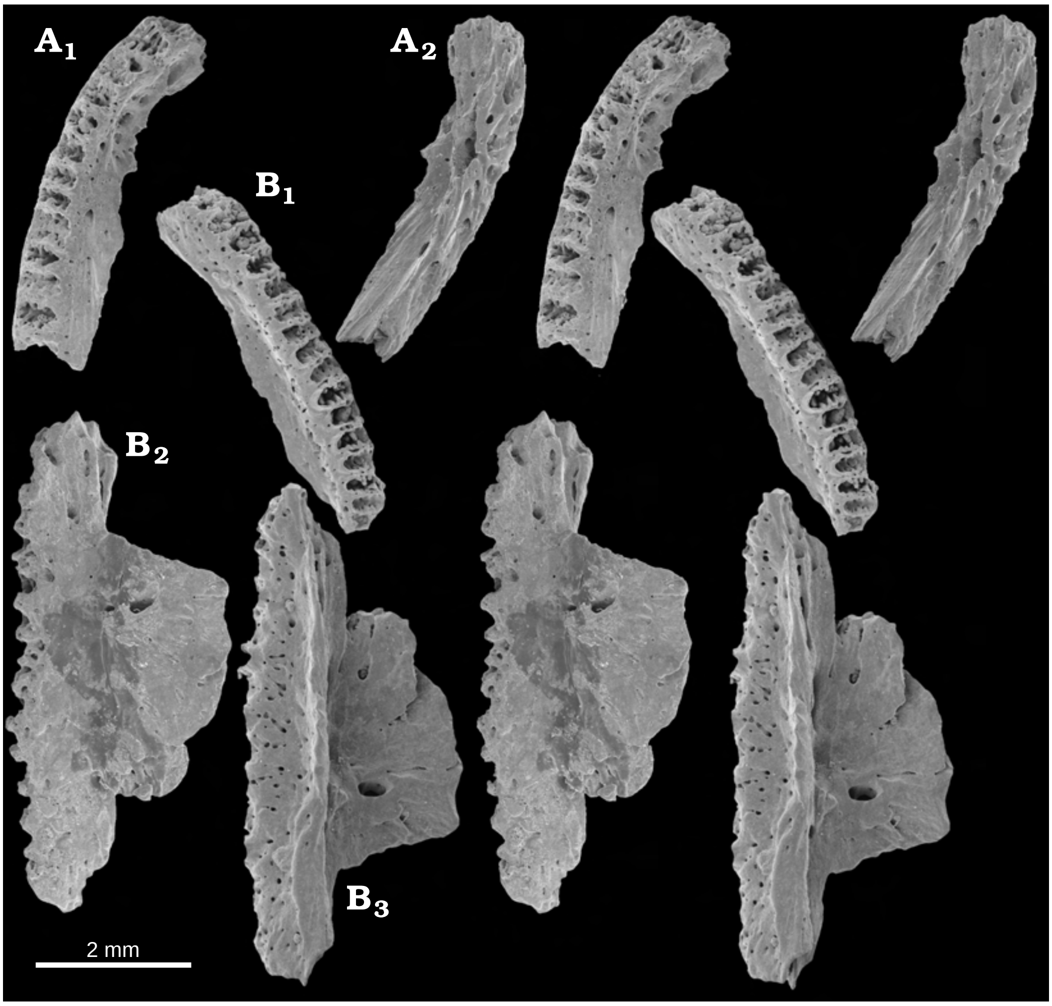

Fig. 17. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Upper jaw bones. **A**. Right premaxilla ZPAL AbIV/92, in ventral (A_1) and dorsal (A_2) views. **B**. Left maxilla ZPAL AbIV/106, in ventral (B_1), labial (B_2), and medial (B_3) views. SEM stereo-pairs.

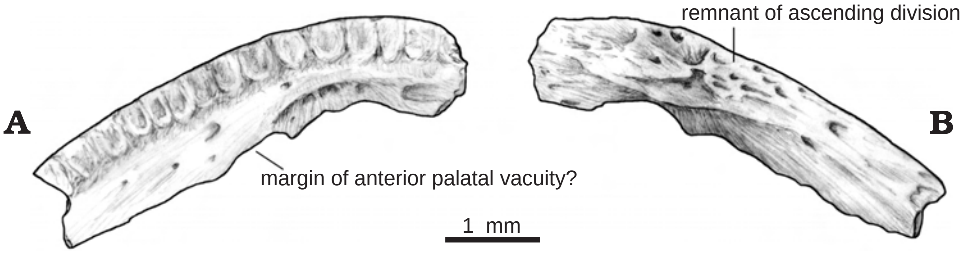

Fig. 18. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Right premaxilla ZPAL AbIV/92, in ventral (A) and dorsal (B) views.

be alternatively attributed either to the dentary or premaxilla. Most of the maxilla is made up of the expanded anterior division. It sends off an ascending plate that contributes to the skull roof and forms the posterior narial margin. The narrowed and shallow posterior division of the maxilla, preserved without its caudal end, was evidently not longer than the anterior (expanded) one, in contrast with the condition in adult capitosauroids. This suggests that the bone hardly extended backwards beyond suborbital portion of the cheek. In the dorsal and palatal views, the maxilla shows a curvature indicating a conspicuous convexity of the skull lateral outlines at the level of the palatine and choana.

The ventral tooth bearing portion of the maxilla is thickened throughout its length and slightly projects medially from the base of the ascending plate (Fig. 20D). As preserved, in our sample, the bone bears from

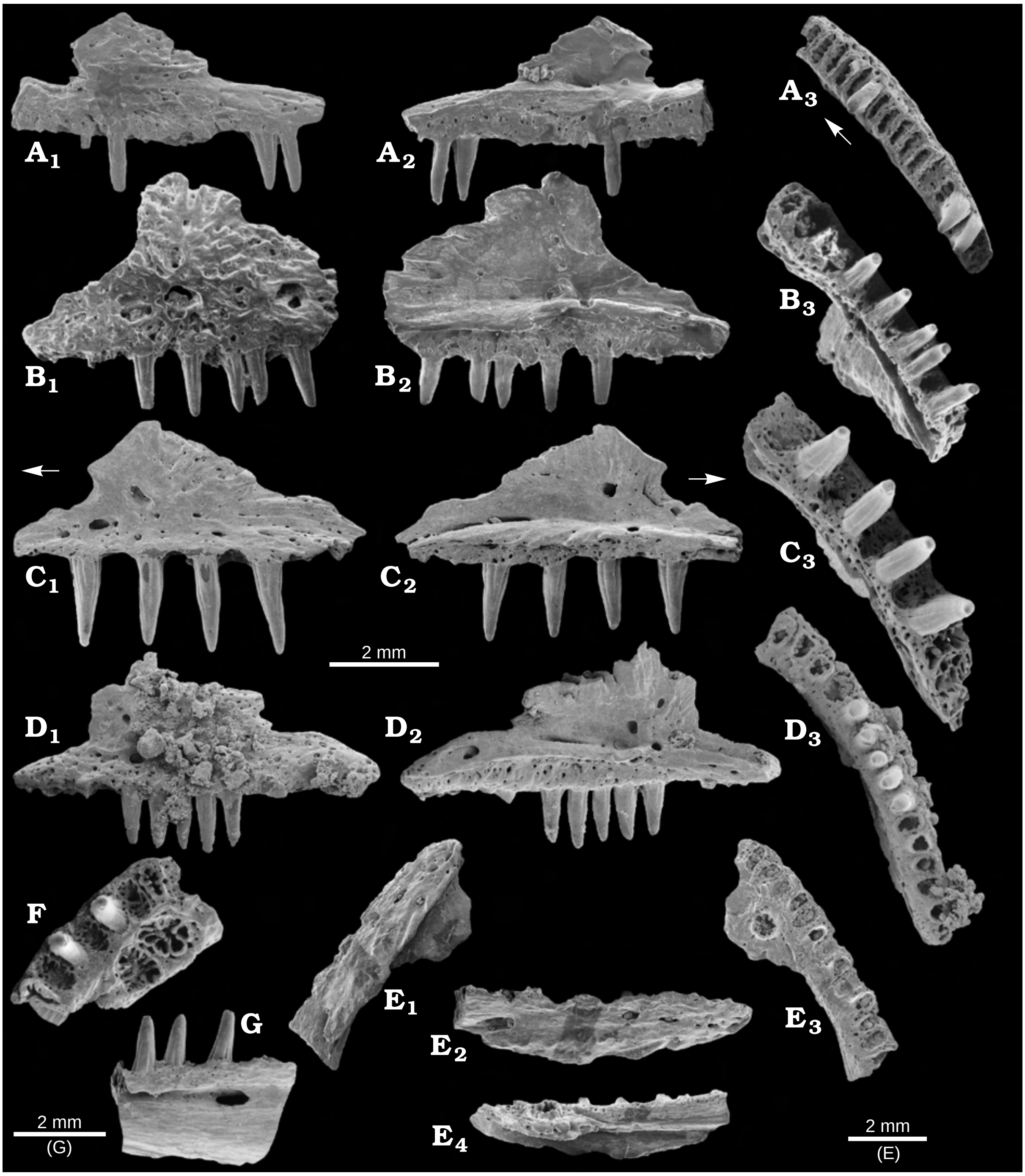

Fig. 19. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Jaw bones: left maxillae ZPAL AbIV/118 (**A**), ZPAL AbIV/31(**B**), ZPAL AbIV/116 (**C**), ZPAL AbIV/153 (**D**); symphyseal portions of dentaries ZPAL AbIV/119 (**E**), ZPAL AbIV/32 (**F**), and fragment of dentary ZPAL AbIV/34 (**G**), in labial (A_1, B_1, C_1, D_1, E_2, G), medial (A_2, B_2, C_2, D_2, E_4), ventral (A_3, B_3, C_3, D_3, E_1), and dorsal (E_3, F) views. SEM micrographs.

12 to 16 teeth and tooth pits showing a trend towards relative growth in size and decrease in numbers with age, as can be indirectly inferred from the series ZPAL AbIV/118, 106, 31, 116, 153 (Figs 17B_1, 19A_3–D_3). In all of these specimens the teeth are compressed to various degrees, without strict correlation with the specimen's size. The medial side of the tooth bearing maxillary base forms a shallow porous wall. Its dorsal margin may project medially into a blade-like palatal articular ledge (Figs 17B_1, B_3, 20A, B, D) that wedges out anteriorly and evidently underlay the marginal articulation area of the palatine (*facies maxillaris*; *cf.* Fig. 10A). Ventral to the anterior portion of the ascending plate and ahead of it the medial wall of the maxillary

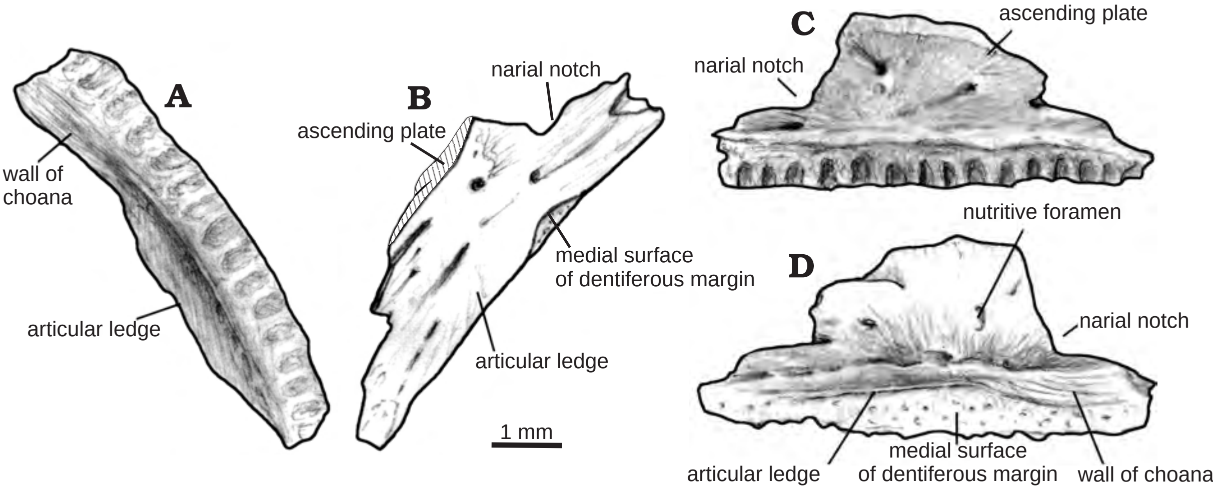

Fig. 20. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Left maxilla ZPAL AbIV/106, in ventral (A), dorsal and slightly medial (B), ventrolabial (C), and medial (D) views.

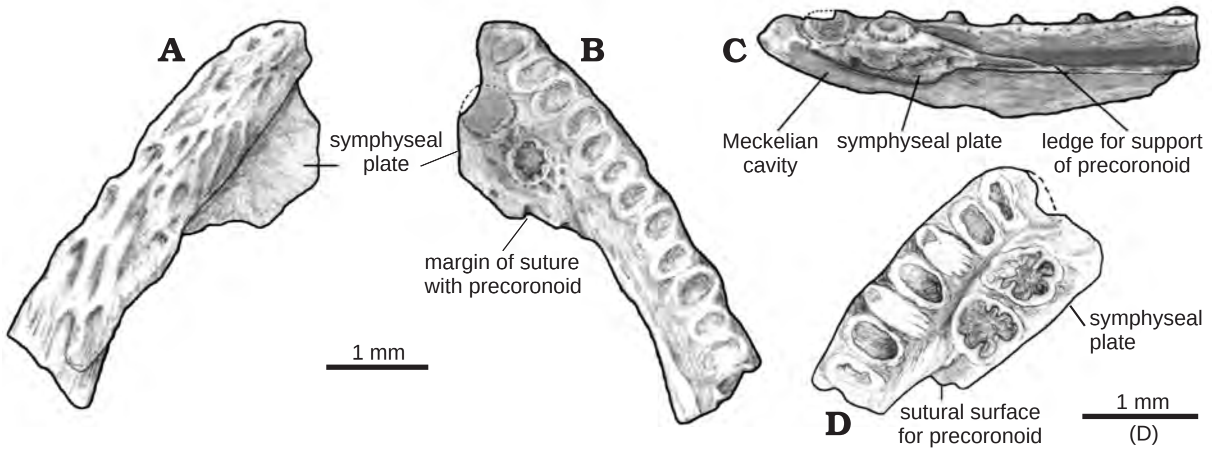

Fig. 21. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Symphyseal portions of right dentary ZPAL AbIV/119 (**A**–**C**) and left dentary ZPAL AbIV/32 (**D**), in ventral (A), dorsal (B, D), and lingual (C) views.

base may form a smooth subvertical surface that shows a gentle anteroposterior concavity and evidently belonged to the lateral choanal wall.

The ascending plate of the maxilla (Figs 17B_2, B_3, 19A_1–D_1, 20C, D) is triangular or trapezoid in side view; in the sample under study its base is from 2.4 to 3.5 mm long. The plate rises vertically from the tooth-bearing maxillary surface, thus demonstrating that the side walls of the juvenile skull in the narial area were much deeper than in adult capitosaurs. The external (dorsolateral) surface of the plate tends to develop rugose or pitted dermal ornamentation, best preserved on ZPAL AbIV/31 and 118 (Fig. 19A_1, B_1).

Anterodorsally, at the contact with the premaxilla, the ascending plate bears a somewhat irregular notch marking the posterior margin of the external naris (Figs 17B_2, B_3, 19A_1–D_1, A_2–D_2, 20C, D). Judging from the condition in ZPAL AbIV/106, the notch lies only slightly in front of presumed posterior end of the lateral choanal margin (Fig. 20D). This is in contrast with the adult capitosauroid pattern showing the nares to be placed mostly, or entirely, in front of the choanae. The posterodorsal margin of the ascending plate (sutured with the nasal and lacrimal in the intact skull) gradually descends backwards, closely approaching the level of the dentiferous portion of the bone. In front of the plate, the maxilla decreases in depth more abruptly, forming a shallow anterior projection to contact the tooth-bearing portion of the premaxilla. It is not clear whether this contact was located at the choanal border or occupied a more anterior position as in adult capitosauroids.

LOWER JAW

Dentary (Figs 19E–G, 21, 22A, B, 23A, 24). — The dentary is known from a suite of fragments exhibiting the symphyseal area and more posterior portions of the bone. The most informative symphyseal fragments are ZPAL AbIV/32 and 119 belonging to the left and right rami of the mandible respectively. Based on the length of their symphyseal plates measuring 3.4 mm in ZPAL AbIV/32 and 2.5 mm in ZPAL AbIV/119, the former specimen represents a somewhat later growth stage. Among other dentary fragments, the most important are ZPAL AbIV/34 and 35.

In the symphyseal area (Figs 19E$_3$, F, 21B, D) the dentition includes the anterior portion of the marginal tooth row and a pair of tusks set on the symphyseal plate. The medial (parasymphyseal) tooth row is lacking. The interrelations of the dentary and its symphyseal plate are unusual. As seen in dorsal aspect of the younger ZPAL AbIV/119, the anterior end of the dentary shaft bearing marginal teeth does not tend to bend around the symphyseal plate as is the case in adult temnospondyls (Fig. 22). Instead, the shaft extends nearly forward, ahead of the anterior limit of the plate. As a result, the plate and the main dentary body appear to be subdivided anteriorly by a shallow notch, marking the position of the anterior end of the meckelian cartilage (Figs 19E$_1$, E$_3$, 21A, 22A). In a larger specimen ZPAL AbIV/32 the integration of the dentary shaft and symphyseal plate is somewhat more complete; but a gentle notch is still detectable (Figs 19F, 21D, 22B).

The above character has never been specifically reported in temnospondyls although it appears to be figured in the adult Australian rhytidosteid *Arcadia myriadens* (Warren and Black 1985, fig. 9A, B). Its occurrence in the juvenile stages of *Parotosuchus* warrants the suggestion that, phylogenetically, the symphyseal plate could have arisen as an independent ossification (see p. 69).

In both ZPAL AbIV/32 and 119, the posterior margin of the symphysial plate abruptly terminates as a free horizontal flange instead of being gradually included into the lingual side of the dentary (Figs 19E$_1$, E$_3$, 21A, B, D). The margin forms a ridged area of sutural articulation with the precoronoid. As seen on the more complete ZPAL AbIV/119, the area continues backwards along the lingual wall of the dentary as a narrow horizontal ledge that afforded support to the coronoid series (Figs 19E$_4$, 21C). Hence, at this developmental stage the precoronoid formed a posterior continuation of the symphysial plate rather than a portion of lingual mandibular wall. Accordingly, like the plate itself, the precoronoid surface faced dorsally rather then lingually. These characters are quite uncommon for adult Triassic temnospondyls (except some rhytidosteids, *cf.* Shishkin 1994); instead, the precoronoid in them is normally removed from contact with the symphyseal plate and belongs to the subvertical lingual wall of the mandible.

On the other hand, the above characters displayed by the *Parotosuchus* juveniles were present in a number of Permo-Carboniferous amphibians (Shishkin 1994). Moreover, as follows from the observations of Ahlberg and Clack (1998), an extensive contact of the dentary plate and the coronoid series was typical for basal tetrapods, including all Devonian forms whose mandibles were properly examined in this respect. The so-called parasymphyseal (adsymphyseal) plate, intervening in the basal forms between the anterior portion of the dentary and the precoronoid, has been inherited from crossopterygians and was unquestionably a member the coronoid series (*cf.* Jessen 1965, p. 333). Its reduction in the course of further evolution resulted in the formation of contact between the symphyseal plate and precoronoid, a condition demonstrated by some early temnospondyls and anthracosaurs (see, for example, Romer and Witter 1941, figs 3A, 19B, C; Ahlberg and Clack 1998, fig. 19). It is also notable that both in crossopterygians and basal tetrapods the elements of the coronoid series largely faced dorsally, in the same fashion as it is demonstrated for the precoronoid of the *Parotosuchus* juveniles.

To sum up, the symphyseal plate of the capitosaurid juveniles under study demonstrates the two most unusual peculiarities: (1) the plate seems to be incompletely integrated anteriorly with the shaft of the dentary, and (2) it is directly sutured with the coronoid series and looks like an anterior termination of the latter. As noted above, both these features are present in the rhytidosteid *Arcadia* (Warren and Black 1985, fig. 9A, B). These facts seem to provide some additional support for earlier hypothesis (Shishkin 1994) that the symphyseal plate might have originated from the coronoid series. Regardless of whether this view be correct, it seems clear that immediate contact between the plate and coronoid series found in early growth stages of *Parotosuchus* recapitulates the ancestral condition.

Other data on the structure of the dentary in the Czatkowice 1 capitosaurid are summarized below. Immediately posterior to the symphysis, the dentary encloses the meckelian cavity for most of its perimeter, form-

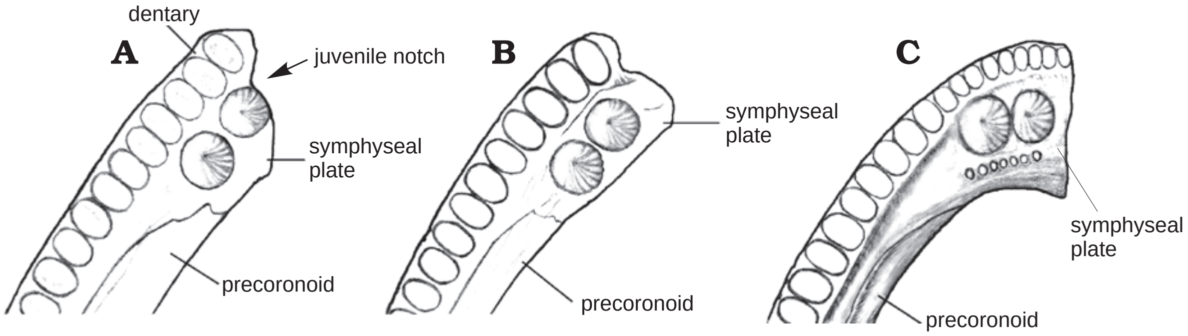

Fig. 22. Ontogenetic changes in the mandible of *Parotosuchus* showing development of the precoronoid into a subvertical position and loss of contact between the precoronoid and symphyseal plate of the dentary. **A**, **B**. Juvenile stages. **C**. Adult stage. A, B reconstructions based on the dentaries of *Parotosuchus speleus* ZPAL AbIV/119 and ZPAL AbIV/32 respectively; C based on the adult mandible of *Parotosuchus panteleevi* PIN 1043/41. Not to scale.

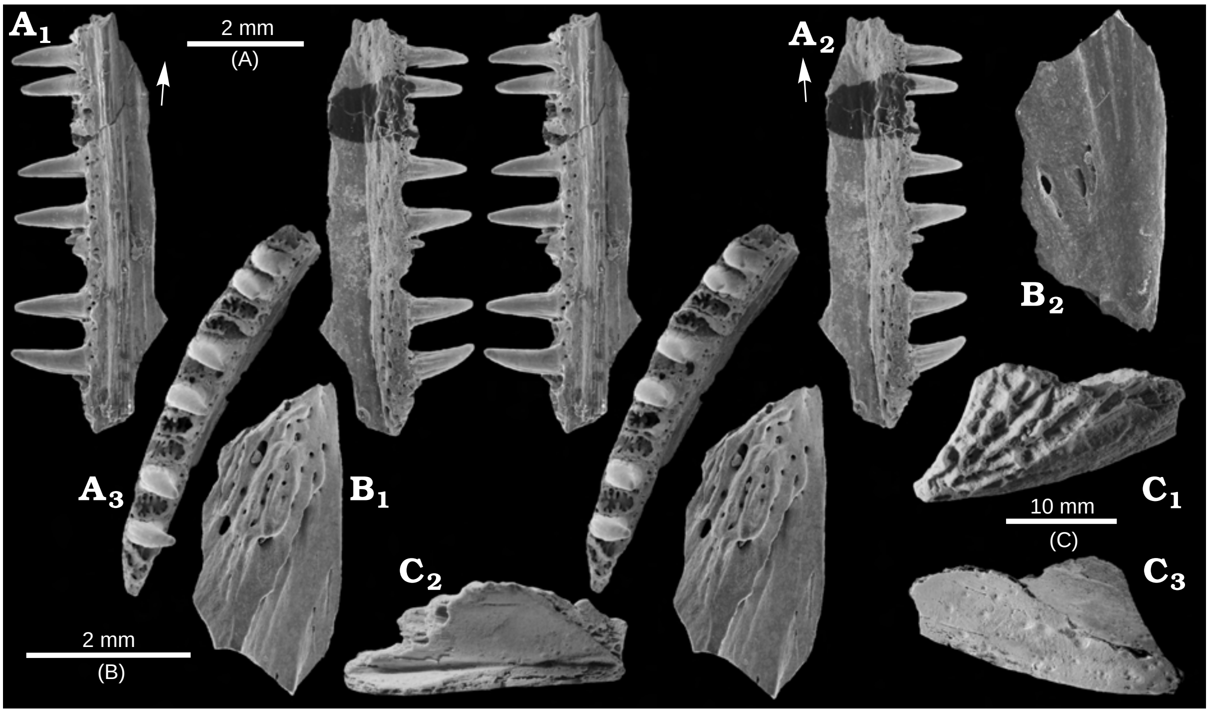

Fig. 23. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Fragments of lower jaw bones: left dentary ZPAL AbIV/35 (**A**), right surangular ZPAL AbIV/68 (**B**), and left angular ZPAL AbIV/63 (**C**), in lingual (A_1, B_2, C_3), labial (A_2, B_1, C_1), and dorsal (A_3, C_2) views. SEM micrographs; A and B_1, stereo-pairs.

ing its dorsal, labial, ventral, and partially lingual sides (Fig. 19E_1, E_4, 21A, C). The labial and ventral aspects of the bone form a gradual transition, with their surface bearing irregular ornamentation; the lingual wall is a strip of smooth surface adjacent to the dorsal (tooth-bearing) side and sutured in life with the precoronoid. The ventral margin of the lingual wall projects medially to produce a horizontal ledge giving support to the precoronoid. An open lingual space between the ledge and the ventral margin of the dentary (meckelian cavity) was closed by the splenial (Fig. 21C).

Compared to the area adjacent to the symphysis, the more posterior portion of the dentary (Figs 23A, 24) exhibits a number of structural changes. The labial wall of the bone does not spread down towards the mandibular floor. Its surface becomes smooth except for the dorsalmost marginal rugose zone that immediately borders the tooth row and projects slightly labially (Figs 23A_2, 24A). The lingual division is not developed and is reduced to a massive longitudinal ridge bordering the tooth-bearing surface (Figs 23A_1, 24B).

In the dorsal view, the posterior part of the dentary shows a significant curvature. This is clearly seen on the fragment ZPAL AbIV/35 (Figs 23A_3, 24C), which bears 14–15 compressed teeth and tooth pits and

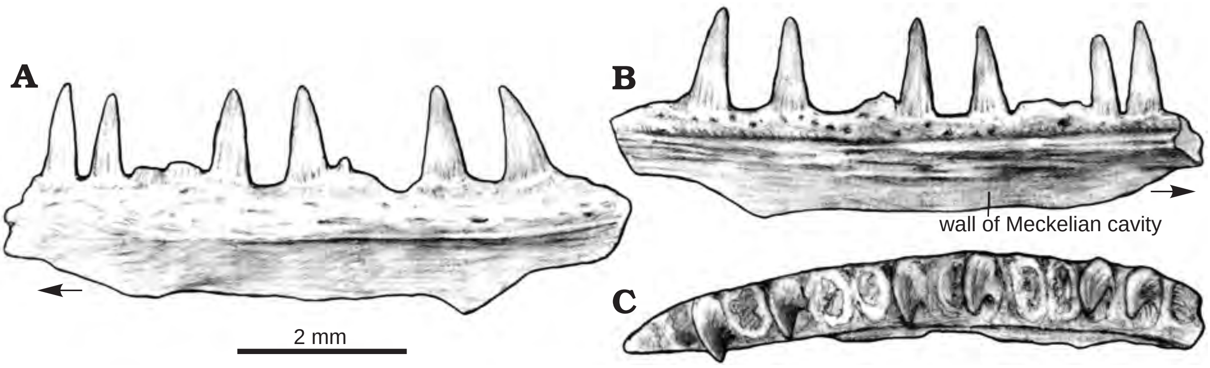

Fig. 24. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Left dentary (posterior portion) ZPAL AbIV/35, in labial (A), lingual (B), and dorsal (C) views.

seems to extend very close to the level of the true posterior end of the bone. In temnospondyls the latter normally reaches the anteriormost part of the mandibular adductor fossa. Based on this, it may be concluded that in juveniles of the Czatkowice 1 capitosaurid the lateral contours of the skull and mandible remained convex as far back as at least the orbital level. This condition is unknown in adult capitosauroids and related forms, but it was restored in small juveniles of *Rewanobatrachus* with skulls about 11 mm long (Warren and Hutchinson 1988a, figs 8–10).

Angular (Figs 23C, 25A–C, 26). — Compared to most other temnospondyl remains identified in the Czatkowice 1 collection, the only available fragment of the angular ZPAL AbIV/63 is exceptionally large (26.4 mm long), which suggests that it may belong to a semi-grown individual. Judging from comparison with the juveniles of *Rewanobatrachus* (Warren and Hutchinson 1988a, figs 1A, C, 2A, C), the skull could have reached about 70 mm in the midline length. The overall design of the angular is typical for early capitosaurids.

The specimen displays only the posterior half of the bone extending to its ossification center. A free posteroventral margin is preserved intact; all other margins show broken surfaces, although some portion of the sutural area for the surangular may be present posterodorsally on the labial side. The bone consists of a massive labial plate and thinner lingual one, forming together the base of the adductor fossa; in a cross section their ventral junction is wedge-shaped like that in all primitive capitosauroids. In a side view, the

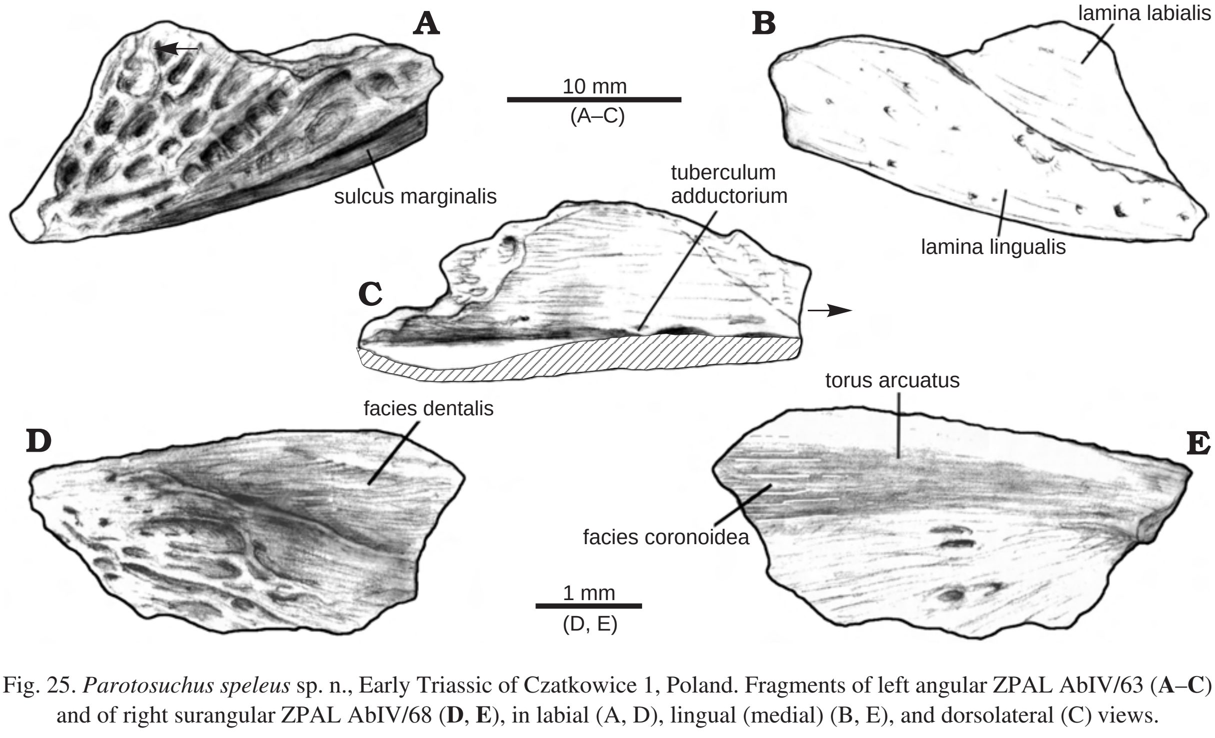

Fig. 25. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Fragments of left angular ZPAL AbIV/63 (**A**–**C**) and of right surangular ZPAL AbIV/68 (**D**, **E**), in labial (A, D), lingual (medial) (B, E), and dorsolateral (C) views.

posteroventral margin of the fragment is moderately curved, thus indicating that the mandible had a convex ventral outline in the angular area.

The labial surface of the bone (Figs 23C$_1$, 25A) is ornamented with coarse irregular ridges radiating posterodorsally from the ossification centre; some of these tend to fork and embrace the unclosed pits. A broad sensory groove (*sulcus marginalis*) with a strongly accentuated dorsal rim passes along the posteroventral margin of the surface. The lingual surface of the angular (Figs 23C$_3$, 25B) is rather smooth and flattened. As preserved, the posterior portion of the lingual plate is unusually deep; the area bordering the posterior meckelian foramen is not preserved.

In a dorsal view showing the floor of the adductor fossa (Figs 23C$_2$, 25C), the zone of junction of the two angular plates forms a straight narrow axial trough. In its anterior part, at the ossification center, the floor of the angular bears a small elongate elevation (*tuberculum adductorium)* preceded and followed by weak elongate pits. A similar elevation is known in many Triassic temnospondyls (Shishkin 1973, p. 88; *cf.* Nilsson 1943, p. 14, figs 10, 13B, 14B, 15, 21). It is thought to have provided an insertion to a main portion of *the musculus pterygoideus posterior*. In a number of Paleozoic temnospondyls, such as dvinosaurids and melosaurids, the homologous projection (*processus adductorius*) is developed as a strong ascending process formed by ossification of the Meckelian cartilage (Shishkin 1973, p. 88, 94; fig. 40c, pl. 5: 2a, pl. 6: 3c).

Surangular (Figs 23B, 25D, E, 26). — The only preserved fragment of the surangular (ZPAL AbIV/68) is the anterior part of the labial plate showing the area of flat contact with the dentary and coronoid. The free dorsal margin of the plate forms the *torus arcuatus* (Figs 23B$_2$, 25E) that bordered the labial wall of the mandibular adductor fossa. It is barely distinguishable on the labial side of the plate and slightly projects medially along the opposite side.

On the labial surface of the surangular (Figs 23B$_1$, 25D) posteroventral and anterodorsal areas can be distinguished. The former belongs to a true labial exposure of the bone and bears ornamentation, which consists of a ridges and elongated pits. Posteriorly, the ornamentation field approaches the level of the *torus arcuatus*. The anterodorsal area of the labial surface (*facies dentalis*) was overlapped in life by the posterior end of the dentary. The area is flat, depressed and forms a caudally pointed wedge. It is demarcated ventrally by a deep groove running along the border of the ornamented division; dorsally the *facies dentalis* extends to the free margin of the bone. As a whole, the described pattern is peculiar in that both the *f. dentalis* and the ornamentation field directly reach the dorsal margin of the surangular. Hence, they left no room for a wide strip of smooth labial surface which usually extends in capitosauroids along this margin.

On the medial surface of the surangular plate (Figs 23B$_2$, 25E), the *torus arcuatus* is seen as a longitudinal thickening of the bone. Anteriorly it broadens and gradually fades away. Its anterior part bearing a number of faint, slightly diverged ridges indicates a zone of contact with the coronoid. Ventral to the *t. arcuatus*, the medial surface of the plate is flattened.

Dentition (Figs 2–4, 9–12, 17–21, 23, 24). — The marginal teeth of the maxilla, premaxilla and dentary conform to a common capitosauroid pattern in being usually compressed anteroposteriorly in a cross section. Only in the youngest individuals the tooth sections remain more or less isometric, as evidenced by the jaw fragments ZPAL AbIV/47, 57, 64. On the other hand, at the somewhat later growth stages represented by

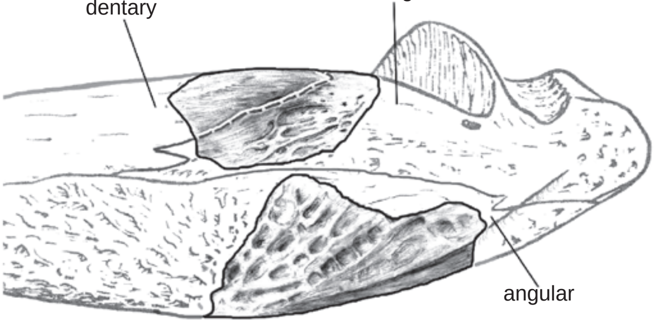

Fig. 26. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Conjectural reconstruction of adductor division of the mandible showing position of preserved fragments of the angular (ZPAL AbIV/63) and surangular (ZPAL AbIV/68, mirror image). Not to scale.

most of the upper jaw specimens, no strict correlation is observed between the individual size and the degrees of tooth compression. For instance, in the series of juvenile maxillae the most compressed teeth are displayed by the smallest specimen ZPAL AbIV/118 (Fig. 19A). In the regular palatal teeth the compression of tooth bases is more weakly expressed or sometimes lacking. The tusks developed on the palatal complex and the dentary symphyseal plate have more or less rounded cross sections. Both the tusks and, typically, the regular teeth have a standard temnospondyl structure with labyrinthine infolding of the dentine. The width of the pulp cavity is variable and generally shows gradual reduction with ontogeny.

POSTCRANIAL ELEMENTS

Of the postcranial amphibian remains recognized in the Czatkowice 1 collection some unquestionably belong to temnospondyls. Those that can be attributed to capitosaurids (obviously, *Parotosuchus*) are the neural arches and elements of the dermal shoulder girdle.

Neural arches (Figs 27, 28). — The three identified neural arches are represented by the left antimeres. Two of them (ZPAL AbIV/158, 159) are reasonably well preserved. They are similarly shaped and pertain to the dorsal vertebrae. In side view, both show a marked slope backward, which is typical for the larval and ju-

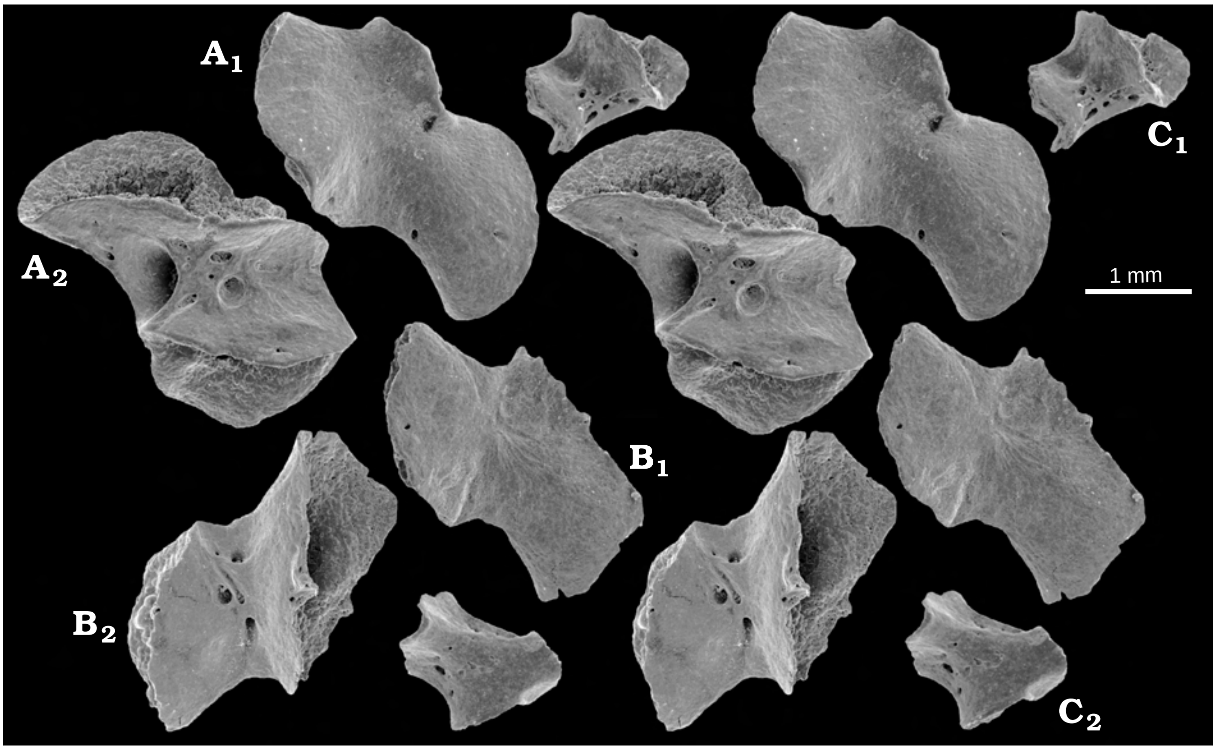

Fig. 27. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Neural arches: ZPAL AbIV/159 (**A**), ZPAL AbIV/158 (**B**), and ZPAL AbIV/160 (**C**), in lateral (A_1, B_1, C_2) and medial (A_2, B_2, C_1) views. SEM stereo-pairs.

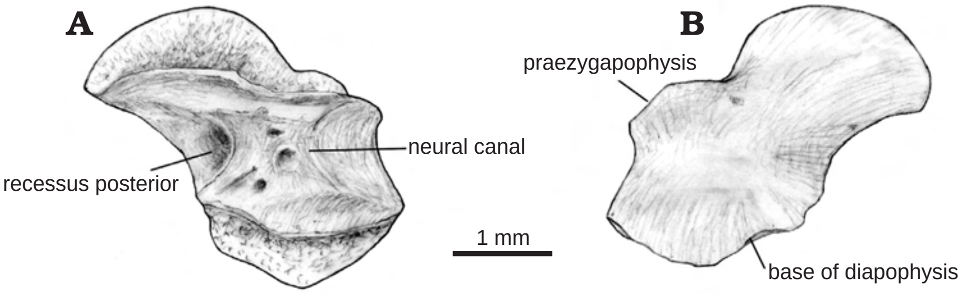

Fig. 28. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Neural arch (left antimere) ZPAL AbIV/159, in medial (A) and lateral (B) views.

venile vertebrae of the trunk division in many temnospondyls, such as dissorophoids, eryopoids and archegosauroids (*cf.* Werneburg 2001, fig.16a; Witzmann 2005b, fig. 4; Witzmann and Schoch 2006b, fig. 10). The presence of this character, otherwise common for the adult caudal vertebrae, seems to show that in temnospondyl ontogeny the change in orientation of the neural arches towards the adult state progressed in a cranio-caudal direction.

As seen on the lateral side of ZPAL AbIV/159 (Figs 27A_1, 28B), the base of the arch bears a barely detectable rudiment of the diapophysis. The prezygapophysis is well differentated, while the postzygapophysis is still not distinctly shaped. The neural spine is short and somewhat broadened anteroposteriorly at its topmost portion. The inner side of the arch (Figs 27A_2, 28A) shows a hollowed lateral wall of the wide neural

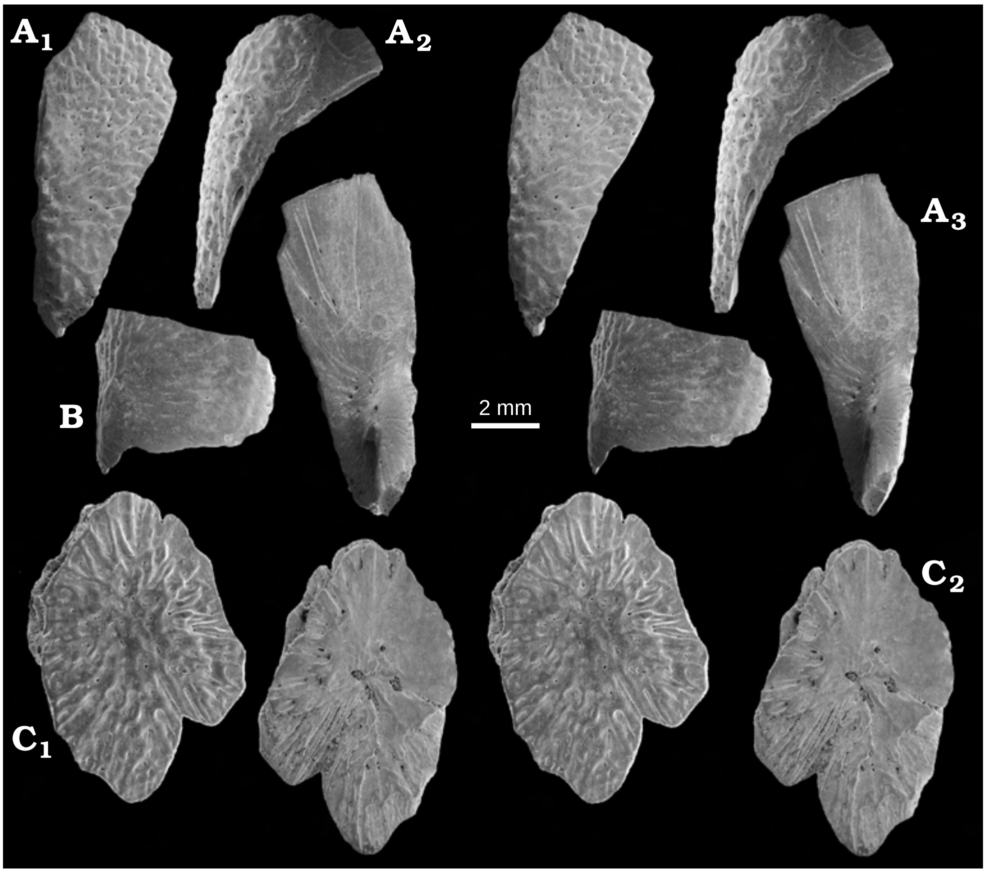

Fig. 29. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Elements of dermal shoulder girdle: right clavicles ZPAL AbIV/87 (**A**), ZPAL AbIV/75 (**B**), and interclavicle ZPAL AbIV/102 (**C**), in ventral (A_1, B, C_1), lateral (A_2), and dorsal (A_3, C_2) views. SEM stereo-pairs.

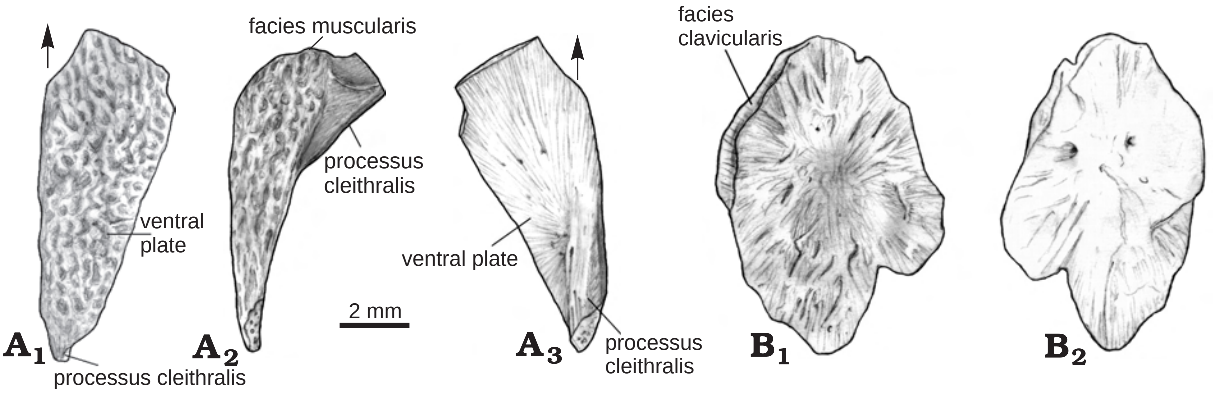

Fig. 30. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Right clavicle ZPAL AbIV/87 (**A**) and interclavicle ZPAL AbIV/102 (B), in lateral (A_2), dorsal (A_3, B_2), and ventral (A_1, B_1) views.

canal. Dorsally the wall is bordered by the overhanging thickened base of the neural spine; anteriorly it bears a broad and shallow longitudinal depression that is rounded or pointed posteriorly. An opposite depression, located on the posterior part of the wall, continues forward into a cone-shaped pit penetrating the wall.

Clavicle (Figs 29A, B, 30A). — A fragment of clavicle, ZPAL AbIV/87 (Figs 29A, 30A) preserves approximately two thirds of bone's anteroposterior extent; it is about 10 mm long. It includes a lateral part of the thoracic plate, uniformly ornamented with irregular pits and ridges on the ventral surface (Figs $29A_1$, $30A_1$), and the basal portion of the dorsal (cleithral) process (Figs $29A_2$, $30A_2$). The latter is broad, smooth and shows a marked slope backwards in side view. The posterior margin of the process bears an embayment, which seems to indicate that the process as a whole had a sigmoid curve typical for capitosauroid clavicles (*cf.* Warren and Hutchinson 1983, p. 41). Another fragment of the right clavicle ZPAL AbIV/75 (Fig. 29B), exhibits the posterior part of the bone. Judging from the width of the dorsal process, it belonged to an individual of similar size. Its shape suggests that, in ventral view, the posterior contour of the thoracic plate was nearly transverse to the body axis. Distinct from ZPAL AbIV/87, the ornamentation of the thoracic plate shows more elongate grooves and retains some traces of a radiating pattern.

Interclavicle (Figs 29C, 30B). — The only interclavicle ZPAL AbIV/102 identified in the collection is a roughly diamond-shaped plate about 10 mm long, with irregular contours and rounded angles. The ventral surface bears an ornamentation formed by radiating irregular ridges on the periphery and smooth pits in the center. The ossification center is slightly shifted to the anterior half of the plate, which is uncommon for temnospondyls and can be explained by incomplete ossification of the anterior division of the bone. The anterolateral marginal zones normally underlain by the clavicles are differently shaped. On the left side (in ventral view), a narrow articulation area (*facies clavicularis*) faces ventrolaterally, while on the opposite side it seems to be located on the dorsal surface of the bone (*cf.* Fig. 30B). The relief of the posterior half of the dorsal side is uneven and irregular.

Elements of primary limb girdles and limbs. — The collection includes a number of bone fragments belonging to other parts of the temnospondyl postcranium. Because of their poor preservation little can be said of their morphology, so that they can be attributed to capitosaurids only provisionally. The material includes, in particular, the fragments of the scapula(?) (ZPAL AbIV/103, 88), humeri (ZPAL AbIV/84, 86), radius (ZPAL AbIV/96) (Fig. 31A–C), and some ribs (ZPAL AbIV/85).

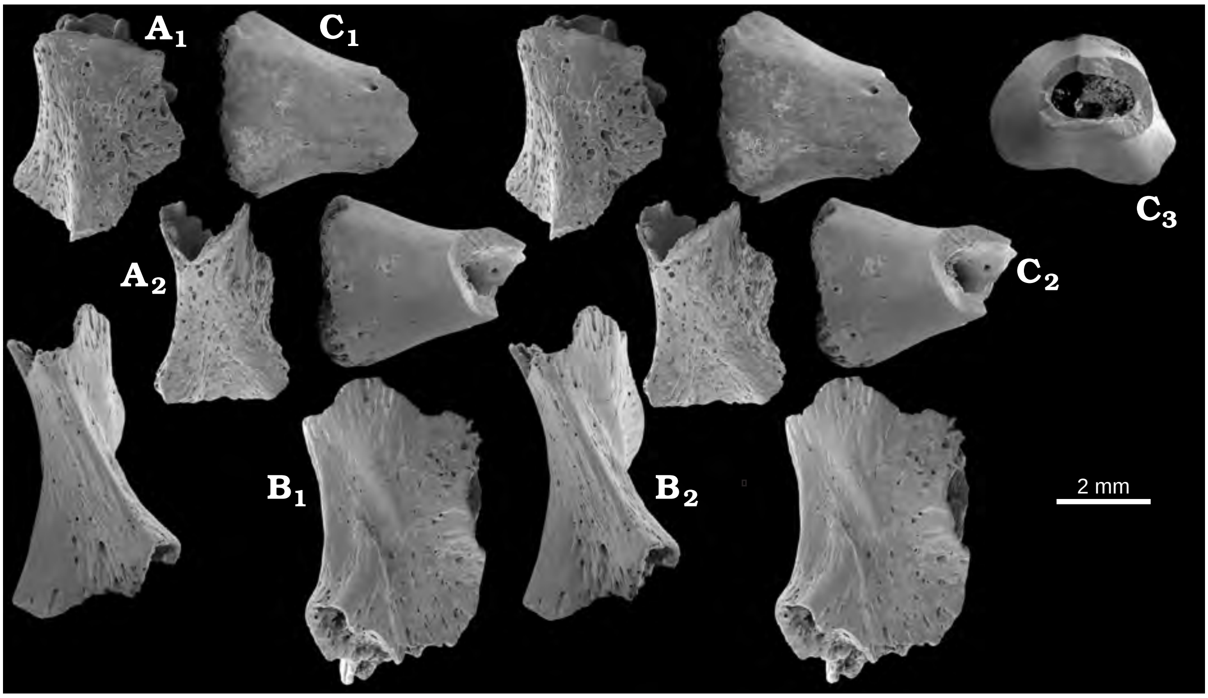

Fig. 31. (?)*Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Fragments of limb bones: scapulae ZPAL AbIV/88 (**A**), ZPAL AbIV/103 (**B**), and radius(?) ZPAL AbIV/96 (**C**). SEM micrographs; all but C_3 stereo-pairs.

MORPHOLOGY OF *BATRACHOSUCHOIDES* SP.

SKULL

Postparietal (Figs 32, 33, 34B). — The right postparietal ZPAL AbIV/101 is the only element of the brachyopid skull roof recognized in the Czatkowice 1 collection. Its attribution to brachyopids is evidenced by the shape of the dorsal plate and by the structure of the occipital flange which is broadened, flattened anteroposteriorly and directed posteroventrally (rather than being rod-like and occupying a subvertical position). In all these respects the bone markedly differs from that in capitosauroids and related forms. It is 5.3 mm wide across the dorsal plate, which is transversely expanded, thickened in the lateral portion and has a gently convex occipital contour. The medial and posterior margins of the plate are somewhat damaged.

The dorsal surface of the bone (Figs 32A, C, 33A, C) is ornamented with short ridges, pustules and semi-closed pits, which irregularly radiate from the base of the occipital flange. The lateral portion of the occipital margin bears a sensory groove (a segment of cranial occipital comissure) that continued to the tabular. Anterolaterally the dorsal surface shows a small attachment area for the supratemporal.

In the posterior view (Figs 32D, 33D, 34B), most notable is the lateral wing of the bone, which roofed the *fenestra posttemporalis* and contacted the tabular. It has a straight (not embayed) ventral margin and much exceeds in length the medial wing that contacted its left counterpart in the assembled skull. These features show that the *f. posttemporalis* was transversely elongate and not rounded dorsally, in contrast to the typical brachyopid condition (see below; *cf.* Fig. 34B, C).

A thickened lateral portion of the occipital flange forms the medial wall of the *f. posttemporalis*. Anteriorly, the wall is limited by an ascending ridge which continues onto the inner (ventral) side of the postparietal

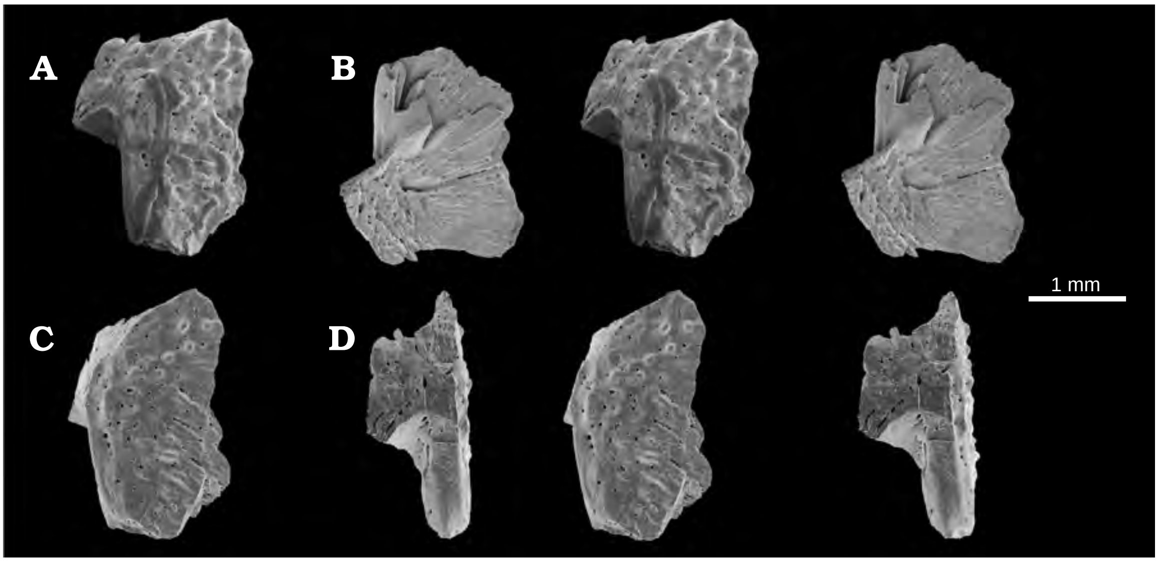

Fig. 32. *Batrachosushoides* sp., Early Triassic of Czatkowice 1, Poland. Right postparietal ZPAL AbIV/101, in posterodorsal (A), anteroventral (B), anterodorsal (C), and posterior (D) views. SEM stero-pairs.

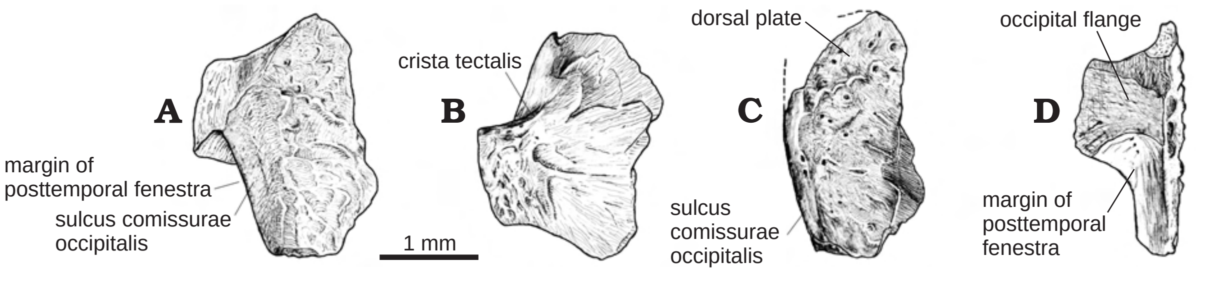

Fig. 33. *Batrachosushoides* sp., Early Triassic of Czatkowice 1, Poland. Right postparietal ZPAL AbIV/101, in posterodorsal (A), anteroventral (B), anterodorsal (C), and posterior (D) views.

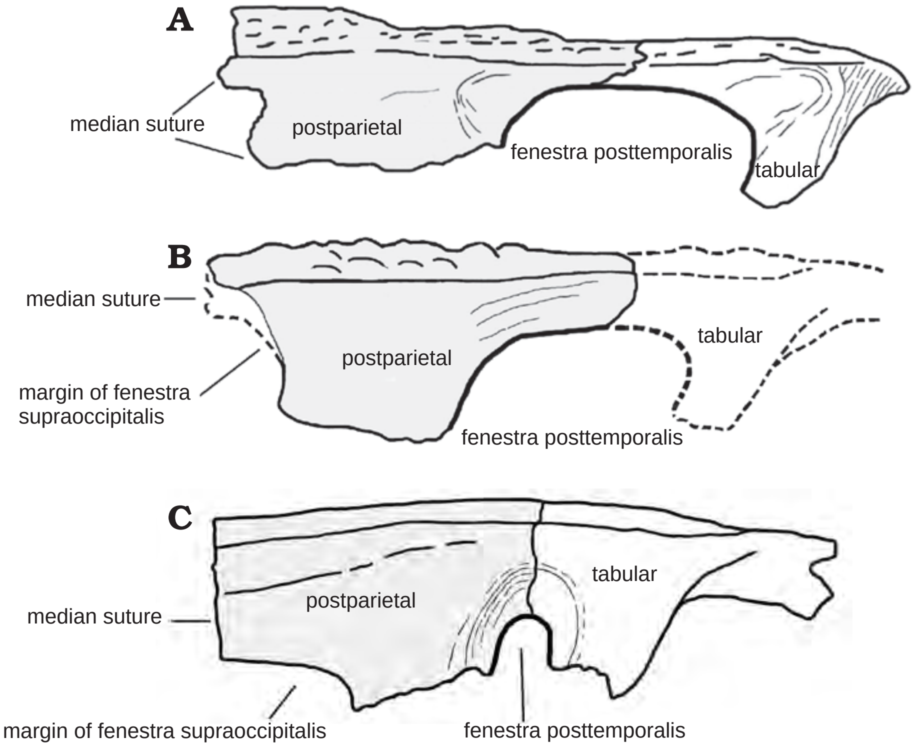

Fig. 34. Recapitulation of ancestral shape of the post-temporal fenestra in ontogeny of brachyopid occiput (**B**, **C**) as demonstrated by comparison with the trimerorhachoid (dvinosaurid) condition (**A**). The postparietal and tabular in occipital view. **A**. Adult *Dvinosaurus*. **B**. Juvenile *Batrachosuchoides*. **C**. Typical brachyopid pattern exhibited by adult *Batrachosuchus* and *Batrachosuchoides*. A based on *Dvinosaurus primus* PIN 3582/78; B based on *Batrachosuchoides* sp. ZPAL AbIV/101; C based on the holotype of *Batrachosuchus watsoni* BMNH R.3589 and, partially, on *Batrachosuchoides lacer* PIN 1043/985. Not to scale.

as the *crista tectalis* (Fig. 33A$_2$, B, D). Although the occipital flange is posteriorly damaged throughout its depth, it seems evident that the medial portion of the flange was flattened anteroposteriorly.

On the ventral surface of the postparietal (Figs 32B, 33B), the occipital flange and most of the dorsal plate form a single shallow depression. The latter is covered by faint ridges, with the occipital flange area being more rugose and irregular. Within the dorsal plate area, the principal demarcation is seen between the larger medial portion and the roof of the posttemporal fossa separated by the *crista tectalis*. This crest, originally described in *Dvinosaurus* (Shishkin 1973, fig. 6), continued laterally onto the tabular and marked the edge of an endocranial sheath (*tectum posterius*) that roofed the posttemporal fossa (Shishkin 1973, figs 47, 49). In front of the *c.tectalis*, the anterolateral portion of the dorsal plate bears ridges that provided sutural attachment to underlying parts of the tabular and supratemporal.

As was already mentioned, the shape of the occipital aspect of the above described postparietal differs from that in the adults of typical (*Batrachosuchus*-grade) brachyopids, in which the lateral wing of the bone is very short and embayed along its ventrolateral margin (*cf.* Shishkin 1967, fig. 2a, b). In line with that, the posttemporal fenestra in these forms is small and rounded, rather then stretched along the horizontal axis, as is the case in the juvenile Polish brachyopid (*cf.* Fig. 34B, C). Since the condition demonstrated by the latter is most common for temnospondyls, it seems justified to ascribe it to the immature state of the specimen. It would then suggest that in advanced brachyopids the early growth stages recapitulated the ancestral design of the posttemporal fenestra, which is known, for example, in the brachyopoid-related *Dvinosaurus* (Fig. 34A).

Ectopterygoid (Figs 35, 36, 37B). — The ectopterygoids attributed to a brachyopid include the specimens ZPAL AbIV/36 and 53. The structure of the bone is best exemplified by an almost complete ZPAL AbIV/36, which is about 9 mm long and seems to represent a rather late juvenile growth stage. The ectopterygoid is much shorter than in *Parotosuchus* from the same assemblage. In the palatal and dorsal aspects (Figs 35A$_1$, A$_2$, 36A, B) it is markedly curved anteroposteriorly, which is in accord with the convex lateral outlines of a brachyopid skull. The true palatal exposure of the bone is limited anteriorly by a short

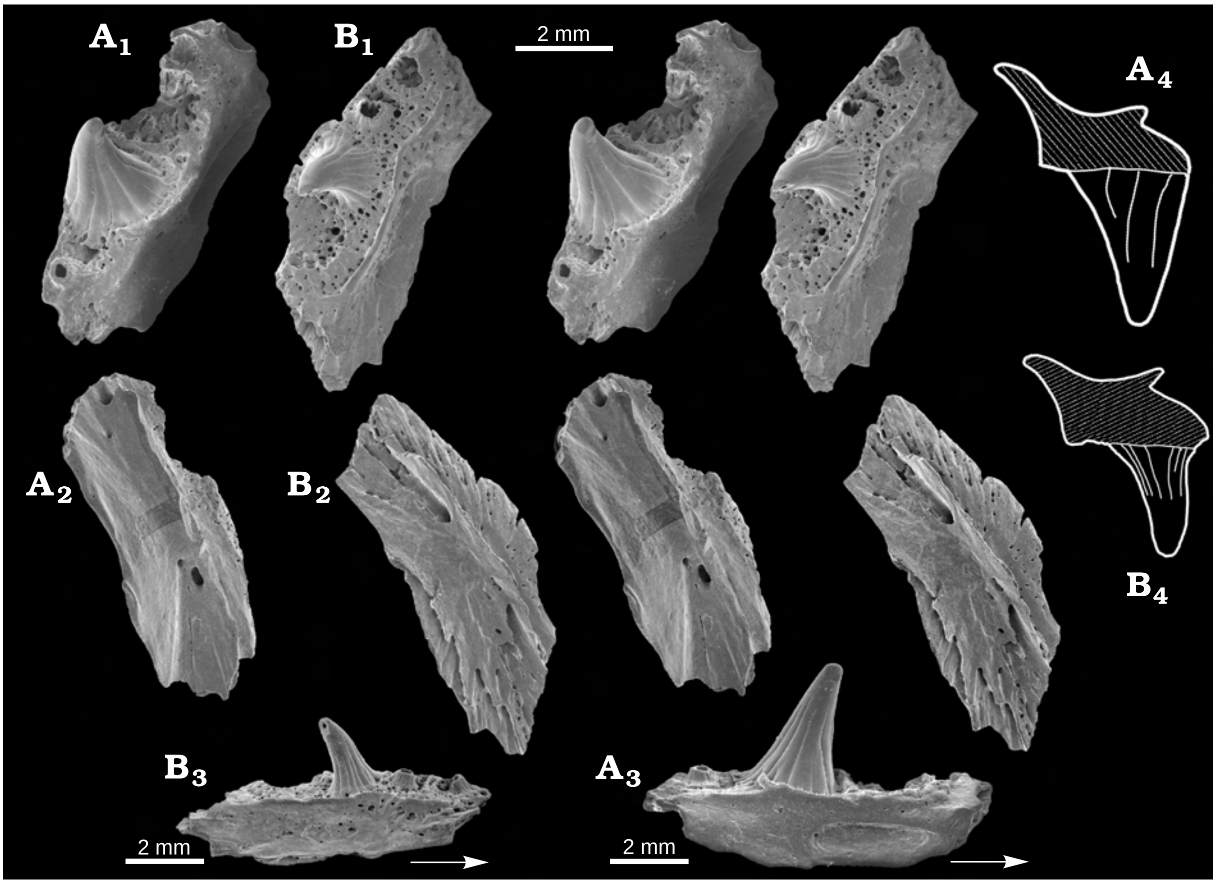

Fig. 35. *Batrachosuchoides* sp., Early Triassic of Czatkowice 1, Poland. Right ectopterygoids: ZPAL AbIV/53 (**A**) and ZPAL AbIV/36 (**B**), in ventral (A_1, B_1), dorsal (A_2, B_2), medial (A_3, B_3) views, and cross sections (A_4, B_4). All but A_4 and B_4 SEM micrographs; A_1, A_2 and B_1, B_2, stereo-pairs.

ridge-bearing a sutural surface for the palatine and, posteriorly, by a surface that was sutured with the jugal palatal process (Fig. 36A, *facies jugalis ventralis*). The shape of the former sutural area indicates that the ectopterygoid-palatine suture ran roughly transversely. The dentition consists of a pair of tusks, the more posterior of which is represented by a pit. Anterior to the tusks are a pair of regular teeth; posterior to them, the palatal exposure of the ectopterygoid is reduced and bears no teeth.

As in the *Parotosuchus* juveniles described above, the bone has a peculiar medial wall (*planum mediale*) lying ventral to the level of the pterygoid-ectopterygoid suture (Figs 35B_1, B_3, B_4, 36A, C, D). The wall is deep and concave dorsoventrally. At the level of the anterior tusk, the ventral portion of the *planum mediale* is nearly vertical; anteriorly it becomes shallower and less steep. In the posterior half of the *p. mediale*, its dorsal margin forms a very weakly expressed posteromedial projection, the incipient *processus pterygoideus*. This condition strongly departs from that in adult brachyopids in which the *proc. pterygoideus* is a long posteromedial branch of the ectopterygoid. (*cf.* Fig. 37B, C). On the other hand, the lack of a well- developed pterygoid process in immature *Batrachosuchoides* from Czatkowice 1 resembles the more generalized morphotype of brachyopid ancestors (Fig. 37A) and thus seems to repeat the ancestral condition.

The dorsal surface of the ectopterygoid (Figs 35B_2, 36B) displays much the same basic pattern as in capitosaurid juveniles. Compared with them, the surface is shorter and more distinctly curved anteroposteriorly, such that its lateral margin shows a strong convexity (indicating a curvature of the adjacent maxilla). The *crista dorsalis*, separating the palatoquadrate area from the *facies maxillo-jugalis*, is also curved and runs almost parallel to the lateral margin of the bone. This ridge is strongly inclined dorsolaterally, forming a longitudinal fissure together with the *f. maxillo-jugalis* that obviously housed the margin of the jugal. The *f. maxillo-jugalis* gently slopes laterally and bears oblique ridges in its anterior half.

In the medial (palatoquadrate) division of the dorsal suface, the zone of its natural exposure is notched by three well-marked sutural areas bearing faint ridges (Figs 35B_2, 36B). The anterior of these, bordered medi-

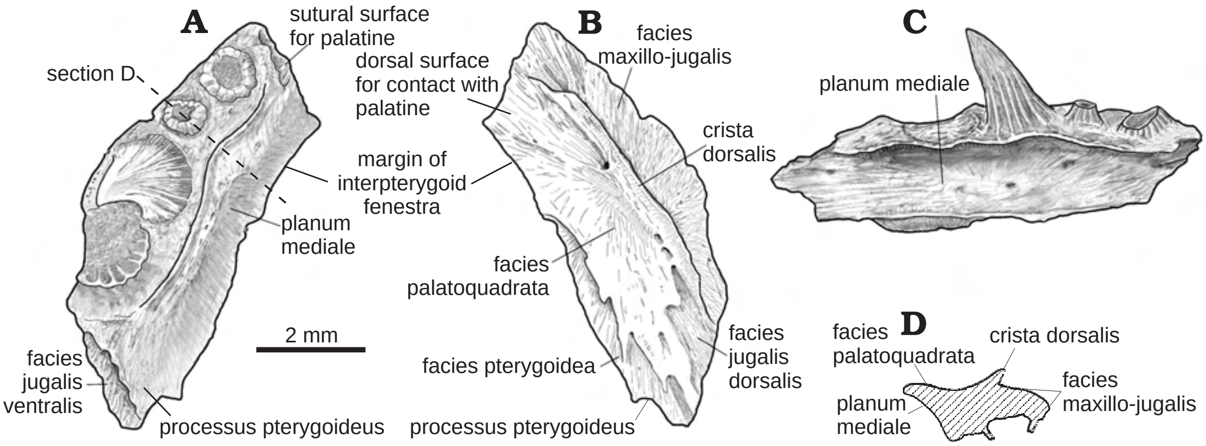

Fig. 36. *Batrachosuchoides* sp. from the Early Triassic of Czatkowice 1, Poland. Right ectopterygoid ZPAL AbIV/36, in ventral (A), dorsal (B), medial (**C**) views, and cross section (D).

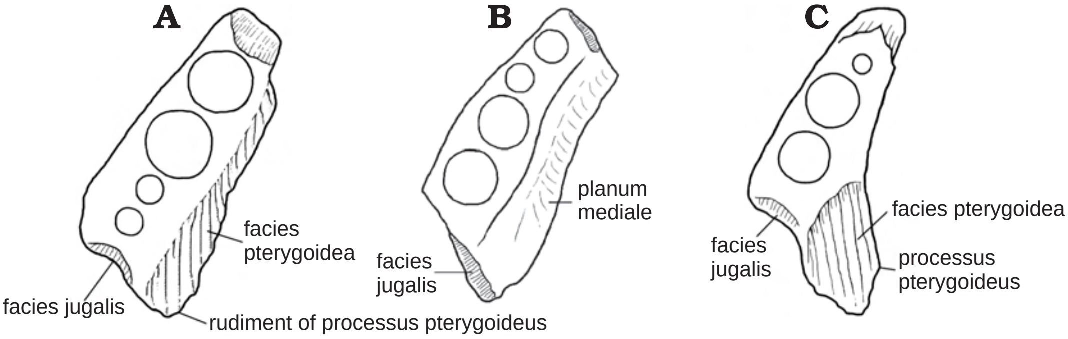

Fig. 37. Modifications of the palatal pterygoid-ectopterygoid suture in trimerhorhachoid and brachyopid temnospondyls as seen from patterns of their ectopterygoids. **A**. *Dvinosaurus primus* (palatal sutural surface for pterygoid narrow and very long; pterygoid process of ectopterygoid rudimentary). **B**. Juvenile *Batrachosuchoides* (palatal surface for pterygoid absent, pterygoid process rudimentary). **C**. Adult *Batrachosuchoides* (palatal surface for pterygoid broad and short, pterygoid process well developed). A based on PIN 522/11 and PIN 4549/1; B based on ZPAL AbIV/36; C based on PIN 953/18. Not to scale.

ally by the *c. dorsalis,* is a narrow wedge pointed backwards; it was evidently overlapped by a flat process from the palatine. The posterior two sutural areas occupy the posterior and medial margins of the rudimentary *proc. pterygoideus*. These are, respectively, the *facies jugalis dorsalis* and *f. pterygoidea* which contacted with corresponding bones. The wedge-shaped *f. jugalis dorsalis* is bordered laterally by the dorsal crest and tapers anteriorly. The *f. pterygoidea* is a narrow depression running along the medial margin of the ectopterygoid for two thirds of its extent. In front of the *f. pterygoidea*, the medial edge of the dorsal ectopterygoid surface is gently concave and smooth, showing no trace of any sutural contact. It certainly entered the margin the interpterygoid fenestra as is typical for brachyopids.

Some variations and/or additional details of the ectopterygoid structure are exhibited by an almost complete specimen ZPAL AbIV/53 (Fig. 35A). Compared to ZPAL AbIV/36, it belongs to a smaller individual and is 5 mm long. It is much similar to the above named specimen in general design and proportions. The dentition includes one regular tooth in front of the tusk pair and one posterior to it. The palatal areas for sutural articulation with the palatine and the jugal are very short antero-posteriorly. The *processus pterygoideus* is barely detectable.

The anterior part of the *planum mediale* on the ectopterygoid ZPAL AbIV/53 is deep, subvertical and longitudinally hollowed (Fig. 35A$_3$, A$_4$). Posteriorly the wall becomes shallow and gently sloped ventrolaterally in top view. As in ZPAL AbIV/36, the anterior portion of dorsal edge of the *p. mediale* contributes to the margin of the interpterygoid fenestra. On the dorsal side (Fig. 35A$_2$), the *crista dorsalis* is developed as a nearly straight ridge directed dorsolaterally. The triangular *facies jugalis dorsalis* is broad but weakly expressed; the *f. pterygoidea* is not detectable and was probably limited to the medial edge of the bone.

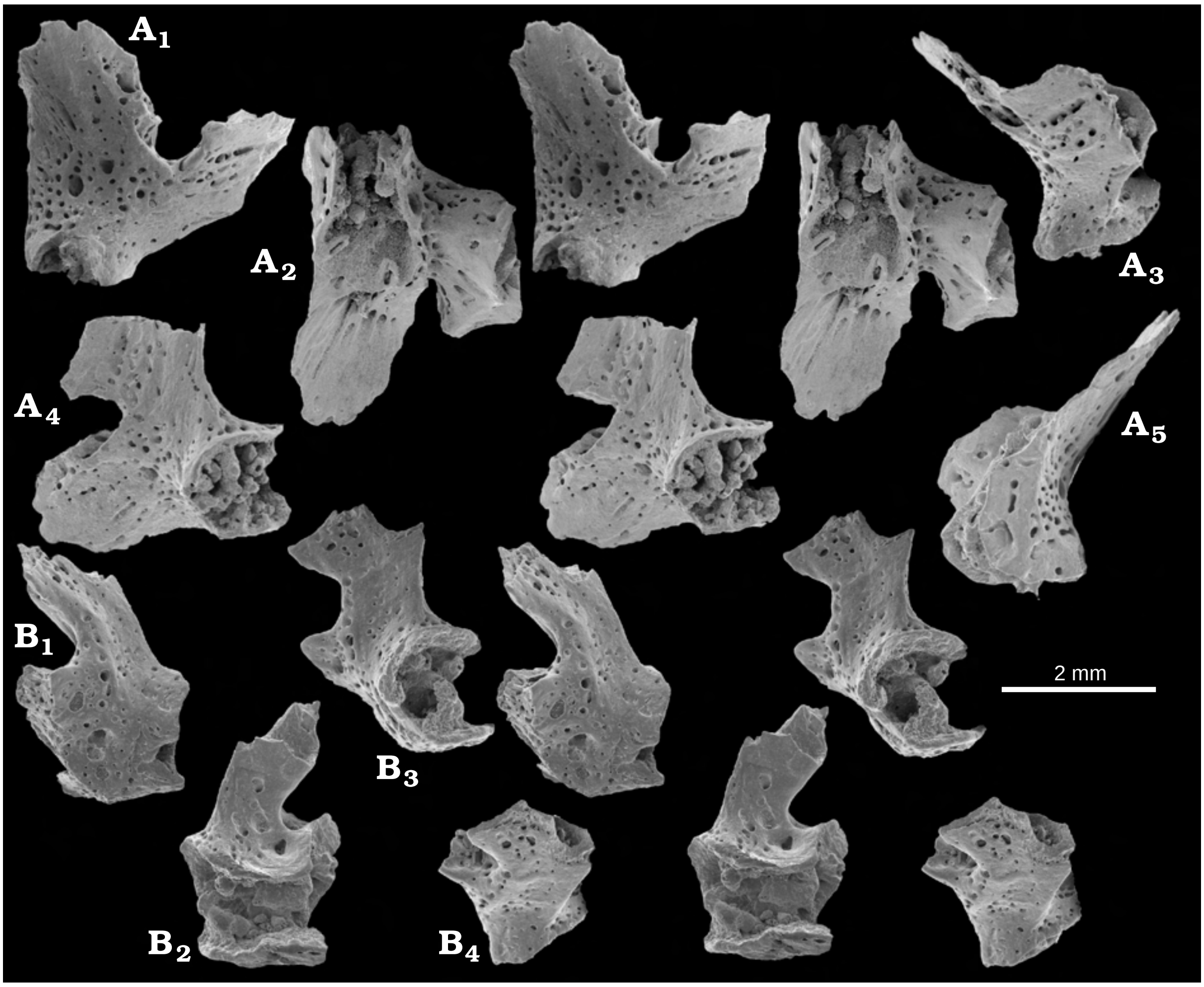

Fig. 38. *Batrachosuchoides* sp., Early Triassic of Czatkowice 1, Poland. Left exoccipitals: ZPAL AbIV/152 (**A**) and ZPAL AbIV/120 (**B**), in lateral (A_1, B_1), medial (A_2, B_2), dorsal (A_3, B_4), posterolateral (A_4), ventral (A_5), and posterior (B_3) views. SEM micrographs; all but A_3 and A_5 stereo-pairs.

To sum up, the attribution of the ectopterygoids ZPAL AbIV/36 and 53 to a brachyopid is substantiated by the following features: (1) palatal exposure of the bone is short; (2) its sutural contact with the palatine is short and nearly transverse; (3) the bone is markedly bent, thus indicating a convexity of the lateral margin of skull; and (4) even at an advanced juvenile stage the ectopterygoid enters the margin of the interpterygoid vacuity.

Exoccipital (Figs 38–41). — Among the exoccipitals recognized in the collection, three left elements have been identified as belonging to brachyopids. These are ZPAL AbIV/48 (about 5 mm long) and the much smaller ZPAL AbIV/120 and 152. All of these are reasonably completely preserved, except that in ZPAL AbIV/120 most of the subotic process is lost.

Although showing some specific characters, the specimens conform to the typical (adult) brachyopid fashion, primarily in the following: marked anteroposterior elongation of the bone; a rather long condylar "neck"; a gentle transition from the subotic process to the condylar division in dorsal view; dorsoventral compression of the condyle; the ascending division of the bone tilted forward (most strongly in younger individuals), the ventral surface of the bone well differentiated and flattened. In all these respects the exoccipitals differ from those in capitosauroids. The description presented below is mainly based on ZPAL AbIV/48 and 152, with some selected references to ZPAL AbIV/120.

In the occipital view (Figs 38A_4, B_3, 39A, 40C), the irregular condylar surface of the exoccipital is expanded transversely rather than dorsoventrally. It is incompletely ossified (especially poorly in ZPAL AbIV/120) and notched medially by the notochordal hollow. The latter is roofed by a strongly projected *processus submedullaris* which underlay the *foramen magnum* in the intact skull. The ascending division of

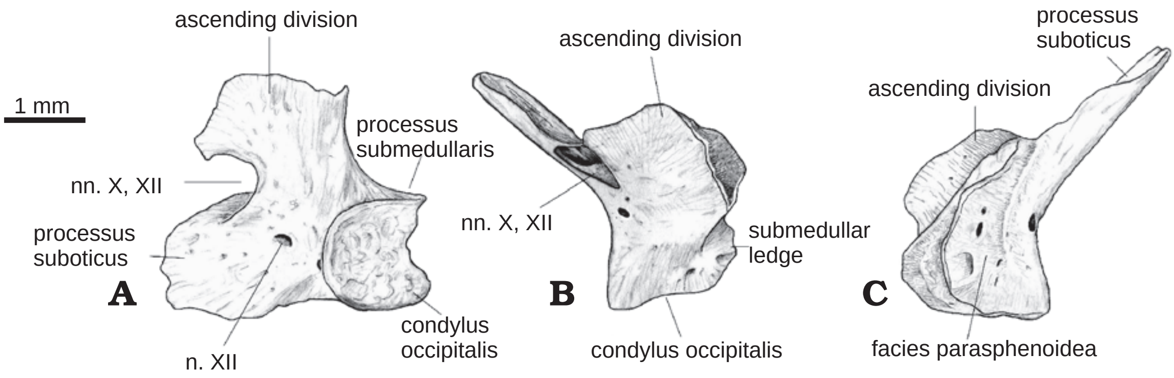

Fig. 39. *Batrachosuchoides* sp., Early Triassic of Czatkowice 1, Poland. Left exoccipital ZPAL AbIV/152, in posterolateral (A), dorsal (B), and ventral (C) views.

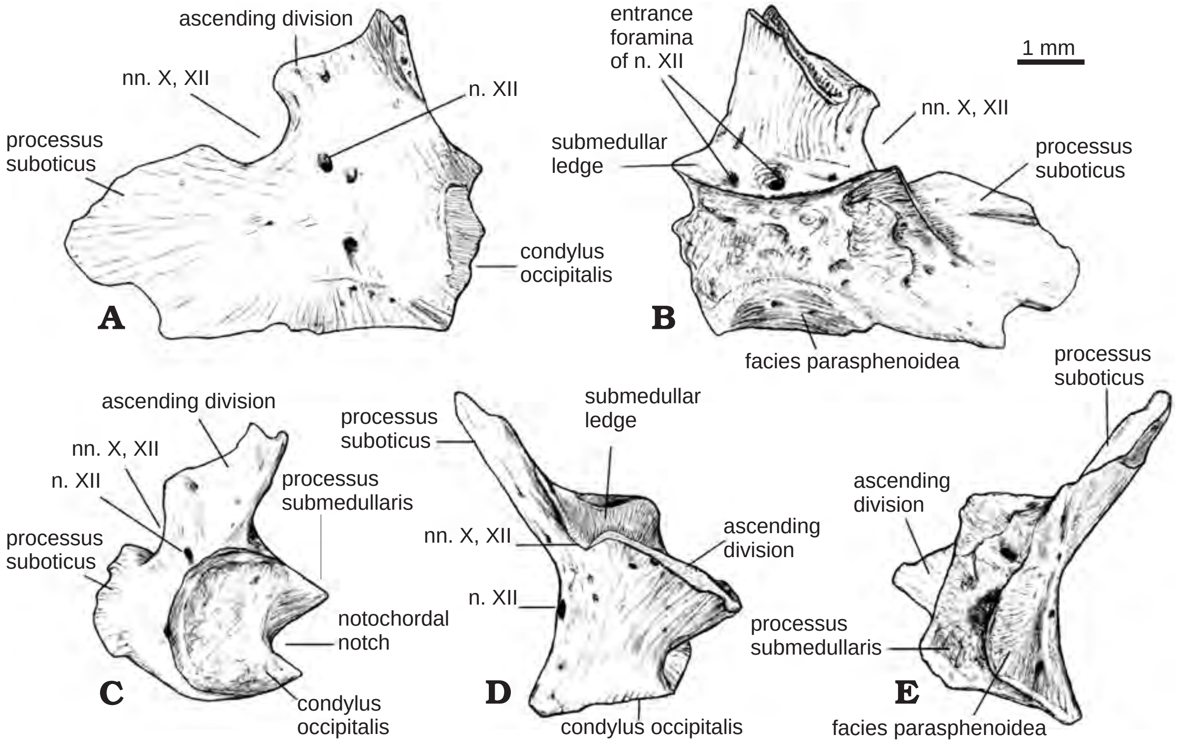

Fig. 40. *Batrachosuchoides* sp., Early Triassic of Czatkowice 1, Poland. Left exoccipital ZPAL AbIV/48, in lateral (A), medial (B), occipital (C), dorsal (D), and ventral (E) views.

the bone is compressed in cross section; its occipital surface faces posterolaterally. Although slightly damaged, the ascending division seems to have been only incipiently forked into the dorsal and paroccipital processes, thus basically forming a single plate, as is common for brachyopids. The medial margin of the division bordering the *foramen magnum* is shaped as a ridge which separates the occipital aspect of the bone from the medial submedullar surface.

In the lateral view (Figs 38A$_1$, A$_4$, B$_1$, 39A, 40A, 41), the base of the exoccipital is strongly stretched anteroposteriorly at the cost of the long *processus suboticus*, which forms much more than one third of the total bone's length. A strong forward projection of the *processus suboticus*, seen already at younger growth stages (ZPAL AbIV/152), may suggest that it could have contacted the pterygoid at the skull base, in a fashion typical for advanced brachyopids. The flattened surface of the process faces ventrolaterally. The ascending division of the exoccipital, seen in lateral aspect, is inclined forward and separated anteroventrally from the subotic process by a huge notch for the exit of the X (*vagus*) nerve and posterior jugular vein. At least in the small specimen ZPAL AbIV/120, showing the column-like ascending division, this notch is not an artefact of preservation, and

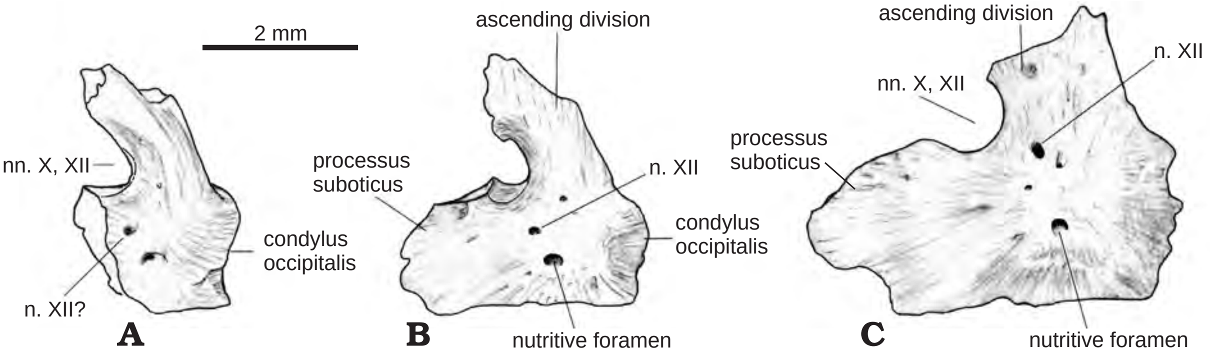

Fig. 41. *Batrachosuchoides* sp., Early Triassic of Czatkowice 1, Poland. Sequence of juvenile growth stages of the exoccipital as documented by specimens ZPAL AbIV/120 (**A**), ZPAL AbIV/152 (**B**), and ZPAL AbIV/48 (**C**), in lateral view.

indicates that the vagus (jugular) canal in the braincase really remained unbordered by the exoccipital anteriorly. This condition is common for Paleozoic temnospondyls and Triassic metoposaurs and is known as a variation in some brachyopids (Shishkin 1967, fig. 3; 1991, fig. 2; Sulej 2007). In the specimens ZPAL AbIV/48 and 152 a more complete enclosure of the vagus exit foramen in the exoccipital seems likely.

Two or three small foramina pierce the lateral wall of the bone. Judging by their position, only the smallest of these (enlarged in ZPAL AbIV/48), lying immediately behind the jugular notch, can be tentatively assigned to the XII (hypoglossal) nerve. Other foramina, situated much lower down, most likely belonged to nutritive vessels. Most roots of the hypoglossal nerve unquestionably left the skull together with nerve X in a manner described in some other brachyopids (Shishkin 1967, figs 3, 4; 1991). This is primarily evidenced by the presence in ZPAL AbIV/120 of a large exit foramen of XII nerve in the posterior wall of the jugular notch.

On the medial surface of the exoccipital (Figs 38A_2, B_2, 40B) three main areas can be distinguished: the posterior, anterior and dorsal. The posterior basal area forms the wall of the notochordal hollow. It is formed by unfinished endochondral tissue and roofed by a smooth dorsal surface of the *processus submedullaris*, which extends forward beyond the anterior limit of the ascending division and borders the latter ventrally. The anterior basal area corresponds to the subotic process; its surface is flattened, faces dorsomedially and bears faint, longitudinal ridges. The dorsal area, showing gentle anteroposterior convexity, is the inner (anteromedial) surface of the ascending division of the exoccipital. On the transition from ascending division to the dorsal surface of the submedullar process there can be situated 3 to 4 entrance foramina for the roots of XII nerve. On the smallest specimen ZPAL AbIV/120, all or most of these are replaced by a single enlarged foramen situated ventral to the vagus notch.

The dorsal and palatal aspects of the exoccipital (Figs 38A_3, A_5, B_4, 39B, C, 40D, E) display some more brachyopid characters, only briefly mentioned above. These primarily include: (1) long base of the exoccipital body; (2) very gradual transition between the latter and the *processus suboticus*, such that in dorsal view they form an angle of about 140–150°. On the other hand, distinct from adult brachyopids (*cf.* Fig. 42), the subotic process is plate-shaped, positioned subvertically, and virtually devoid of a palatal portion overlying the parasphenoid plate. Given that similar design of the *processus suboticus* has been also found in the *Parotosuchus* juveniles (see above), it may be regarded as a normal character of early development in advanced temnospondyls.

Lastly, a very spectacular brachyopid feature is demonstrated by the palatal aspect of the exoccipital (Figs 38A_5, 39C, 40E). In contrast to the condition in capitosaurids, the ventral surface of the bone is markedly flattened and separated by a shallow ridge from the lateral surface, such that there is no gradual transition between them. The ventral surface, somewhat damaged medially on ZPAL AbIV/48, is best preserved in the younger spec-

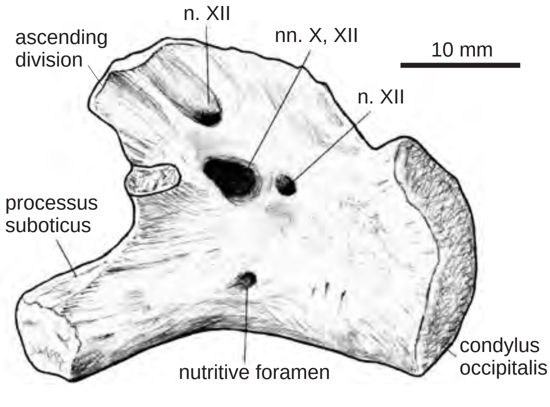

Fig. 42. *Batrachosuchoides* sp., Lower Triassic of Don River Basin, Russia. Adult left exoccipital PIN 1043/653 in lateral view.

imens ZPAL AbIV/120 and especially ZPAL AbIV/152 (Fig. 38A_5, 39C). They demonstrate that even at the earliest growth stages documented by our material the flat area predestined to contact the parasphenoid (*facies parasphenoidea)* was already well developed, extending forward to the base of the subotic process. However, it was still smooth and devoid of sutural ridges.

In summary, comparison of the above described juvenile pattern with that in adult brachyopids seems to imply that in the Brachyopidae the exoccipital primarily underwent the following growth changes (*cf.* Figs 39–42): (1) with the progress of ossification, the condylar surfaces became more compressed dorsoventrally; (2) transformation of a wide jugular embayment between the ascending and subotic processes into closed foramen (when attained) was very gradual; (3) the subotic process appeared as a deep, nearly steep plate which only later tended to have converted into a more shallow and rod-like structure; and (4) on the ventral side of the bone, the flat area for sutural contact with the parasphenoid had already arisen in early stages, but the contact probably remained loose until late ontogeny.

Surangular (Fig. 43). — The presence of a brachyopid in the collection is further evidenced by the incomplete left surangular ZPAL AbIV/69. The specimen is 7.3 mm long and displays roughly a half of the bone's extent. It comprises most of the anterior labial plate (bordering the adductor fossa), the labial wall of

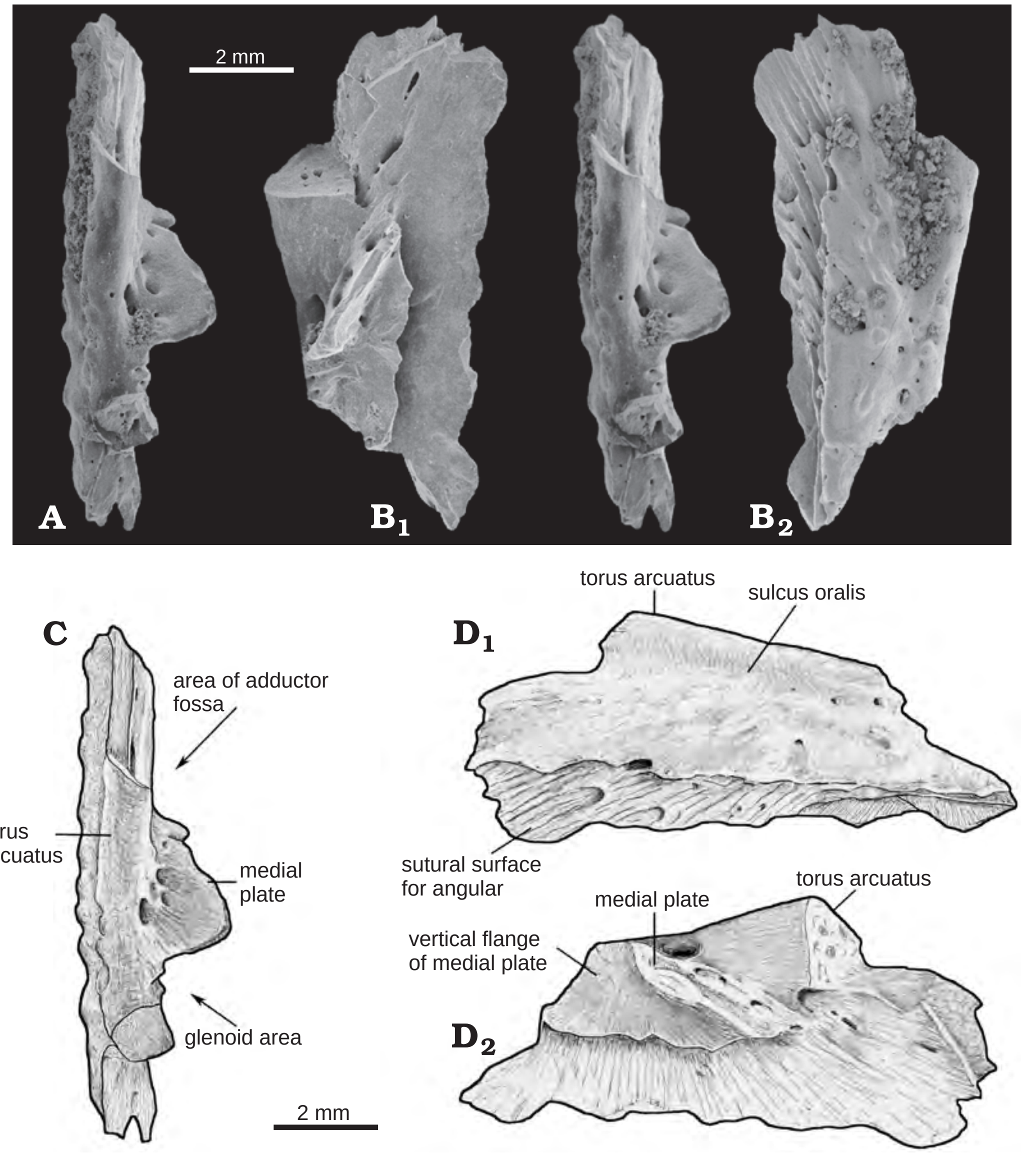

Fig. 43. *Batrachosuchoides* sp., Early Triassic of Czatkowice 1, Poland. Left surangular ZPAL AbIV/69, in lingual (B_1, D_2), labial (B_2, D_1), and dorsal (A, C) views. A, B, SEM stereo-pairs.

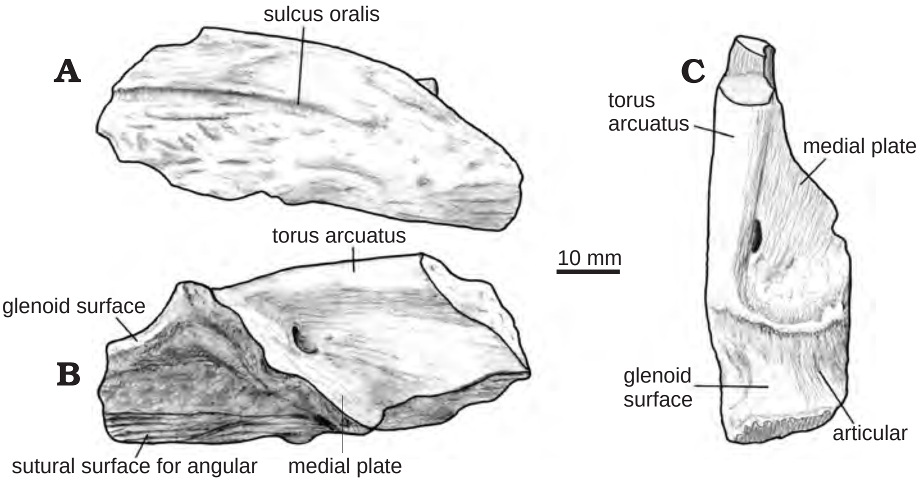

Fig. 44. *Batrachosuchoides lacer* Shishkin, 1966, Lower Triassic of Cis-Urals, Russia. Incomplete left surangular of adult individual PIN 2649/1, in labial (A), lingual (B), and dorsal (C) views.

the glenoid area, and the transverse medial plate separating the two former divisions. Damage to the specimen affected the anterior end of the labial plate and, largely, the postglenoid division, which is not preserved.

In its shape and structure, the surangular much resembles that in *Batrachosuchoides* and other brachyopids (*cf.* Figs 43, 44; see also Watson 1956; Shishkin 1973, pl. 9: 3a–c). In labial view (Fig. 43B$_2$, D$_1$) the area of true exposure of the bone is bordered ventrally by a marginal sutural surface that faces ventrolaterally and was overlapped in life by the angular. The exposed area is rather narrow and decreases in depth posteriorly toward the glenoid region, a condition opposite to that in capitosauroids and their derivatives (MAS personal observations). Another difference relates to the position of the oral sensory groove. It runs close to the margin of the adductor fossa as is typical for brachyopids, but in contrast to most other Triassic temnospondyls, in which it passes along the angular-surangular suture. The dermal ornamentation is barely detectable and built up of smooth shallow ridges.

As seen from the line of demarcation between the true labial surface of the surangular and the sutural area, the angular-surangular suture was straight as is common for brachyopids. The sutural area bears multiple subparallel ridges directed anteroventrally. Its uppermost zone, immediately bordering the labial surface, faces nearly ventrally rather than sidewards. This feature may be a developmental stage towards a condition seen in adult *Batrachosuchoides*, in which the entire sutural surface for the angular attains a largely ventral position (*cf.* Figs 43D$_1$, 44B). A thickened dorsal margin of the anterior surangular plate (*torus arcuatus*) has a rounded subtriangular cross section.

The medial surangular plate forming the posterior wall of the adductor fossa is seen in the dorsal and lingual aspects of the bone (Fig. 43A, B$_1$, D$_2$, C). In side view, it gently slopes forward (at an angle of 40°or so), thus demonstrating again a typical brachyopid pattern. A row of nutritive foramina occurs along the oblique line of the junction of the medial plate with the anterior surangular plate, and on the medial surface of the latter. In the dorsal view, the position of the medial plate indicates that the posterior wall of the adductor fossa was situated more or less transversely. Although this character is common for a number of late temnospondyls, it is not shared by the Early Triassic capitosaurids, in which the wall extends anterolingually (*cf.* Maryańska and Shishkin 1996, fig. 22E, B, G; Shishkin *et al.* 2004, p. 12).

The most unusual feature of the surangular medial plate is the presence of a blade-like vertical flange that projects from the plate downwards throughout its entire anteroposterior extent (Fig. 43B$_1$, D$_2$). It also continues some distance posterior to the plate, being here produced directly by the lateral glenoid wall. The flange runs in parallel with, and in a close proximity to, the glenoid wall, such that they embrace together a slit-like longitudinal vertical space closed dorsally. In life, the observed lingual surface of the flange contacted the labial side of the articular division of the Meckelian cartilage. It seems almost certain that the above space bordered by the flange transmitted the blood vessels and nerves which supplied the glenoid division of the mandible. Apparently, with age, the space underwent transformation into a canal or a set of canals, whose entrance foramina normally occur in temnospondyls in the posterior wall of the adductor fossa (*cf.* Shishkin 1973, figs 40g, 41; *foramen paraarticulare*).

POSTCRANIUM

Clavicle (Fig. 45). — The clavicle ZPAL AbIV/61 can be attributed to *Batrachosuchoides* only on indirect evidence as the dermal shoulder girdle in brachyopids is very poorly known. The bone markedly differs from its homologue described above for *Parotosuchus*. Along with a different kind of ornament on the thoracic plate (in which the pustules dominate over pits), of principal importance are specific features of the ascending process (Fig. 45B). The latter is tall, broad and straight, very gradually narrowed dorsally and only weakly tilted backward. The boundary between the ornamented basal portion of the process and its main body is situated much higher up than in *Parotosuchus*; the muscular depression on the process (common in capitosaurids) is lacking. Lastly, the process is devoid of embayment on the posterior margin and thus evidently did not form the sigmoid curve typical for capitosaurids and some related groups. In most of these characters the ascending process is very similar to that in the clavicle restored by Warren and Marsicano (2000, fig. 6D) for *Batrachosuchus*.

We agree with Warren and Hutchinson (1983) that the pattern of clavicular dorsal process was correlated in temnospondyls with the structure of the occiput, such that a tall process showing only a weak backward slope backward (as is the case in the above-decribed clavicle) should be considered as evidence of a deep occiput. As is well known, it is the latter character that is typical for brachyopid skulls.

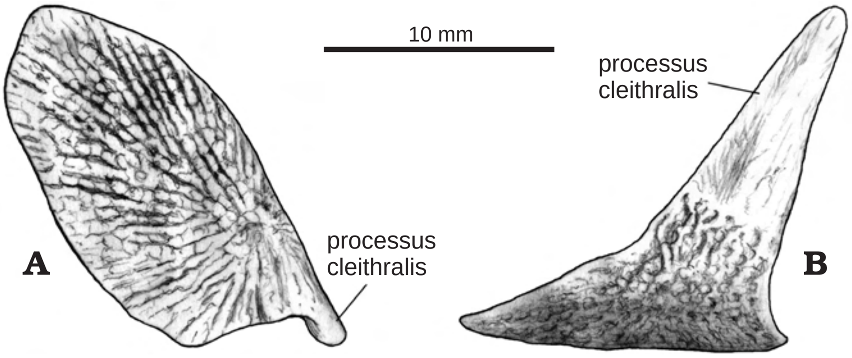

Fig. 45. (?)*Batrachosuchoides* sp., Early Triassic of Czatkowice 1, Poland. Left clavicle ZPAL AbIV/61, in ventral (A) and lateral (B) views.

TEMNOSPONDYL SKULL DEVELOPMENT

The Czatkowice 1 material provides some new data on skull development in Early Triassic temnospondyls, primarily the capitosaurids. This information has been inferred from a study of selected bones of the palatal complex, jaws and occipital arch, represented by one or more juvenile stages. The most specific of these observations cannot be assessed by comparison with previously published data, as they relate to ontogenetic changes that have never been examined before.

A study of ontogeny in temnospondyls, started as early as the 19th century, is primarily based on examination of extensive growth series. It remains almost entirely confined to the Paleozoic taxa, including various members of paedomorphic dissorophoid lineages (Branchiosauridae and Micromelerpetontidae), the Eryopidae, Archegosauridae, Zatrachydidae, and related groups (for some recent accounts and reviews see Boy 1972, 1974, 1988, 1989, 1990; Boy and Sues 2000; Schoch 1992, 2001, 2002a, b, 2003; Werneburg and Steyer 2002; Witzmann 2005a, b; Witzmann and Schoch 2006a, b). Studies conducted on these forms substantiate the present idea of temnospondyl ontogeny. These are mostly centered on such aspects as the patterns of ossification sequence and allometric growth, the evidence of metamorphosis, and the development of the dentition. These studies contain little information on structural (qualitative) growth changes of particular bones.

The same problem arises to an even greater extent when we turn to typical Triassic groups. Some aspects of their development have been surveyed only in a limited set of papers, such as those of Wagner (1935), Bystrow and Efremov (1940), Warren and Hutchinson (1988a), Warren and Schroeder (1995). The rest of the relevant information is confined to sporadic comments scattered over a variety of descriptive papers, including, for instance, the accounts of Welles and Cosgriff (1965); Shishkin *et al.* (1996, 2004); Damiani and Warren (1997); Shishkin and Rubidge (2000); Morales and Shishkin (2002); Steyer (2003); Schoch (2006). This state of things complicates the evaluation of our results in a wider developmental context.

An approach to assessment of ontogenetic variations seen in the Czatkowice 1 temnospondyls much depends on one‘s idea of evolution and diversification of cranial structural patterns within the group overall. In this light, the provisional (juvenile) characters surveyed in the preceding section may be subdivided into several categories. The first one embraces the best evidenced palingeneses in Haeckel’s (1866) sense, *i.e.*, the characters bearing a resemblance to ancestral adult states. The next group includes the characters thought to be more or less common for temnospondyl ontogeny, regardless of whether they reflect the adult ancestral patterns or not. Such evaluation is mostly based on comparison with the growth stages or paedomorphic morphotypes known in various lineages. An additional category includes evolutionary novelties (Haeckel‘s caenogeneses in a broad sense) that arose due to a change in timing of specific transformations involved in the development of a given structure (heterochrony). Lastly, some features, first revealed in the Polish material, pertain to those aspects that have never been specifically examined in the juvenile stages of other taxa. Tentative attribution of such features to juvenile morphotypes may be justified at least in some cases.

The analysis of these developmental data suggests some evolutionary implications. In particular, it may shed light on the origin of particular structures. Similarly, it allows one to speculate on the order of some evolutionary changes, which is not directly derivable from the fossil record. The data on juvenile patterns of capitosaurid skull bones may elucidate the evolutionary trends that underlay the origin of some derived groups.

The results obtained in the course of our analysis are surveyed below. Unless stated otherwise, these relate to the ontogeny of the capitosaurid *Parotosuchus*.

PALINGENETIC CHARACTERS

Palatal dentition. — An evident example of the repetition of the remote ancestral state in ontogeny of the Czatkowice 1 capitosaurid is provided by the juvenile dentition of the ectopterygoid. The tooth set borne by the bone comprises a pair of large tusks combined with one or two minor regular teeth anterior or/and posterior to the tusks (Figs 11A_2, A_3, A_5, B_1, B_3, 12A, C). With growth, this arrangement tends to grade into a more standard capitosauroid design by increase in the number of teeth within a regular row, along with moderate reduction of tusks (*cf.* Figs 12E, G, 14). A similar pattern including the tusks and, occasionally, a few regular teeth (or shagreen field) is fairly common in the adults of Permo-Carboniferous temnospondyls (*cf.* Holmes 2000). It is also known in a number of distantly related Triassic forms, such as the brachyopids, some rhytidosteids and a relict dissorophoid (Schoch and Rubidge 2005, p. 507). This suggests that such an ancestral type of dentition might have represented a rather generalized early stage in temnospondyl ontogeny.

Structure of the mandibular symphyseal plate. — As was shown in the Morphology section, the growth changes observed in the symphyseal portion of the mandible provide a basis for some evolutionary implications. In contrast to a normal temnospondyl condition, with the symphyseal plate of the dentary entirely incorporated in an adjacent portion of this bone, the young juveniles of *Parotosuchus speleus* (ZPAL AbIV/119 and 31) show these parts to be subdivided anteriorly by a notch (Figs 19E_1, E_3, F, 21A, B, D, 22A, B). This may give support to a suggestion that in temnospondyl ancestors the symphyseal plate of the dentary was an independent ossification.

Some additional support to this view may be indirectly derived from specific interrelations of the symphyseal plate and precoronoid found in *P. speleus* juveniles. Unlike nearly all advanced temnospondyls, but in accord with the primitive condition demonstrated by some Paleozoic forms (edopids and zatracheids, *cf.* Shishkin 1994, p. 135), these elements are widely sutured in dorsal view, forming together a single plate-like longitudinal shelf facing dorsally rather than lingually. This looks like a simplified version of the earliest structural pattern known in stem tetrapods (acanthostegids, ichthyostegids, baphetids, colosteids, etc.) and their sarcopterygian (elpistostegid) ancestors, in which the precoronoid and anterior tusk-bearing end of the dentary are similarly orientated and linked via an intervening additional derivative of the coronoid series, the parasymphyseal plate (Ahlberg and Clack 1998, figs 1–3, 5, 9, 13, 14, 16, 18, 19). In temnospondyls the latter was either lost or included in the symphyseal plate.

Hence, in the archaic type of temnospondyl dentary, recapitulated by the Triassic capitosaurid juveniles, the symphyseal plate was directly sutured and aligned with the dorsally exposed coronoid series, thus appearing as an anterior member of the latter (or at least including such a member). Recognizing this homology would imply a conclusion that the symphyseal plate or some its portion originated independently from the rest of the dentary.

Shape of the posttemporal fenestra in *Batrachosuchoides*. — In the adults of advanced brachyopids and supposed dvinosaurid derivatives (*Batrachosuchus*, *Batrachosuchoides*, *Hadrokkosaurus*) the posttemporal fenestrae piercing the occiput above the otic capsules are much reduced in size and rounded in shape. Accordingly, the lateral wing of the postparietal contributing to the roof of the posttemporal fenestra is very short and ventrally concave in occipital aspect (Fig. 34C). By contrast, in the juvenile postparietal of *Batrachosuchoides* sp. (ZPAL AbIV/101) the lateral wing is transversely elongate and straight, thus indicating that the fenestra was expanded mediolaterally (Figs 32A, D, 33A, D, 34B). This type of fenestra is the most common for temnospondyls, including the Paleozoic trimerorhachoids, which are close to brachyopid ancestry (Fig. 34A). Hence, we can suppose that this condition was recapitulated in the brachyopid ontogeny.

Position of the jugular canal in *Batrachosuchoides*. — Examination of the exoccipitals (Figs 39–41) suggests that in the smallest juveniles of Polish brachyopid (Figs 38B$_1$, B$_2$, 41A) the jugular canal transmitting the X nerve and posterior jugular vein was not incorporated into this bone, in contrast to a standard condition observed in Triassic temnospondyls. Instead, the nerve and vein emerged via a broad notch between the subotic process and straight ascending division of the exoccipital. In the next stages (Fig. 41B, C) the notch becomes more distinctly cut into the anterior margin of the ascending division, thus showing that the jugular canal tends to be included in the exoccipital.

An initial position of the canal seen in younger juveniles (Fig. 41A) is otherwise typical for Paleozoic temnospondyls and reflects a common embryonic tetrapod condition, under which the X nerve leaves the skull via the metotic fissure between the otic capsule and occipital arch (*cf.* de Beer 1937). Even in some Triassic forms that show the widening of the jugular canal, its complete incorporation in the exoccipital might have been retarded or arrested. As a common variation this occurs in some brachyopids, such as *Batrachosuchoides* and *Gobiops* (Shishkin 1967, fig. 3; 1991, fig. 2) in which the vagus foramen may look like a notch. The only Triassic group in which the enormously expanded jugular passage in the exoccipital always remains unclosed anteriorly is the Metoposauridae (Shishkin 1967); a small foramen attributed in metoposaurids by most authors to the vagus nerve is actually the exit of the XII nerve.

CHARACTERS NOT NECESSARILY REFLECTING THE ADULT ANCESTRAL STATES

Juvenile structure of the vomer. — As was emphasized above, all the vomers identified in the collection seem to be formed mainly by a thickened marginal tooth-bearing portion, with only a rudimentary contribution from a medial plate of the bone. These two subdivisions are demarcated on the palatal surface by a step-like boundary (Figs 2A$_1$, A$_3$, B$_1$, B$_3$, 3A$_1$, A$_3$, B$_1$, B$_3$, C, 4B, D, 5). Although poor development of the medial plate may be accentuated by its incomplete preservation, it seems certain that ossification of the vomer had started from its marginal (dentiferous) portion and later spread over the plate area. This is a standard condition for temnospondyls as evidenced by the pattern of lines of growth on the vomerine dorsal surface, examined in many taxa (MAS personal observation).

These facts imply that at the earliest growth stages the extent of the vomer in temnospondyls was mostly confined to its tooth-bearing field as is observed in the ontogeny of recent urodeles (Lebedkina 1979, figs. 33–35, 48, 50, 51A, B, 63). The condition found at the youngest ontogenetic stages of branchiosaurs closely approaches this pattern by showing the vomerine rudiments separated and extended along the choanal margin (Schoch 1992, figs 4, 5; Boy and Sues 2000, fig. 8). In many of the Branchiosauridae, the vomer basically retains the same juvenile outline throughout the life cycle, (Fig. 7A; *cf.* Boy 1972, figs 30–32, 35, 36; 1986, fig. 14; Werneburg 1989, figs 7, 8). Contribution from the medial plate seems here rather limited. A similar condition is seen in neotenous trimerorhachoid *Dvinosaurus primus* (Fig. 7B; *cf.* Shihkin 1973, fig. 4, pl. 4a, b). In all these instances the structure of the vomer much resembles that preserved in juveniles of the Czatkowice 1 capitosaurid. Much the same shape and orientation of the vomer are also exhibited by the Devonian stem-tetrapod *Acanthostega* (Clack 2000, fig. 21B).

To evaluate the evolutionary significance of these facts, it should be remembered that the vomer evidently arose as an exoskeletal element of the visceral skeleton. Jarvik (1954) regarded it as a derivative of the epibranchial dermal ossifications of one of the premandibular arches incorporated into the skull in the Gnathostomata. Providing this view is correct, the narrowness and oblique ("visceral') orientation of the primitive vomer seem predictable. Coupled with the above discussed data, this may justify the assumptions that (a) in primitive temnospondyl ontogeny, the early ossification of the vomer was limited to its external zone adjacent to the upper jaw, and (b) this initial ossification recapitulated the archaic type of the vomer.

The above analysis makes it evident that the stout palatine process of the vomer (formed in juveniles of the Czatkowice 1 capitosaurid mostly from the thickened tooth-bearing portion of the bone) is an ancient structure which arose much earlier than the posterior vomerine process, adjacent to the parasphenoid. All known data on the cranial development in branchiosaurs seem to corroborate this conclusion. Retention of the primitive (narrow and elongate) palatine process in adults may be exempified by a number of very distantly related Paleozoic forms such as, for example, *Trimerorhachis* and *Doleserpeton* (Holmes 2000). A further evolution of the vomer, which proceeded in parallel in many temnospondyl groups, including the Capitosauridae, resulted in the appearance of the posterior process and broadening of the palatine process at the cost of the medial vomerine plate (Fig. 8D). Steps toward this condition are exemplified by rhinesuchids and some paedomorphic dissorophoids (Figs 7C, D, 8A).

In capitosaurid ontogeny, an intermediate growth stage between the formation of an early rudiment of the vomer (see above) and the adult structure of this bone may be represented by the stage known in juvenile *Rewanobatrachus*, which seems to combine the narrow palatine process with the presence of an incipient posterior process (Fig. 8B; *cf.* Warren and Hutchinson 1988a, fig. 8D).

Juvenile structure of the ectopterygoid. — In both of the temnospondyl taxa detected in the Czatkowice 1 assemblage, the early growth stages of the ectopterygoid show the presence of an unusual subvertical medial surface (*planum mediale*) which borders the interpterygoid (palatal) vacuity and to some extent contacts the pterygoid along the dorsal margin (Figs 11A$_3$, A$_4$, 12C, D, 13A, 35A$_1$, A$_3$, A$_4$, B$_1$, B$_3$, B$_4$, 36A, C, D). With growth, this surface becomes shallower and grades into the marginal medial zone of the palatal surface of the bone (Fig. 12G, H, *cf.* Fig. 13A, B).

As the growth changes of the temnospondyl ectopterygoid have never been studied in three-dimensional aspect, the above observations remain unparallelled in the literature. Nevertheless it seems highly probable that the *planum mediale*, recognized in so distantly related forms as capitosaurids and brachyopids, belongs in fact to generalized characters of the early cranial development in temnospondyls. A variety of paedomorphic cranial morphotypes known in short-faced trimerorhachoids and their derivatives (dvinosaurids, tupilakosaurids, brachyopids) strongly suggests that in temnospondyl larvae the posterior part of the palate was deeply vaulted in a cross section, due to downturn of the lateral pterygoid portions bordering the palate at the level of the subtemporal fossae. It seems almost certain that the portion of palate in front of the fossae was also involved in formation of the vault, which resulted in appearance of the deep medial surfaces of the ectopterygoids (Fig. 13A). In adult individuals of the short-faced paedomorpic groups listed above the presence of such medial walls is not known with confidence. This may be accounted for by the trend to flattening of the palate which proceeded in craniocaudal direction during ontogeny.

The vaulted shape of the posterior part of the palate, demonstrated by temnospondyl larvae, resembles the adult condition in many primitive tetrapod lineages, such as early temnospondyls (*e.g.*, dendrerpetontids), colosteiforms and anthracosaurs, and was evidently inherited from the condition in sarcopterygian ancestors. However, no data is known so far which could confirm that the ectopterygoids had ever contributed to the formation of the vault in adult protetrapods. For this reason the occurrence of a medial surface of the ectopterygoid seen in temnospondyl ontogeny cannot be interpreted with certainty as a recapitulation of ancestral state.

Maintenance of larval skull shape at the advanced juvenile stages. — As is well known (Bystrow 1935; Boy and Suess 2000, fig. 4), at early ontogenetic stages the temnospondyl skulls were proportionally much shorter than in the adults and most often had a parabolic shape with markedly convex side contours. The same was obviously the case in the earliest juveniles of capitosaurids, in contrast to the nearly straight elongate postnarial contours of the skull in their adults. Such a pattern of growth change is suggested by a restoration of the youngest known individual of the capitosaurid *Rewanobatrachus*, with a skull 11 mm long, published by Warren and Hutchinson (1988a, figs 8–10). The data from the present study provide similar evidence for a more advanced capitosaurid, *Parotosuchus*.

The most important piece of such evidence is the shape of posterior division of the dentary, whose contour is markedly bent in dorsal view (Figs 23A$_3$, 24C). Even given slight damage to the posterior end of the bone, it is safe to conclude that the lateral outlines of the skull and mandible were convex for the entire extent of their marginal dentition, *i.e.*, up to the beginning of the postorbital zone. The capitosaurid maxillae from Czatkowice

1, albeit incompletely preserved, are also convex along the labial surface (Figs 17B$_1$, 19A$_3$, B$_3$, C$_3$, D$_3$, 20A). The shortness of the skull is also indirectly implied by the crescent-shaped design of the postorbital (Fig. 1B) resembling that in the early stage of *Rewanobatrachus* (Warren and Hutchinson, 1988a, figs 9B, 10A, 11A).

The above conclusion about the shape of the juvenile *Parotosuchus* skull is corroborated by the pattern of the ectopterygoid specimens. Both the smallest and that belonging to a much more mature stage (Fig. 12) show various degrees of convexity along the lateral side, which implies the same contour for the lateral skull margin. This again is in contrast to the condition in adult capitosaurids, in which the ectopterygoids are straight in palatal view.

EVOLUTIONARY NOVELTIES RESULTING FROM HETEROCHRONY

An example of such a newly arisen feature is a temporary or permanent entrance of some portion of the ectopterygoid into the interpterygoid (palatal) fenestra. The feature is observed in the early juvenile stages of both the capitosaurid and brachyopid from the Czatkowice 1 assemblage. In the former such a condition ceases in later ontogeny due to spreading forward of the palatal branch of the pterygoid. The latter reaches the palatine along the border of the palatal fenestra (*cf.* Figs 6, 12A, B, E, F, 14) and thus separates it from the ectopterygoid. The same order of events obviously took place with growth in the Australian capitosaurid *Rewanobatrachus* (Warren and Hutchinson 1988a). On the other hand, in all brachyopids the ectopterygoid remains included in the margin of the palatal fenestra.

These facts strongly suggest that, historically, an entrance of the ectopterygoid into the palatal fenestra resulted from interplay of two processes, the growth of the palatal rami of the pterygoids and the expansion of the palatal fenestrae. Early tetrapods, including most of the Paleozoic temnospondyls, typically possessed small or moderate fenestrae combined with strongly developed pterygoids. The ontogenetic expansion of the fenestrae evidently proceeded at a very slow rate. As a result, in no stage of ontogeny could it prevent continuous contact of the pterygoids with the entire series of palatal bones, from the ectopterygoid to vomer (see, for example, Schoch 2003, p. 1061, fig. 3A, B). In Triassic temnospondyls, which show large palatal fenestrae, the latter became greatly expanded in early developmental stages, when the slowly growing pterygoids remained too short to preclude the ectopterygoids from entering the fenestrae. With later ontogeny, when expansion of the fenestrae became retarded or completed, the continuing growth of the palatal pterygoid branches could restore the ancestral condition (the pterygo-palatine contact) as is observed in capitosaurids. Alternatively, if the development of the pterygoids underwent further slowing down, this finally resulted in their failure to reach the palatines. This caused retention in the adult of the juvenile condition (entrance of ectopterygoid into palatal fenestra) as is exemplified by brachyopids.

Some poorly known juvenile characters. — Study of all tooth-bearing palatal elements of *Parotosuchus* and the brachyopid ectopterygoids from Czatkowice 1 demonstrates that in juvenile stages these bones were devoid of subvertical lateral surfaces, which in adult temnospondyls usually form most of the sutural contact with the maxillary-premaxillary complex. Instead, the palatal elements had flattened lateral edges and displayed different modifications of the contact with the upper jaw.

Specifically, the vomer of juvenile *Parotosuchus* bears a marginal area for attachment of the premaxilla (*facies articularis*; Figs 4B, D, 5) on the ventral surface. The posterior continuation of this area that served for contact with the maxilla (*f. maxillaris*) is developed on the ventral side of the palatine (Figs 9B$_1$, 10A). By contrast, in the juvenile ectopterygoids, both in the capitosaurid and brachyopid examined, the zone of contact with the maxilla (*facies maxillo-jugalis*) is developed on the dorsal or dorsolateral surface of the bone (Figs 11A$_1$, A$_4$, B$_2$, B$_4$, 12B, D, 35A$_2$, A$_4$, B$_2$, B$_4$, 36B, D). As can be extrapolated from the growth series of the ectopterygoids in *Parotosuchus* (Fig. 12D, H), in the course of ontogeny all these sutural patterns tended to grade into a more uniform one, in which the upper jaw bones were largely attached to the lateral side of the palatal complex.

Additional implications. — As seen from the above analysis, the data on developmental changes provided by the Czatkowice 1 temnospondyl material may substantiate some speculations on the patterns of cranial evolution within the group. One more possible implication of this sort relates to parallels between the capitosaurid juvenile morphology and that known in the adult Trematosauridae. The origin of typical (non-lonchorhynchine) trematosaurids from primitive capitosaurids seems unquestionable (Shishkin 1980). The same holds for the fact that the formation of the trematosaurid cranial pattern was strongly influenced by paedomoprhic trends, as is manifested, for example, by the type of their dermal ornamentation and otic notches. Comparison with data on the Czatkowice 1 material allows for extention of the list of such trends by inclusion of many further parallels between capitosaurid juvenile characters and the typical trematosaurid pattern. These include: the vaulted shape of the palate; retention of the ectopterygoid tusks; entrance of the ectopterygoids in the palatal fenestrae; flatness and vertical position of the subotic process of the exoccipital; and, possibly (by analogy with juvenile ectopterygoid dentition), reduction of the tooth count on the palatines.

In conclusion, summarizing the available data on the juvenile cranial morphology in *Parotosuchus*, we should stress that it looks more primitive than the comparable juvenile morphotypes of related genera from the basal Lower Triassic, such as *Rewanobatrachus*, *Edingerella* and *Benthosuchus*. The most obvious contrast relates to the ectopterygoid dentition. This difference may be primarily explained by a more retarded (paedomorphic) and prolonged development in geologically younger *Parotosuchus*.

DATING AND CORRELATION

Assessed in terms of evolutionary level, the temnospondyl amphibians of the Czatkowice 1 vertebrate assemblage allow for new refinement of the dating of the entire community. The most recent concept of its age (Borsuk-Białynicka *et al.* 2003) was focused on the presence of the jaws of advanced procolophonids with reduced tooth count in association with the toothplates of the dipnoan *Gnathorhiza*. In the European part of Russia (Eastern European Platform and Cis-Uralian Foredeep) which displays the best calibrated tetrapod succession of the continental Lower Triassic (Shishkin *et al.* 2000), the ranges of the above fossils show an overlap in the interval from the Upper Vetlugian stage of the regional scheme (Rybinskian-Sludkian stages) to the Lower Yarenskian stage (Fedorovskian substage). This corresponds to most of the Olenekian, including the early half of the Late Olenekian.

As the Polish finds of *Gnathorhiza* were not accompanied by the toothplates of *Ceratodus,* the typical dipnoan genus of the Yarenskian time, it has been tentatively suggested that a Late Vetlugian (Early Olenekian) age of the Czatkowice 1 assemblage was most probable. However, this view should be now revised owing to the discovery in the assemblage of the unquestionable Late Olenekian temnospondyl genera, the capitosaurid *Parotosuchus* and brachyopid *Batrachosuchoides*, both known to be typical members of the Yarenskian *Parotosuchus* Fauna.

To this end, two more points should be stressed with reference to the Eastern European Triassic faunal succession: (1) in the units older than the Late Olenekian (Yarenskian) no brachyopids at all have been recorded; and (2) these older (Vetlugian) units include no capitosaurids other than the primitive genus *Wetlugasaurus*.

Some further comments on the comparison of the Polish assemblage with the Eastern European faunal succession can be based on the age limitations superimposed by the dipnoan *Gnathorhiza*. As said above, the presence of this genus suggests that the Czatkowice 1 assemblage should be not younger than the early Late Olenekian (Yarenskian). Providing this is correct, one can suppose that the local capitosaurid species *Parotosuchus speleus* belongs to primitive (Yarenskian) members of the genus, showing skulls with the narrow tabular horns and constituting the "*helgolandiae*"-group, distinct from the later "*nasutus*"-group (Ochev *et al.* 2004). In this case *P. speleus* is expected to be close to such Russian species as *P. bogdoanus* and *P. orientalis*. To test this assumption, more diverse skeletal material of the Polish species is needed.

LANDSCAPE SETTING OF THE CZATKOWICE 1 TETRAPOD FAUNA

As was already noted (p. 32), the Czatkowice assemblage is peculiar for a very modest role played by its amphibian component. In this respect it markedly differs from the typical Scythian–Early Anisian tetrapod faunas of Euramerica. These are entirely dominated by the aquatic temnospondyl amphibians, whose bones may amount to over 90% of collected material.

This kind of taphonomic bias, giving preference to inhabitants of aquatic or subaquatic biotopes, is fairly common for the continental fossil record overall, since the bulk of it has been linked in geological history with the lowland territories adjacent to terminal basins. Positioned close to the erosional base, they were the zones of most continuous accumulation of continental sediments.

Distinct from that, on geological evidence, the Czatkowice area in the Early Triassic belonged to low upland (Borsuk-Białynicka *et al.* 1999; Paszkowski 2009) which was dominated by destructive processes. The sediments were accumulated only in local depressions (presumably small lakes) within the karstified relief and subject to quick erosion with time. As a consequence, they have been preserved only in the karst fissures.

In general, the tetrapod communities of the upland biotopes are poorly represented in the fossil record. Ecologically, when documented, they can show rather weak links with the aquatic environment, as distinct from coeval lowland burials.

The composition of the Czatkowice 1 assemblage is consistent with its presumed geographical setting. It is entirely dominated by terrestrial reptiles, primarily euparkeriid archosaurs (most probably facultative bipeds), a group, which is otherwise known nowhere in the Early Triassic of Euramerica.

Another point important for estimating the local environment is the presence in the assemblage of the early salient amphibian, *Czatkobatrachus* (Evans and Borsuk-Białynicka 1998; Borsuk-Białynicka and Evans 2002). *Czatkobatrachus* is a rather routine, although subordinate, member of the local tetrapod community, comparable in number of fossils with the record of accompanying temnospondyl amphibians. (This condition much differs from that displayed by *Triadobatrachus*, the only other Triassic stem-frog so far known, detected by but a single specimen).

The fact that *Czatkobatrachus* is not uncommon in the assemblage may provide support to the hypothesis suggesting that the anurans originated in upland habitats (Eaton 1959, p. 170; Schmalhausen 1964). This concept assumes that the structural pattern of primitive anuran larvae along with the mode of their feeding (scraping algae from the rock) arose as an adaptation to living in mountain brooks. It can be admitted that the type of environment exemplified by the Czatkowice biotope did not depart too much from conditions under which the anurans are thought to have originated.

No direct data are available on the relief of the vicinity that surrounded the local Scythian lake. However, the evidence of water transport documented by the bone-bearing rock (fissure infillings) indicates sporadic floods that most probably occurred in the rainy seasons. It seems obvious that during such seasons the shoreline was crossed by some temporary streams which conveyed the flood waters to the lake. The streams could have been maintained long enough to afford a necessary swift-water setting for development of the salientian larvae.

Hence, both the ecological features and taxonomic composition of the Czatkowice 1 vertebrate assemblage corroborate the conclusion that its habitat was distinct from that typical of the lowland biotopes.

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THE EARLY TRIASSIC STEM-FROG *CZATKOBATRACHUS* FROM POLAND

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Evans, S.E. and Borsuk-Białynicka, M. 2009. The Early Triassic stem-frog *Czatkobatrachus* from Poland. *Palaeontologica Polonica* **65**, 79–105.

Czatkobatrachus polonicus Evans *et* Borsuk-Białynicka, 1998 is a stem-frog from the Early Triassic karst locality of Czatkowice 1 (southern Poland). It was described and named on the basis of a small collection of vertebrae, ilia, and forelimb bones, with subsequent description of the scapulocoracoid. Further skeletal elements have now been recovered. Here we present a complete overview of the available material of *Czatkobatrachus*, give an extended diagnosis of the genus, and provide an assessment of its relevance to our understanding of the early stages of salientian evolution. *Czatkobatrachus* has an anuran type ilium, a urodelan-like scapulocoracoid, unfused epipodials, a moderately shortened presacral column, and a very short tail of separate caudal vertebrae. The strongly ossified ends of the proximal limb bones suggest terrestrial life. The skull is unknown.

Key words: Stem-frogs, Anura, Salientia, Lissamphibia, Triassic.

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INTRODUCTION

Czatkobatrachus polonicus Evans *et* Borsuk-Białynicka, 1998 is a stem-frog described from the Early Triassic microvertebrate locality of Czatkowice 1 in southern Poland (Paszkowski and Wieczorek 1982). It is the earliest lissamphibian known from Northern Pangaea, and only the second recovered from Triassic deposits, the roughly contemporaneous salientian *Triadobatrachus massinoti* (Piveteau 1936) from Madagascar being the first. To date, only a few postcranial bones of *Czatkobatrachus* (ilia, distal humeri, ulnae, vertebrae, scapulocoracoid) have been described (Evans and Borsuk-Białynicka 1998; Borsuk-Białynicka *et al.* 1999; Borsuk-Białynicka and Evans 2002). Incomplete as they are, the remains of *Czatkobatrachus* are generally similar to those of *Triadobatrachus* but are significantly smaller and appear more derived (or at least better ossified) in rib, vertebral structure and limb morphology.

The objective of the present paper is to describe newly discovered material of *Czatkobatrachus polonicus*, as well as give a more detailed description of skeletal elements only briefly discussed in the original paper, most notably parts of the vertebral column and limbs.

Institutional abbreviations. — MNHN, Museum National d'Histoire Naturelle, Paris, France; UCMP, University of California, Museum of Paleontology, Berkeley, USA; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

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GEOLOGICAL SETTING

The Triassic deposits filling the karst fissures developed in the Early Carboniferous limestones at Czatkowice 1 (southern Poland) were discovered by a team from the Jagiellonian University, Kraków, and were first described by Paszkowski and Wieczorek (1982). The material described herein comes from the largest of the karst fissures called Czatkowice 1. This material has been dated as probably Early Olenekian in age (Borsuk-Białynicka *et al.* 2003). A more detailed account of the geology may be found elsewhere in this volume (Cook and Trueman 2009; Paszkowski 2009).

MATERIAL AND METHODS

The bone material from the karst deposits of Czatkowice 1 consists of the completely disarticulated skeletons of several small vertebrates, most of them reptiles (Borsuk-Białynicka *et al.*1999). Salientian postcranial bones are easily discriminated from reptilian ones by their anatomical structure, further supported by their size range (all but one of the Czatkowice 1 reptiles are larger as adults); their frequency (*Czatkobatrachus* remains are comparatively scarce); and the type of bone tissue in terms of surface appearance. The skeletal elements were compared with those of both extant and fossil frogs, particularly the earliest known Jurassic frogs: *Notobatrachus degiustoi* Reig, 1955 and *Vieraella herbsti* Reig, 1961 (Báez and Basso 1996), and *Prosalirus bitis* Shubin *et* Jenkins, 1995 (Jenkins and Shubin 1998). Most informative was a comparison with the Early Triassic Malagasy basal salientian *Triadobatrachus massinoti* (Piveteau, 1936) (Rage and Roček 1989; Roček and Rage 2000).

The puzzling absence of skull bones cannot be explained as the effect of chemical preparation in acetic acid, because equally small and fine reptilian elements are perfectly preserved. It may be partly an artifact of the relative scarcity of *Czatkobatrachus* remains overall. Although all crown-group frogs have lost the lower dentition, most basal taxa, as well as many neobatrachians, retain teeth in the maxilla, and these toothed elements are both common and distinctive in microvertebrate assemblages, even when fragmented. Nonetheless, despite a careful scrutiny of all toothed elements from Czatkowice 1, none are attributable to *Czatkobatrachus*. Rage and Rocek (1989) found no trace of teeth in *Triadobatrachus*, but only the most posterior part of the maxilla is preserved, and no teeth are expected in this part (Roček personal communication 2007).

The scanning electron microscope was used extensively for illustrations and studies of surface texture.

Terminology used follows Sanchiz (1998).

PHYLOGENETIC BACKGROUND

No-one has ever seriously doubted the monophyly of Anura, and although the status of *Triadobatrachus* as a stem-frog has occasionally been challenged (*e.g.*, Hecht 1960), most authors accept also the monophyly of Salientia, including *Triadobatrachus*, and now *Czatkobatrachus*, along with crown-group Anura (*e.g.*, Duellman and Trueb 1986; Milner 1988; Rage and Roček 1989; Sanchiz 1999; Roček 2000; Carroll 2007; Anderson *et al.* 2008). There is also a general consensus that Salientia were derived from temnospondyl, or more precisely dissorophoid, ancestors (Bolt 1969, 1977, 1991; Bolt and Lombard 1985; Daly 1994; Milner 1988, 1990, 1993; Carroll 1999; but see Laurin and Reisz 1997; Laurin *et al.* 2000; Yates and Warren 2000; Anderson *et al.* 2008).

The monophyly of the Lissamphibia as a whole (Salientia, Caudata and Gymnophiona) was proposed by Parsons and Williams (1962, 1963), Szarski (1962), and Bolt (1969), and has been supported by many authors (*e.g.*, Milner 1988; Rage and Janvier 1982; Gauthier *et al.* 1989; Trueb and Cloutier 1991; Cannatella and Hillis 1993; Ford and Cannatella 1993; McGowan and Evans 1995; Gardner 2000). Others have rejected or questioned lissamphibian monophyly (*e.g.*, Shishkin 1973; Bolt and Lombard 1985; Carroll and Holmes 1980; Carroll 1999; Carroll *et al.* 1999), and the debate is ongoing. The recovery and description of early representatives of major lissamphibian lineages are clearly critical to the discussion of their ancestry.

SYSTEMATIC PALEONTOLOGY

Class **Amphibia** Linné, 1758

Order **Salientia** Laurenti, 1768

Family uncertain

Genus ***Czatkobatrachus*** Evans *et* Borsuk-Białynicka, 1998

Czatkobatrachus polonicus Evans *et* Borsuk-Białynicka, 1998

Holotype: ZPAL Ab IV/7, a right ilium.

Type horizon and locality: Olenekian karst deposits at Czatkowice Quarry (locality 1), Kraków region, Poland.

Material. — 76 catalogued specimens, including 15 presacral vertebrae, 2 sacral vertebrae, 9 scapulocoracoids, 11 humeri, 2 ulnae, 19 ilia, 5 femora.

Emended generic and specific diagnosis. — Small stem-frog (less than 50 mm snout-vent length) that resembles *Triadobatrachus* and all other salientians in having an anteriorly extended iliac shaft. It resembles

Triadobatrachus and differs from crown-group anurans in retaining relatively long neural arches, unfused epipodials, a series of unfused caudal vertebrae instead of an urostyle (Lynch 1973; Trueb 1973; Sanchiz 1998), a scapulocoracoid that is a single ossification, and an ilium with very strong dorsal prominence and a slender elongate shaft, rounded in cross-section. It differs from *Triadobatrachus* in having a long slender scapular blade (short and broad in *Triadobatrachus*), in having a single atlas ossification with no trace of rib facets (bipartite atlas with a rib processes reported in *Triadobatrachus* by Rage and Roček 1989, and Roček and Rage 2000, but see below for different view), in having a higher level of ossification, long fused posterior transverse processes and sacral ribs, fully ossified components in elbow joint, ischium fused to ilium (the last feature unique within the Salientia; Roček, personal communication 2007) despite its much smaller size, and in having longer, more slender limbs. As reconstructed, the ilio-sacral joint of *Czatkobatrachus* has a morphology quite distinct from that of *Triadobatrachus*, in that the sacral rib is short and fused to the vertebral centrum (rather than free and posteriorly elongate), and has an expanded distal end that is both dorsoventrally and anteroposteriorly bifurcate, with a posterior notch and groove. *Czatkobatrachus* also differs from *Triadobatrachus* and resembles many crown-group frogs in having a fully ossified, capitate eminence (*eminentia capitata*) that equals or exceeds 60% of the width of the distal end of humerus, and asymmetrical epicondyles (ulnar epicondyle larger). It differs from crown-group frogs in having the anterior margin of atlas pedicel notched for the exit of the first spinal nerve and spinal nerve notches or foramina in some posterior vertebrae, and in retaining an ossified remnant of the pubis, fused to the body of the pelvis and perforated by an obturator canal.

Occurence. — Only type locality.

VERTEBRAL COLUMN

The vertebral column of *Czatkobatrachus* is represented by isolated elements that have been ordered (Fig. 4B) partly on the basis of morphology (neural arch and centrum length, posterior zygapophysial size, transverse processes, and the presence or absence of free ribs) and partly by comparison with *Triadobatrachus* (Fig. 4A). On this basis, the atlas (Fig. 1), anterior, middle and posterior presacrals (Fig. 2), sacrals (Fig. 3), and caudals have all been identified. They are all fully ossified, and share a distinctive domed neural arch, a weak dorsal midline ridge, and a cylindrical perichordal (ectochordal) centrum perforated by a large unconstricted notochordal canal. The anterior zygapophyses are horizontal and vary in size along the column. Between them, the anterior border bears a deep V- or U-shaped notch that extends to the level of the base of the transverse processes. Behind the notch, there are bilateral depressions, some more marked than others, that mark the attachment of intervertebral muscles or ligaments. More posteriorly, the neural arch becomes strongly domed but curves down at the posterior margin. This posterior margin is usually slightly indented, but in the vertebrae immediately following the sacrum, it develops a small median process (Fig. 2C, G). The centrum is rounded in cross-section. Seen in anterior view, however, the lateral walls of the cylinder are usually thicker than the dorsal and ventral walls, giving the centrum a slightly depressed shape (see *e.g.*, Fig. 2A_1, C_1). In general morphology, the vertebrae closely resemble those of *Triadobatrachus*, except that the transverse processes, and in some cases the ribs, are fused to the vertebra rather than free. A few specimens (*e.g.*, ZPAL AbIV/6, Fig. 2A_1, A_2) show a bulbous region part way along the transverse process that marks the point of fusion, although subsequent remodelling apparently removes this to leave a single smooth, but actually compound, process.

Atlas. — Three atlantes have been recovered (ZPAL Ab IV/15, 112, and 126). None of these preserves a complete neural arch, but ZPAL Ab IV/126, the right half of an atlas, retains the neural arch pedicel and its posterior tip (Fig. 1B). The centrum is shorter than it is wide and fully notochordal. Anteriorly, the atlas bears paired, subcircular cotyles for the exoccipital condyles (Fig. 1A_2). As these surfaces are anterolaterally directed it suggests that the articular surfaces of the occipital condyles were themselves divergent. There is no interglenoid tubercle and the interglenoid region is perforated by an almost unconstricted notochordal canal (Fig. 1A_2, A_3). The neural arch pedicels are narrow but the edges are intact and are located at about the mid-length of the centrum. This centrum obviously corresponds to an intercentrum, even if the pleurocentrum contributed to its posterior part. There is no hint of the bipartite structure that has been interpreted for *Triadobatrachus* (Rage and Roček 1989), nor any trace of an atlantal rib (Fig. 1A). In ZPAL AbIV/126,

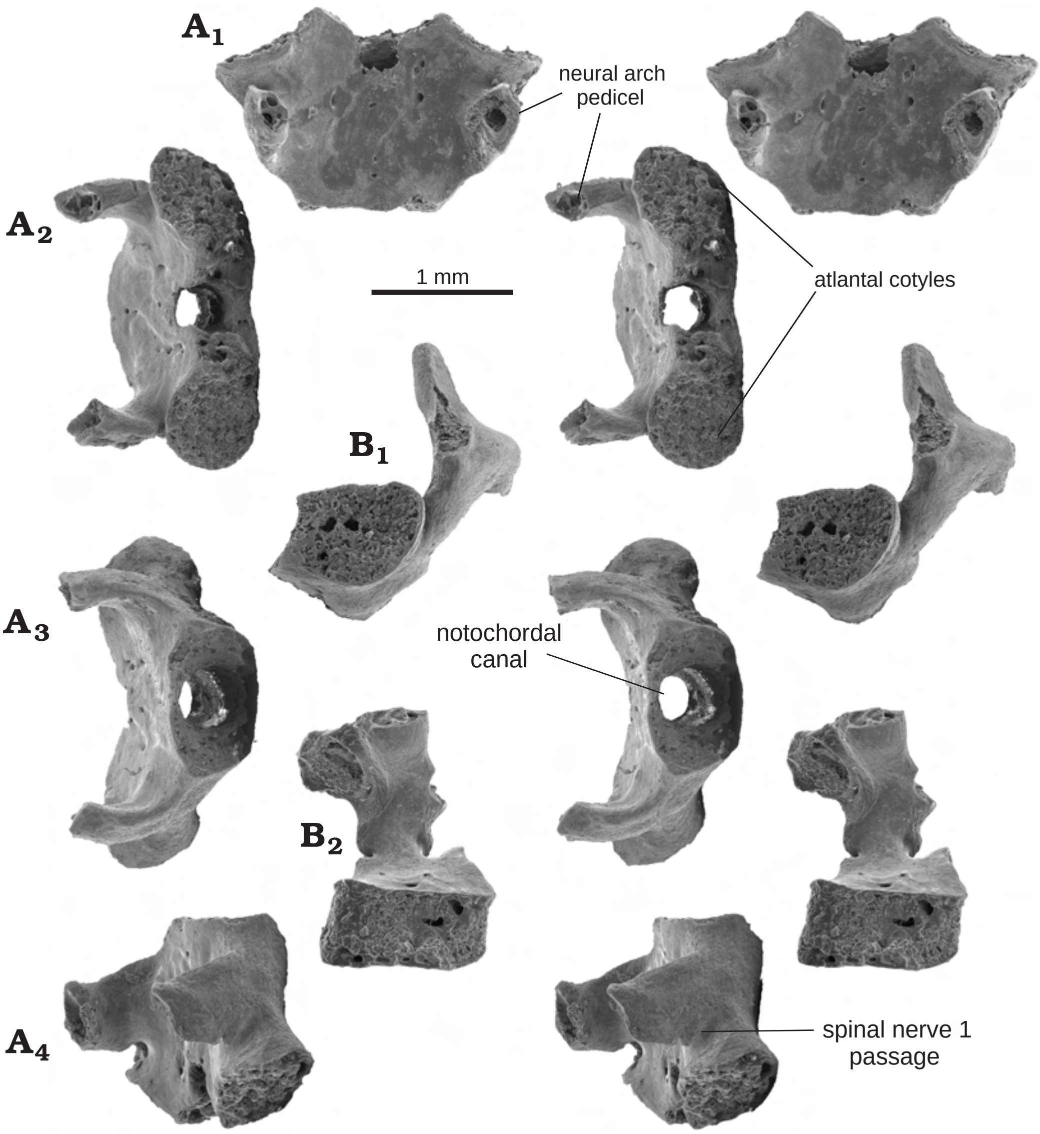

Fig. 1. *Czatkobatrachus polonicus* Evans *et* Borsuk-Białynicka, 1998, Early Triassic of Czatkowice 1, Poland. **A**. Atlas ZPAL Ab IV/15, in dorsal (A_1), cranial (A_2), caudal (A_3), and left lateral (A_4) views. **B**. Atlas ZPAL IV/126, in cranial view (B_1) and medial view of the left neural arch pedicel (B_2). SEM stereo-pairs.

the posterodorsal margin bears a postzygapophysis (Fig. 1B_2). Above and lateral to the cotyles the surface of the centrum bears a shallow groove that leads into a small notch in the anterior margin of the pedicel (Fig. 1A_4). This matches the groove and notch (or foramen) found in the atlas of most salamanders and caecilians for the passage of the first spinal nerve although this is the first time the condition has been recorded in a salientian. Ritland (1955a) describes the nerve as running in front of the arch and above the centrum in the modern *Ascaphus*, but no obvious canal or incision is shown in his fig. 2.

Postatlantal presacral vertebrae. — Given the general similarity between the vertebrae of *Czatkobatrachus* and *Triadobatrachus*, it is likely that the vertebral column was of similar length. Using the criteria listed above, the presacral vertebrae can be roughly divided into anterior, middle and posterior elements.

Anterior presacrals are represented by several specimens (*e.g.*, ZPAL AbIV/6, 108–110; Figs 2A, B, 4). They have centra and arches shorter (anteroposteriorly) than those that follow them. Their zygapophyses are expanded and the transverse processes are robust, ovoid in cross-section (longest axis dorsoventral), and end in a pitted surface to which a free rib would have been attached — although immovably. ZPAL AbIV/108 (Fig. 2B_2) is an example of this morphology, and would have been located in an anterior position (Fig. 4B). In crown-group frogs presacrals 2–4 usually bear enlarged transverse processes/ribs to provide support for

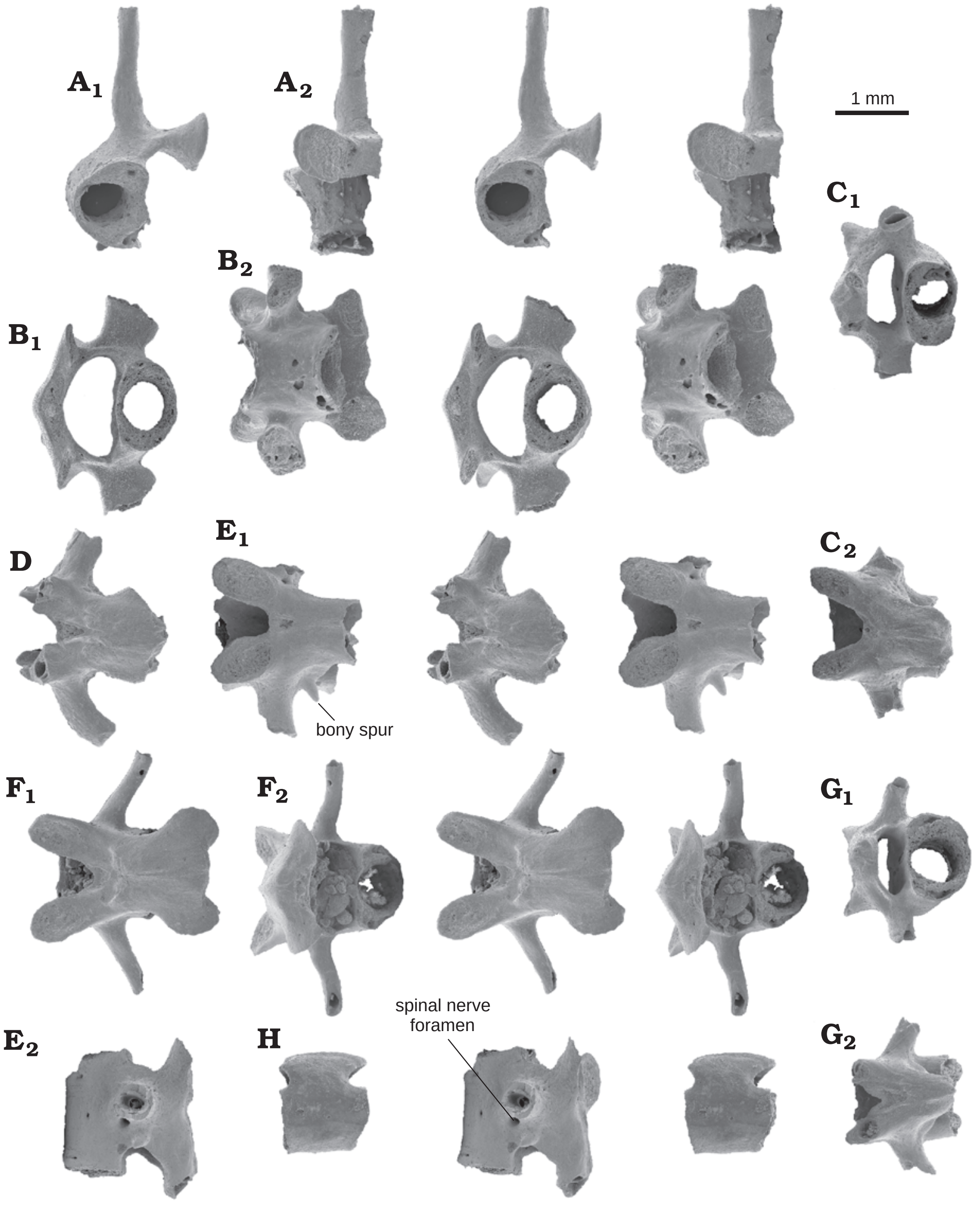

Fig. 2. *Czatkobatrachus polonicus* Evans *et* Borsuk-Białynicka, 1998, Early Triassic of Czatkowice 1, Poland. **A**. Anterior dorsal ZPAL Ab IV/6, in caudal (A_1) and dorsal (A_2) views. **B**. Anterior dorsal ZPAL Ab IV/108, in caudal (B_1) and ventral (B_2) views. **C**. Anterior caudal ZPAL Ab IV/135, in posterior (C_1) and dorsal (C_2) views. **D**. Posterior presacral ZPAL Ab IV/127, in dorsal view. **E**. Directly presacral or anterior caudal vertebra ZPAL Ab IV/115, in dorsal (E_1) and left lateral (E_2) views. **F**. Middle presacral vertebra ZPAL IV/128, in dorsal (F_1) and caudal (F_2) views. **G**. ?the second caudal vertebra ZPAL Ab IV/134, in caudal (G_1) and dorsal (G_2) views. **H**. Posterior caudal ZPAL AB IV/20, in left lateral view. SEM micrographs; all but C_1, C_2, G_1, G_2 stereo-pairs.

the pectoral girdle. Of these, the strongest rib/process is usually that of presacral 3 (*e.g.*, Ritland 1955a). The condition in the Malagasy stem-frog *Triadobatrachus* is similar although whether the vertebra bearing the largest rib is presacral 3 or 4 depends on the interpretation of the atlas as single or bipartite. According to our

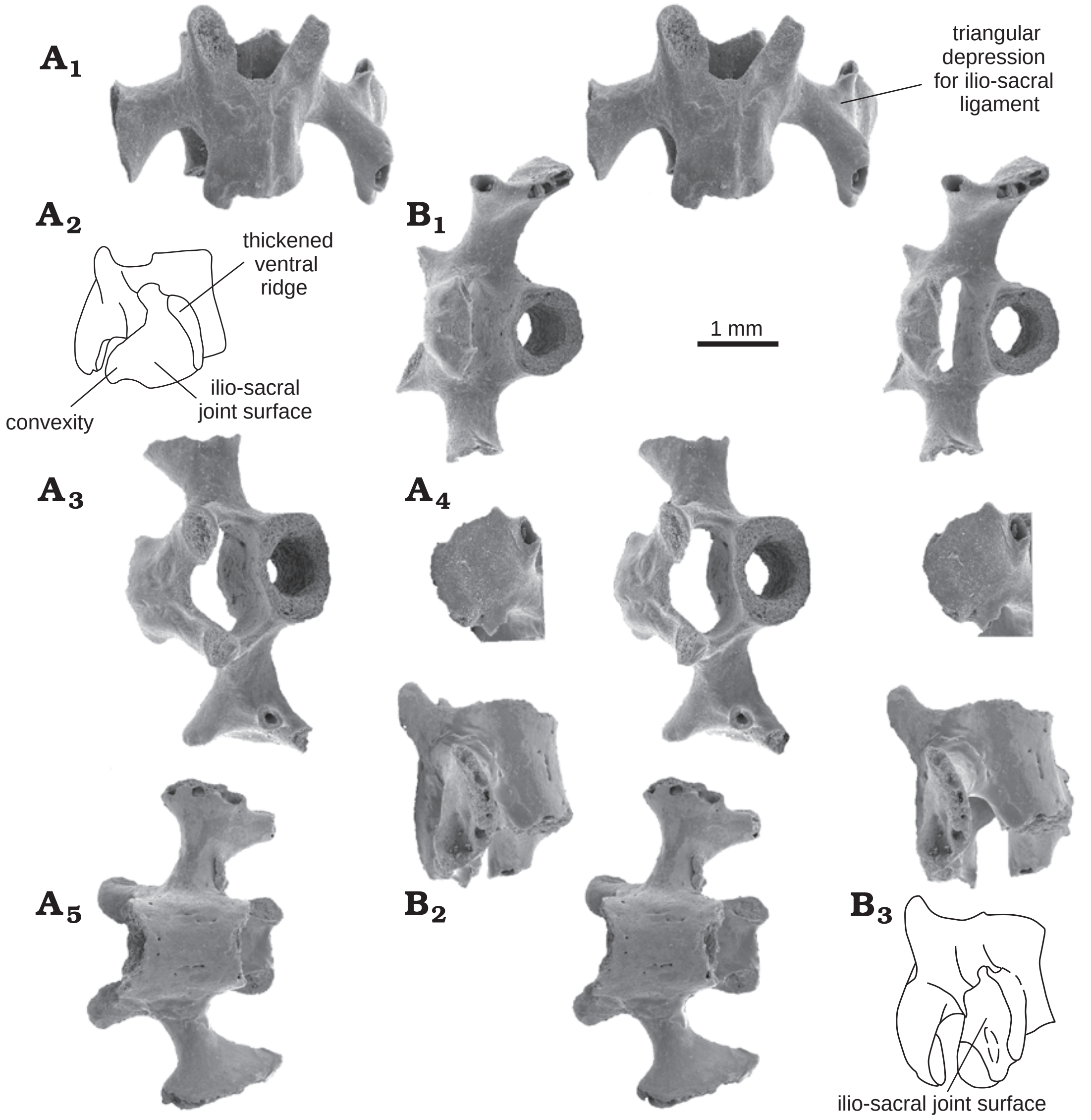

Fig. 3. *Czatkobatrachus polonicus* Evans *et* Borsuk-Białynicka, 1998, Early Triassic of Czatkowice 1, Poland. **A**. Sacral vertebra ZPAL Ab IV/79, in dorsal (A_1), caudal (A_3), and cranial (A_5) views; right iliac surface in lateral view (A_2, A_4). **B**. Sacral vertebra ZPAL Ab IV/76, in caudal view (B_1); right iliac surface in lateral view (B_2, B_3). All but A_2 and B_2 SEM stereo-pairs.

interpretation, it is presacral 4 (Fig. 4A). Amongst the Polish material, specimen ZPAL ABIV/6 bears the longest transverse process, probably including a fused rib. In the reconstruction (Fig. 4), this element has been located posterior to ZPAL AbIV/108, which had either the third or fourth position, the exact number of anterior vertebrae being unknown. The length of processes and their dorsoventral flattening suggest they supported the pectoral girdle as they do in crown-group frogs.

Strong bifurcate ribs and/or uncinate processes (Ritland 1955a) are found on the third presacral of the Jurassic *Vieraella* and *Notobatrachus* (Báez and Basso 1996), and isolated ribs of similar morphology have also been described and illustrated for the Jurassic *Prosalirus* (Jenkins and Shubin 1998). In the living *Ascaphus*, the second rib is generally the largest and possesses a sharp, posterolaterally directed uncinate process, but the fourth rib is sometimes equally large. This compares closely with the structure in *Leiopelma* (Ritland 1955a) and discoglossids, The bifurcations that relate to the attachment of muscles connecting the scapula to the spine (*m. serratus*, Ritland 1955a), have not been recorded in *Czatkobatrachus*.

A third set of vertebrae (*e.g.*, ZPAL AbIV/11, 14, 26, 128, and 146; for the latter two see Figs 2F, 4B) show a fairly consistent morphology and are the most common. The neural arch is longer than it is wide (unlike the more anterior presacrals), and this is matched by a slightly longer centrum. The transverse processes are shorter than those on ZPAL AbIV/6, are distally subcircular in section, vary in width, and are directed posterolaterally. The anterior zygapophyses vary slightly in shape, but seem to have decreased in size towards the rear of the column.

A fourth group of vertebrae, *e.g.*, ZPAL AbIV/8 and10, tentatively considered a sacral by Evans and Borsuk-Białynicka (1998, fig. 3B, E), and ZPAL AbIV/127 (Fig. 2D) is characterised by a somewhat shorter arch and centrum than those of the mid-trunk, smaller postzygapophyses that are closer to the midline (distinguishing them from anterior presacrals) and a more robust posteriorly curved transverse processes probably with no free ribs contacting them. We interpret these elements as posterior presacrals.

ZPAL AbIV/115 (Fig. 2E) has two unusual features. The first is a small additional bony spur (Fig. $2E_1$) on the left side between the transverse process and the posterior margin of the pedicel (on the right only a slight tuberosity). The second is the presence of a distinct foramen, possibly for a spinal nerve, perforating the neural arch pedicel on each side behind the transverse process (Fig. $2E_2$). From its morphology, this vertebra is a posterior presacral or an anterior caudal (Fig. 4B). Rage and Roček (1986) reported that such foramina were not visible in *Triadobatrachus*.

Sacrum. — Two almost complete sacral vertebrae have been recovered, ZPAL AbIV/76 and 79 (Fig. 3B, A), and ZPAL AbIV/123. The main body of the bone is slightly shorter than that of the presacrals, but is otherwise similar in morphology. The arch has a low midline ridge and is slightly domed (Fig. $3A_1$). The horizontal anterior zygapophyses are ovoid, long axis slightly divergent, and the U-shaped notch more open than in presacrals (Fig. $3A_1$). Postzygapophyses are present (as in some basal frogs, *e.g.*, *Ascaphus*, Ritland 1955a) but small and more closely placed than in most presacrals. The centrum is spool-shaped like those of other vertebrae and shows a normally developed posterior joint surface (*i.e.*, no specialised sacro-caudal articulation). The notochordal canal continued into the tail (Fig. $3A_3$, B_1).

In spite of variation (see below), the basic, highly unusual, morphology of the sacral transverse processes (diapophyses) is the same. The processes are short and strong, proximally almost circular in cross-section, but they expand and bifurcate distally, in both dorsal and anterior/posterior views (Fig. $3A_1$, A_3, B_1). The posterodorsal margin of the process extends first laterally and then curves strongly posteriad (to be continued further in cartilage, as shown by a pitted, unfinished surface). The anteroventral margin of the process angles slightly posterolaterally and then curves anteriad. Between these margins, the dorsolateral surface of the process bears a triangular depression (or furrow) that opens outward into a large distal concavity facing laterally (Fig. $3A_1$) or dorsolaterally (Fig. $3B_2$, B_3). The concavity creates a subhorizontal passage oriented anteroventrally, and open posteriorly (Fig. $3A_2$, B_3), that could have admitted the anterior tip of the ilium (the diameter of which is consistent). It is bordered ventrally by the thickened, shelf-like edge of the process and posterodorsally by a convexity (Fig. $3A_2$, A_4, B_2). However, its surface is completely smooth, without the pitting that characterises a surface bearing joint cartilages (*e.g.*, that of the pelvic acetabulum). Rather, the morphology suggests that the tip of the ilium was suspended in position by ligaments, the chief of which ran from the dorsomedial surface of the transverse process in the triangular depression noted above (as in the type IIA iliac suspension of Emerson 1979). A small anterior tubercle may have limited forward movement (Figs $3A_4$, B_2, $4C_2$). However, given the importance of sesamoid cartilages in the ilio-sacral articulation of extant frogs (Emerson 1979, 1982), there is a possibility that the distal concavity of the sacral processes included a sesamoid which allowed a more anterior position of the ilium (Fig. $4C_1$) or a shift of the ilium shaft relative to the sacrum. The position of the iliac facet varies (see above) from directly lateral facing (Fig. $3A_1$, the distal flange particularly broad dorsoventrally Fig. $3A_2$), to dorsolateral (Fig. $3B_2$, the distal flange dorsoventrally less extensive Fig. $3B_3$), However, according to Ritland (1955a, p. 138), "no other parts of the skeleton of *Ascaphus* are subject to greater variation than the sacrum and the coccyx", and the variability of the sacral processes in *Czatkobatrachus* is most probably intraspecific. There is nothing to suggest a ventral position of the ilium joint with respect to the sacrum in *Czatkobatrachus*, but the arrangement of the iliosacral joint offers a perfect transitional stage towards an eventual position of the ilium ventral to the sacrum. Aquisition of this ventral position was an important element in the evolution of the anuran locomotor apparatus (Shubin and Jenkins 1995), already present in the Early Jurassic species *Prosalirus bitis*. The arrangement of the ilio-sacral joint was markedly different from that reconstructed for *Triadobatrachus* (Rage and Roček 1986) in which the ilium simply abuts the lateral surface of a sacral transverse process that is not fused to the body of the vertebra. In its larger size (relative to body size), the complete fusion of the sacral ribs, and the larger, more complex, ilio-sacral contact, the sacrum of *Czatkobatrachus* appears to be better adapted to terrestrial locomotion.

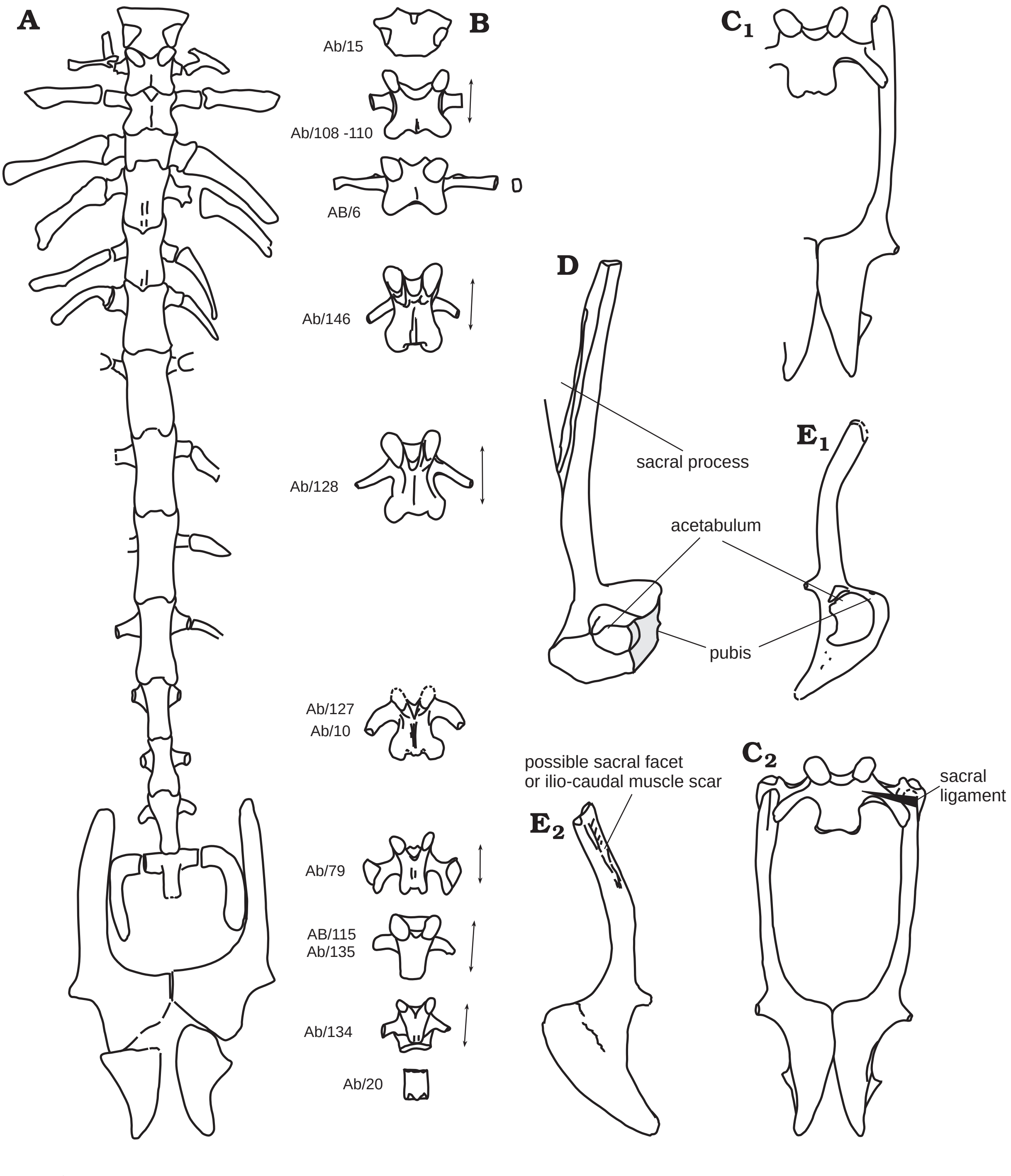

Fig. 4. **A**. *Triadobatrachus massinoti* (Piveteau, 1936), Early Triassic of Madagascar. Vertebral column with pelvis according to Rage and Roček (1989) with a hypothesised reinterpretation of two anterior cervicals based on *Czatkobatrachus* structure. **B**, **C**, **E**. *Czatkobatrachus polonicus* Evans *et* Borsuk-Białynicka, 1998, Early Triassic of Czatkowice 1, Poland. **B**. Vertebrae arranged in natural sequence. **C**. Possible sacro-pelvic configuration with a connective tissue pad filling up the distal concavity of the sacral transverse process (C$_1$), the same with the distal end of the ilium located in the concavity (C$_2$). **E**. Reconstruction of right innominate bone, in lateral (E$_1$) and medial (E$_2$) views. **D**. *Pelobates fuscus* ZPAL Ab III/6, Recent, right innominate bone and sacral process in lateral view. All but D, E in dorsal view.

Caudal series. — In all crown-group frogs, the caudal vertebrae are fused into an elongated urostyle, although some (*e.g.*, the Jurassic *Notobatrachus*) are recorded as retaining one free caudal vertebra behind the sacrum (Báez and Basso 1996) and the condition occurs as a variant in the living *Ascaphus* (Ritland 1955a). In *Triadobatrachus*, however, the caudal vertebrae are unfused and form a short series of at least

6 small vertebrae showing a sharp posterior decrease in diameter and a reduction in the neural arch and transverse processes. Posterior caudals are thus little more than double cylinders. We have recovered two kinds of caudal element from Czatkowice 1 (*e.g.*, ZPAL AbIV/134, 135, and 20; Evans and Borsuk-Białynicka 1998; Fig. 2C, G, H, respectively), and we interpret *Czatkobatrachus* as having had a short tail like that of *Triadobatrachus*, rather than a urostyle. Anterior postsacrals (*e.g.*, ZPAL AbIV/134 and 135, Fig. 2C, G) resemble posterior presacrals in having a relatively short arch and centrum and a thickened transverse process, but differ in that the postzygapophyses are even smaller and lie close to the midline on a tapering posterior spur. Further posteriorly, the transverse processes are reduced and then lost. As represented by ZPAL AbIV/20 (Fig. 2H), posterior caudals also lack anterior or posterior zygapophyses, and their anteriorly and posteriorly tapering arches would have been held together by ligaments.

The robustness of the transverse processes of the vertebrae immediately in front of and behind the sacrum suggests they were involved in some way with the support of the ilium, perhaps providing additional attachment points for stabilising ilio-lumbar and sacro-coccygeal musculature (Emerson and de Jongh 1980).

PECTORAL GIRDLE AND LIMB

Scapulocoracoid. — The pectoral girdle of *Czatkobatrachus polonicus* has been described in detail elsewhere (Borsuk-Białynicka and Evans 2002), but its morphology is summarised here for completeness.

The bone is represented by many fragmentary specimens, the most complete of which is ZPAL AbIV/26 (Fig. 5A). It is a single ossification and consists of a subtriangular ventral plate and a narrow blade that widens distally along its vertebral border to about twice the proximal width, although no specimen has the distal end preserved. The scapular blade is unusually long and slender (ZPAL AbIV/29, Fig. 5B). In life, it was inclined posterodorsally, its axis making an angle of about 65° with the long axis of the coracoid plate.

A large glenoid cavity occupies much of the postero-ventral region of the scapulocoracoid, extending well posteriorly. It is subcircular in outline, much deeper dorsoventrally than is usual in lower tetrapods, and is hemispherical rather than funnel shaped (in contrast to urodeles). It faces directly laterad, in contrast to the posterolateral orientation in non-lissamphibian temnospondyls. A distinct anteroventral glenoid tubercle seems to belong to the scapular component of the glenoid and contributes a small articular surface to its anteroventral border.

Anterodorsal to the glenoid is a large supraglenoid foramen that forms a subvertical cleft partly separating the glenoid region of the scapula from its acromial part, homologous and similar in position to the scapular cleft of Anura (Borsuk-Białynicka and Evans 2003; Carroll 2007). The acromial part is a long, laterally (or slightly anterolaterally) flattened process extending ventrally from the scapula, of which it is an integral part. Ventral to the supraglenoid foramen, the acromial process fuses with the procoracoid part (anteroventrally), and with both the scapular and coracoid parts of the glenoid (posteroventrally). Separating the procoracoid region from the coracoid, the supracoracoid foramen leads into a short canal directed toward the supraglenoid foramen. Both open on the medial surface of the scapula in the subscapular fossa. The procoracoid region faces almost laterally, but the coracoid itself turns ventromedially to lie at an angle of about 110° to the plane of the scapula. Its ventromedial margin ends in a strip of unfinished bone that would have been continued in cartilage in life Fig. 5C), rather than forming a transverse bar as it does in anurans. The retention of the supracoracoid foramen, which is included within the scaphoid fenestra in anurans, provides further evidence that an independent coracoid bar was not yet developed. Furthermore, it suggests that the arciferal contact of the *Czatkobatrachus* scapulocoracoids was of a caudate rather than anuran pattern. No clavicles have been identified for *Czatkobatrachus*, but they were probably present, given the high degree of ossification of the skeleton, and their retention in *Triadobatrachus* (Rage and Roček 1989). These elements have been lost in caudates, but in arciferal frogs, clavicles are necessary to retain the structural integrity of the girdle, given the mobility of the epicoracoid cartilages with respect to each other during locomotion (Emerson 1983). Their possible role in *Triadobatrachus* and *Czatkobatrachus* remains obscure.

Humerus. — The humerus was one of the first bones to be recognised for *Czatkobatrachus* because it is characteristically salientian. The majority of specimens preserve only the distal ends (*e.g.*, ZPAL AbIV/2–3, 12–13, and 55), but ZPAL Ab IV/78 is a complete humerus that permits a detailed description and also a discussion of forelimb-hind limb ratios.

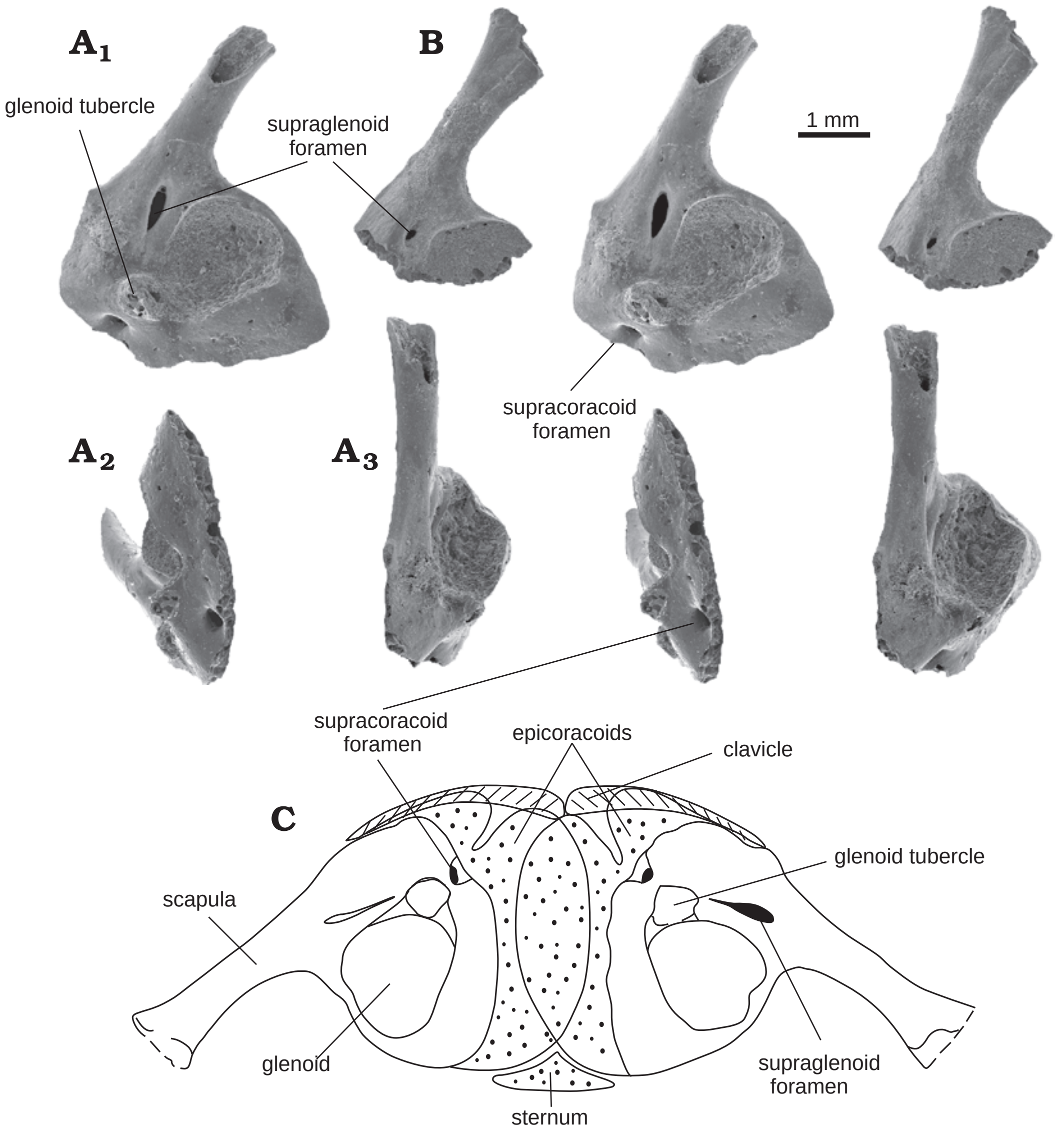

Fig. 5. *Czatkobatrachus polonicus* Evans *et* Borsuk-Białynicka, 1998, Early Triassic of Czatkowice 1, Poland. **A**. Left scapulocoracoid ZPAL Ab IV/26, in lateral (A_1), ventral (A_2), and anterior (A_3) views. **B**. Left scapula ZPAL AB IV/29, in lateral view. **C**. Reconstruction of pectoral girdle in ventral view. All but C SEM stereo-pairs.

ZPAL AbIV/78 (Figs 6 and 7A) is a complete left bone roughly 11 mm in length and a little over 0.5 mm in width at its narrowest point. The proximal and distal ends are gracile, separated by a long and slender shaft. The proximal end has a dorsoventrally flattened terminal condyle that is much more tightly co-ossified with the shaft than is usual in extant frogs (*e.g.*, *Rana*, *Bufo*, and *Pelobates*). A ventral humeral crest (*crista humeralis ventralis*; of Sanchiz 1998) is present but is very low both proximally and distally. However, in the extant *Rana* the proximal part of the crest is intimately connected with the articular condyle, protruding over it proximally, and sharing its delayed ossification. No such connection is evident in *Czatkobatrachus*, but the crest looks proximally unfinished. The relative weakness of the crest may reflect the size of the associated musculature. The muscles that attach to the crest (*mm. pectoralis*, *deltoideus*, *coracobrachialis*, *supracoracoideus*, *scapulohumeralis*, *dorsalis scapulae*, *latissimus dorsi*; Ritland 1955b) are mostly postural muscles, supporting the body in standing. If the body was light, strong musculature may not have been necessary. The scars of the pectoralis muscle — on the crest edge, and that of the deltoideus, on the anterior side of the crest, are the only ones tentatively recognized here (Fig. 6B_1, C) on the basis of *Ascaphus* structure (Ritland 1955a).

The humeral shaft is circular in cross-section, but is otherwise featureless. It expands gradually into a slender distal end. Ventrally there is a large capitate eminence (65% or more than the total width of the distal

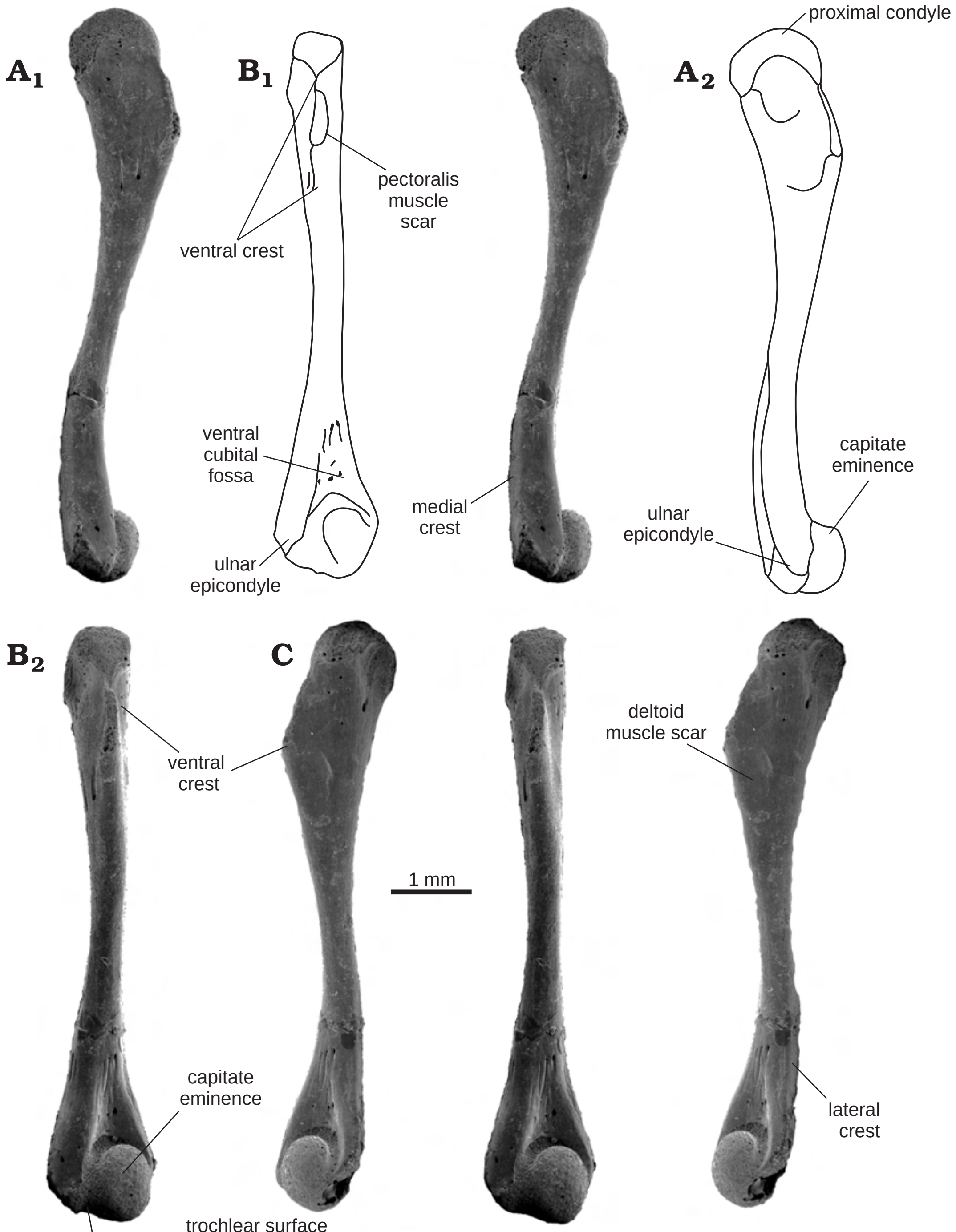

Fig. 6. *Czatkobatrachus polonicus* Evans *et* Borsuk-Białynicka, 1998, Early Triassic of Czatkowice 1, Poland. Left humerus ZPAL Ab IV/78, in posterior = medial (A), ventral (B), and anterior = lateral (C) views. A_1, B_2, C, SEM stereo-pairs.

end). The remaining some 35% of the distal end is occupied by the ulnar epicondyle, contacting the eminence ventrally through a small trochlear surface (Figs 6B, $7A_3$). Dorsally, there is a short triangular olecranon scar (Fig. 7B). The radial epicondyle — the site of origin of many extensor muscles (*e.g.*, *mm. extensor carpi radialis*, *extensor carpi ulnaris*, *extensor digitorum communis longus*), is very small (suggesting weak extensor muscles) while the ulnar epicondyle (mostly for flexor muscles) is more prominent. These differences may relate to sexual behaviour (amplexus) and may be subject to sexual dimorphism (Roček, personal communication 2007). The longitudinal medial and lateral distal muscle crests are quite feeble (Fig. 6A, C), and thus the forelimbs were probably not heavily muscled.

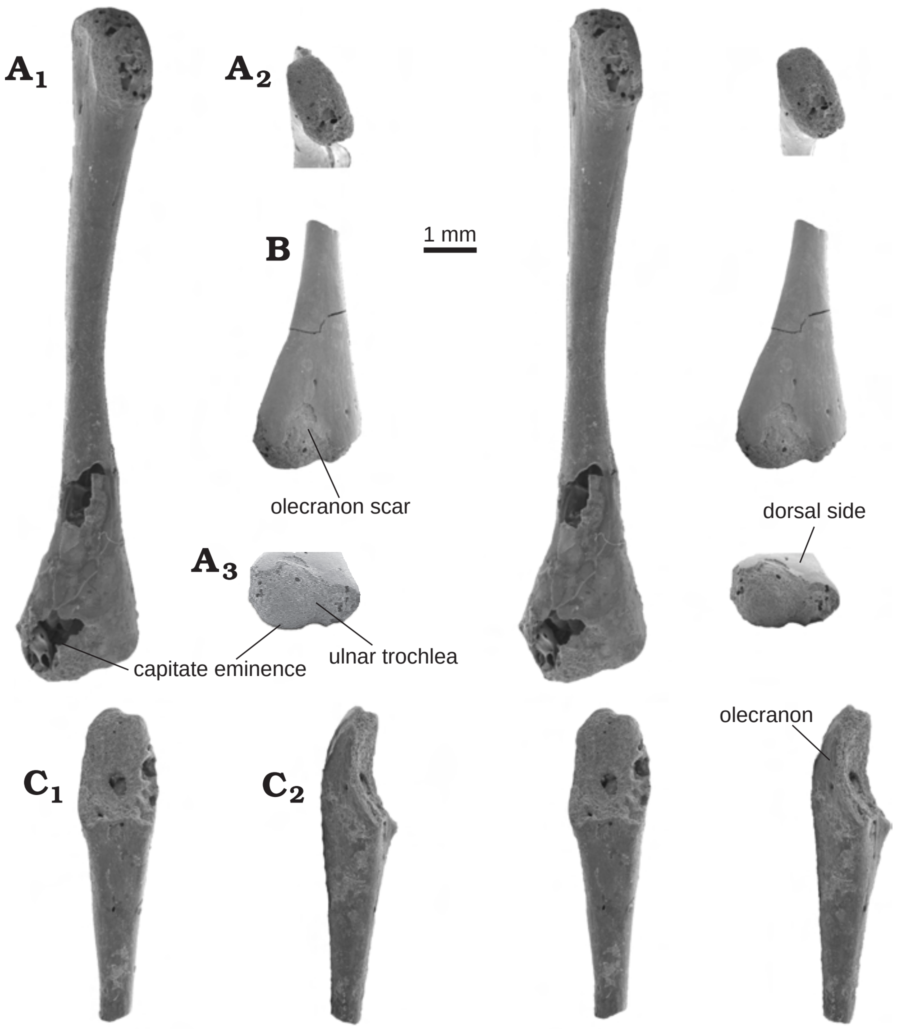

Fig. 7. *Czatkobatrachus polonicus* Evans *et* Borsuk-Białynicka, 1998, Early Triassic of Czatkowice 1, Poland. **A**. Left humerus ZPAL Ab IV/78, in dorsal view (A_1), proximal end (A_2), and distal end (A_3). **B**. Distal part of the left humerus ZPAL Ab IV/55, in dorsal view. **C**. Ulna ZPAL Ab IV/22, in anterior (C_1) and lateral (C_2) views. SEM stereo-pairs.

Antebrachium. — The ulna of *Czatkobatrachus* is represented by three specimens of the proximal end (*e.g.*, ZPAL AbIV/22, Fig. 7C). Like the humerus, the bone is well ossified with a strong elongated olecranon process, providing the lever arm for the triceps muscle (*m. anconeus*; Duellman and Trueb 1986) and a concave articular surface for the humeral articulation. The elbow joint seems to have been stable. No radius has been recognized as yet.

PELVIC GIRDLE AND HIND LIMB

Pelvic girdle. — The pelvic girdle of *Czatkobatrachus* is represented by many distinctive ilia (some 18 specimens), some specimens having the puboischiadic plate fused in place (*e.g.*, ZPAL AbIV/111 and 129; Fig. 8D and B, respectively). At the time of the original description (Evans and Borsuk-Białynicka 1998), the most complete ilium was the holotype, ZPAL AbIV/7, but more complete specimens have been found subsequently. ZPAL AbIV/114 (Fig. 8A) is one of the most complete, the delicate iliac shaft usually breaking at or close to its junction with the acetabular region. The acetabular region is expanded, with a large shallow lateral acetabular surface, little development of a supra-acetabular buttress, and no extension of the anterior or posterior acetabular margins (into *partes descendens* or *ascendens*; Sanchiz 1998). The medial surface is smooth with no trace of an interiliac synchondrosis. The most obvious feature is a large protruding dorsal prominence (also present in *Triadobatrachus*; Rage and Roček 1989, fig. 3) for the gluteus magnus muscle or

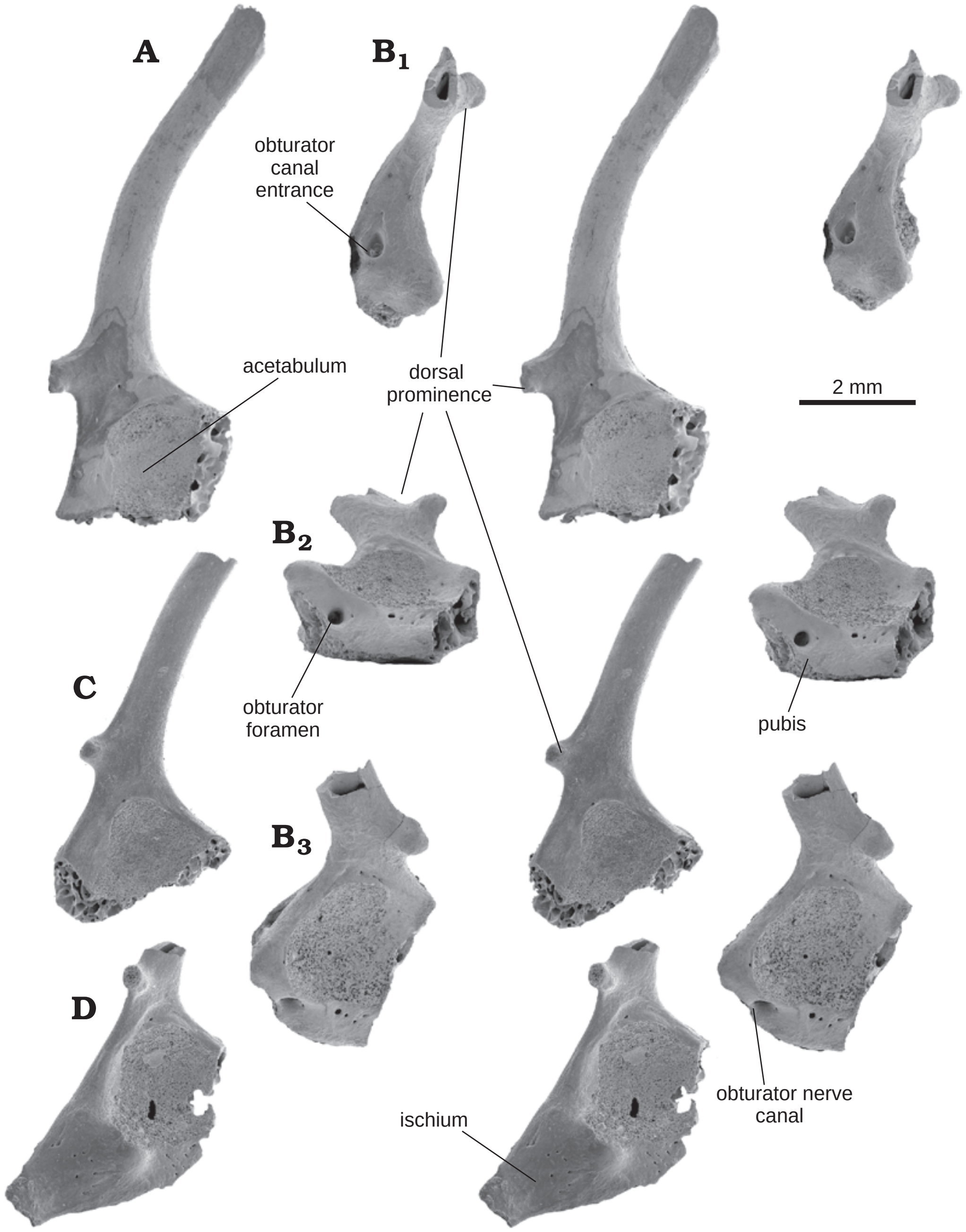

Fig. 8. *Czatkobatrachus polonicus* Evans *et* Borsuk-Białynicka, 1998, Early Triassic of Czatkowice 1, Poland. **A**. Right ilium ZPAL Ab IV/114, in lateral view. **B**. Left acetabulum ZPAL Ab IV/129, with proximal part of ilium and pubis preserved, in anterior (B_1), medial (B_2), and reversed lateral (B_3) views. **C**. Right ilium ZPAL Ab IV/54, in lateral view. **D**. Right acetabulum ZPAL Ab IV/111 with proximal part of ilium and ischium preserved, in lateral view. SEM stereo-pairs.

for its accessory tendon (Ritland 1955b; Duellman and Trueb 1986). The iliac shaft is somewhat longer than that of *Triadobatrachus* (6.5 *versus* 4.9 times dorsal vertebral lengths), and is more slender. The shaft is ovoid in cross section with no traces of either crests or rugosities, except for a faint trace on the dorsomedial side of the distal end (Fig. $4E_2$), left by the sacral transverse process or by the ilio-caudal muscle. As described for *Triadobatrachus* (Rage and Roček 1989, p. 11), the end of the shaft is open and hollow. It was presumably completed by a cartilaginous plug or extension of some form.

Specimens ZPAL AbIV/16, 111, and 129 add further to our knowledge of pelvic structure, and in combination with the ilia permit a complete reconstruction of the pelvis. ZPAL AbIV/129 (Fig. $8B_3$) preserves the almost square anteroventral tip of the pelvic plate. This is thickened in anterior view (Fig. $8B_1$) and grooved. In the upper part of the groove, hidden in direct medial view, there is a large foramen. This leads into a short

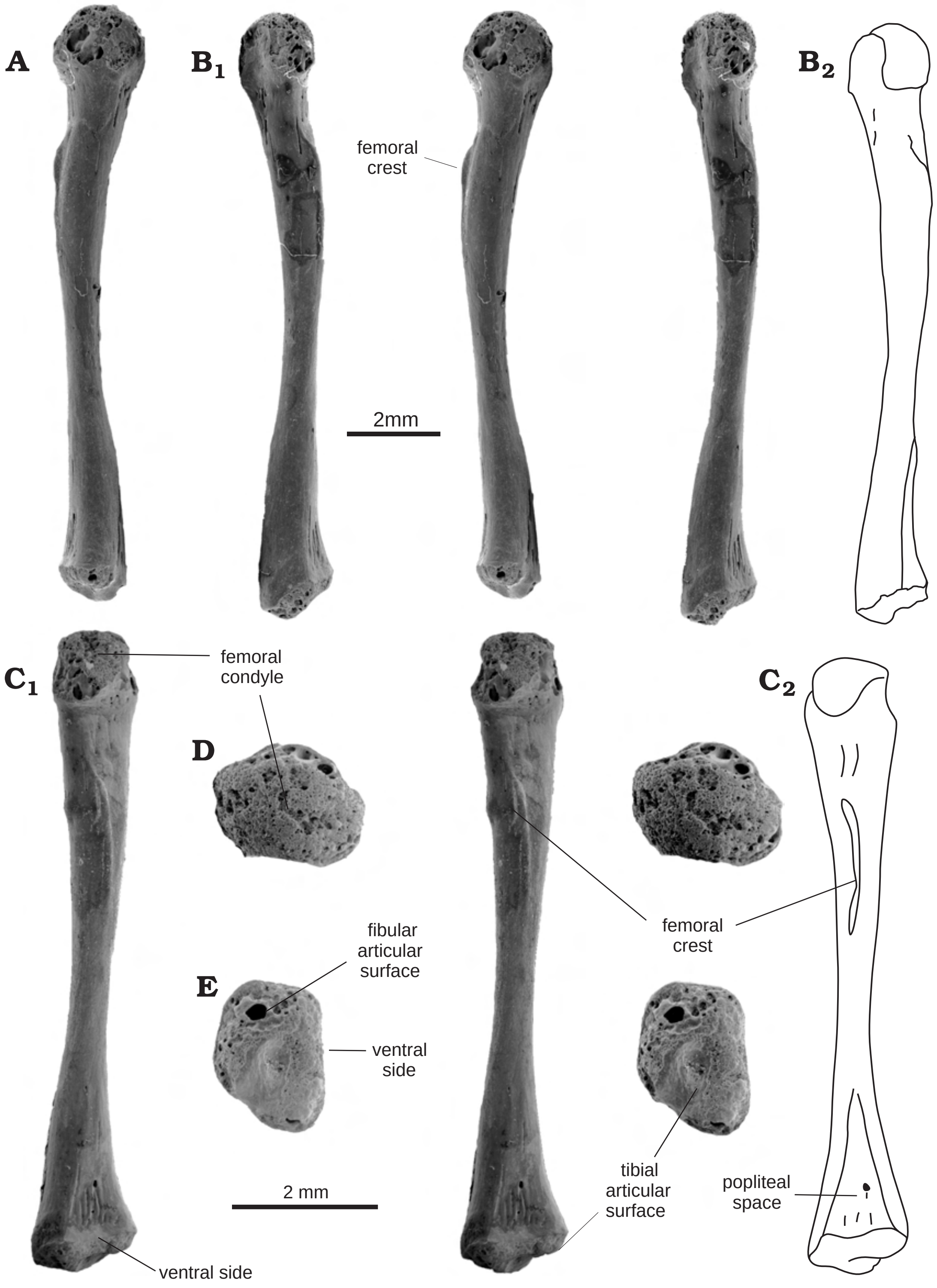

Fig. 9. *Czatkobatrachus polonicus* Evans *et* Borsuk-Białynicka, 1998, Early Triassic of Czatkowice 1, Poland. Left femur ZPAL AB IV/25, in anterior (A), posterior = lateral (B), ventral (C), proximal (D), and distal (E) views. All but B_2, C_2 SEM stereo-pairs.

canal that runs through the anterior pelvic margin at roughly 45 degrees and emerges on the lateral surface (Fig. $8B_3$) just below the anterior rim of the acetabulum. This canal is not present in crown-group anurans and is not described for *Triadobatrachus*, but from its course and position must have carried the obturator nerve and blood vessels from out of the pelvic cavity. In non-lissamphibian temnospondyls and amniotes, this canal perforates the pubis, suggesting that the anterior corner of the pelvic plate in *Czatkobatrachus* is an ossified remnant of this bone (cartilaginous in crown-group frogs), not a calcified prepubis as found in

Ascaphus and *Xenopus* (Ritland 1955a). Posteriorly, ZPAL AbIV/16 (not figured) and 111 (Fig. 8D) preserve the almost complete posteroventral, ischiadic part of the pelvic plate. They show that the acetabular surface is not rounded in the complete pelvis but instead has a posterior triangular extension formed by the ischium. This, in turn, suggests that there was an anteroposterior component to the femoral movement as well as the dorsoventral one. The triangular ischium closely resembles the same element in *Triadobatrachus*, except that the ischium is free from the rest of the pelvis in the Malagasy genus.

In crown-group frogs, the two halves of the adult pelvis meet posteroventrally at a steep angle, with a deep synchondrosis of the pubo-ischiadic plate that may or may not extend to the base of the ilium. As described by Green (1931) for *Rana*, this synchondrosis deepens gradually during development, with only the edges of the pubo-ischiadic plate meeting initially but then incorporating more and more of the plate until the two halves are completely fused. This articulation is not discussed for *Triadobatrachus* (Rage and Roček 1989). The only visible articular surface on the pubo-ischiadic plate of the Polish form is a recessed pitted strip along the ventromedial margin (Fig. 8B_2). The two pelvic plates clearly met at an angle (a horizontal orientation would render the pelvis too wide), but with a relatively weak synchondrosis, like that of the larval *Rana*.

Femur. — The only hind limb element to be identified with any certainty is the femur (Fig. 8), but a second element closely matches the fibulare (Fig. 10) of modern frogs. No conjoined tibiofibulae have been recovered. Since these are among the most characteristic and common frog elements preserved in microvertebrate assemblages, we are confident that in *Czatkobatrachus*, as in *Triadobatrachus*, these two bones were not fused.

The femur is represented by two complete specimens, ZPAL AbIV/25 (Fig. 9) and 125, and several fragments. By comparison with the modern *Bufo punctatus*, the complete specimens are both right femora. However, the attribution of femora to right or left can be somewhat problematic, because of the lack of landmarks, and the variability of bone curvature in extant frogs. In *Rana*, the bone is S-shaped in a dorso-ventral plane, but is curved in both dorso-ventral and lateral planes in *Bufo*, and in only one plane in *Pelobates*. Perhaps the type of locomotion, and the size have a bearing on this character, but the relationships are obscure. In *Czatkobatrachus*, the femur is only slightly bowed dorsoventrally (dorsally concave Fig. 9A, B), and probably twisted, the axes of the ends being subperpendicular to each other. The torsion is less obvious in *Bufo* but is difficult to observe in extant frogs because their epiphyses are usually lost. In contrast to them, *Czatkobatrachus* femora have completely fused epiphyses and their articular surfaces are at least partly finished (although in life they were certainly coated with articular cartilage).

ZPAL Ab IV/25 (Fig. 9) is long and slender, ca. 12.5 mm in total length with small proximal and distal ends of equal width (ca. 2 mm). The shaft is 0.8 mm at its narrowest point. The femur is thus only slightly longer than the humerus and of very similar proportions. The proximal end bears a proximally convex, slightly bilaterally flattened, condyle (Fig. 9D). The femoral crest (corresponding to the trochanter) extends down the ventral surface beginning proximally from a point about 1/5 of the femoral length and fading out at about 3/5 femoral length. By comparison with extant frogs (*Ascaphus* as illustrated by Ritland

Fig. 10. *Czatkobatrachus polonicus* Evans *et* Borsuk-Białynicka, 1998, Early Triassic of Czatkowice 1, Poland. Possible fibulare ZPAL Ab IV/138, in proximal (A) and lateral (B) views. SEM stereo-pairs.

1955a, b), the crest is for the attachment of hip muscles (*mm. pectineus*, *gluteus minimus*, *iliofemoralis*, *pyriformis*, *quadratus femoris*, and *obturator externus*; Ritland 1955b). The distal end has its surface differentiated (Fig. 9E). By comparison with a *Bufo* femur, a large concavity in the anteroventral part of distal surface was probably for the tibia, whereas a second, posterior, convexity articulated in some way with the fibula. As noted above, there is no evidence that the crural bones were fused.

Possible additional element. — ZPAL AbIV/138 (Fig. 10) is a long bone of similar overall morphology and bone type (density and surface texture) to that of the other limb elements of *Czatkobatrachus*, but it is much shorter than either the humerus or femur (roughly 45% of the femoral length). Like the femur, the shaft is bowed, with one edge almost straight and the other strongly concave. Both heads are compressed, with a possible distal head broader than the proximal one. This bone does not show any obvious match to either of the epipodials in *Triadobatrachus* (and is relatively shorter) or modern frogs (where they are rounded but always co-ossified), although it does show some resemblance to the epipodials of salamanders. The closest match in a modern frog is to the fibulare, one of the two ankle bones that become elongated in crown-group frogs. These bones are apparently only slightly elongated in *Triadobatrachus* so their extension in *Czatkobatrachus* would represent an advance, although it would be consistent with the generally longer and more gracile limbs of the Polish form.

CHARACTER ANALYSIS

Axial length. — Crown-group frogs are characterised by a very short vertebral column (typically 6–9 presacrals, Griffiths 1963; Kluge and Farris 1969; Lynch 1973). The number of presacral vertebrae in *Czatkobatrachus* but it was probably similar to that of *Triadobatrachus* (14–15), because their vertebrae are very similar both in length and morphology. If this is correct, then the body axis of basal salientians was much shorter than that of many outgroup taxa (*e.g.*, 19–24 in branchiosaurs, Boy and Sues 2000), a shortening that would have involved a reduction in the number of trunk somites (Richardson *et al.* 1998). The recently described amphibamid *Gerobatrachus* has 17 presacrals, intermediate between the primitive condition and that in basal salientians (Anderson *et al.* 2008).

The first spinal nerve. — The notch in the anterior margin of the atlas in *Czatkobatrachus* is reminiscent of the morphology of crown-group salamanders (but not stem taxa) and caecilians. In salamanders and caecilians the atlantal foramen transmits a spinal nerve, but the identity and homology of this nerve is still disputed. According to Duellman and Trueb (1986), the first spinal nerve (here called the transatlas nerve to avoid confusion later) emerges through the atlas in salamanders, but between the atlas and second presacral in frogs. Deuchar (1975), however, argued that the disposition of the anterior spinal nerves in frogs is similar to that in salamanders, the difference being that the first nerve (between the occiput and atlas; sometimes called the suboccipital nerve, *e.g.*, Mookerjee 1930, 1931; Fox 1954) usually gets lost in anuran metamorphosis. Whether this nerve really exists in frogs, and which nerve, if any, is its equivalent in salamanders and caecilians is a problem on which *Czatkobatrachus* structure sheds some light. This, however, requires a brief diversion into cranial embryology.

In the embryonic amphibian head, there are four segments (somitomeres) (Jacobson 1993 and personal communication 2003), three preotic and one subotic. These are followed by two postotic somitomeres that become the first two somites. A preoccipital arch forms between the first and second of these (somitomeres 5 and 6), the occipital arch forms between the second and third somite (somitomeres 6 and 7), and the atlas arch forms between the third and fourth somites (somitomeres 7 and 8) (Goodrich 1911; Wake and Lawson 1973).

According to Jacobson (1993) the first spinal nerve emerges from the third somite, and thus at the level of the anterior part of the atlas (see Burke *et al.* 1995 for different opinion). Francis (1934) claimed that salamanders had a still more anterior nerve (in front of the atlas, in addition to the transatlas nerve), equivalent, according to him, to the suboccipital nerve, and thus to the spinal nerve 1. The transatlas nerve would thus correspond to spinal nerve 2 (although Francis chose to designate it as spinal nerve 1 as it was the first nerve visible in the adult). However, Wake and Lawson (1973) found no evidence for the existence of any nerve in front of the atlas in salamanders, and identified the suboccipital nerve with the transatlas nerve, as spinal nerve 1, with nerve 2 passing behind the atlas. This is the homology accepted herein.

This accepted homology also agrees with the pattern of innervation of the atlanto-occipital muscles, and with morphology. The transatlas nerve of salamanders has only a ventral root, and the first spinal nerve in frogs has lost the dorsal root and dorsal root ganglion during metamorphosis (Mookerjee 1930, 1931; Fox 1954). Wake and Lawson (1973) also suggested that the first spinal nerve originally lay in front of the atlas arch in salamanders (within the range of the third somite), moving back into the atlas pedicel through time (possibly to protect it from the cranio-cervical joint surfaces). A similar process has been assumed by Ritland (1955a) in crown-group frogs (*e.g.*, *Rana* and *Xenopus*) in which the fibers of the first spinal nerve fuse with the spinal nerve 2 (Ritland 1955, pp. 160–163) completely losing their individuality during metamorphosis, except in *Ascaphus* and *Leiopelma* in which they are very much reduced. According to Ritland (1955a, p. 163) "the way in which change may occur at any level of the cord is by a gradual shift of fibers to the next posterior exit from the spinal canal".

The alternative scenario by Francis (1934) would require that the second spinal nerve moved forwards through the atlas from back to front (to become transatlas nerve *i.e.*, his spinal nerve 1 in adults). This is not the pattern seen in the embryonic development of salamanders, where the notch in the front edge of the atlas gradually becomes enclosed (*e.g.*, Mookerjee 1930, 1931). The same transition is seen in salamander evolution where an anteriorly open notch (SEE) may present an intermediate stage between the unnotched condition in some karaurids (Evans *et al.* 1988, SEE personal observations) and the perforating foramen of crown-group urodeles (SEE). The presence of a notch in the anterior margin of the atlas in *Czatkobatrachus* provides evidence that the condition in stem-frogs was not dissimilar to the condition in most salamanders, with the first spinal nerve (= suboccipital nerve, *i.e.*, transatlas nerve) notching the anterior margin of the atlas. A fully enclosed atlantal foramen is also found in basal caecilians (Jenkins and Walsh 1993; Evans and Sigogneau-Russell 2001), and could be a basal lissamphibian feature. However, the absence of either a notch or foramen in the stem-caudate *Marmorerpeton* (Evans *et al.* 1988, and SEE personal observations) renders this character problematic, as does the two-state condition (anterior incision or closed foramen) in salamanders, and its ontogenetic variation.

Subdivision of the atlas. — Rage and Roček (1989) and Roček and Rage (2000) interpreted the atlas of *Triadobatrachus* as being bipartite, with a single arch but with the centrum divided into anterior and posterior parts, and with a dichocephalous atlas rib (see also Estes and Reig 1973) meeting both components. This would be an unusual morphology, and it is certainly not the condition in *Czatkobatrachus* where the atlantal centrum is a single entity with a short neural arch bearing the postzygapophysis but no rib. According to Shishkin (2000, pp. 543–544) one of the few apomorphies that can be attributed with confidence to temnospondyls (including lissamphibians, Duellman and Trueb 1986) is the absence of transverse processes on the atlantal neural arch. Fusion of the first two vertebrae can occur in frogs (*e.g.*, palaeobatrachids, rhinodermatids, brachycephalids, and some bufonids, myobatrachids, and pipids, Duellman and Trueb 1986, p. 470; rarely in *Ascaphus*, Ritland 1955a), and is probably associated with a strong shortening of both the centra and neural arches (Ritland 1955a, fig. 4). Such fusion does lead to the presence of a transverse process, but it is associated with the second vertebral segment. Contrary to the opinion of Rage and Roček (1989), the neural arches were certainly present on the first two vertebrae in *Triadobatrachus*, as shown by what is probably the pedicel of atlantal arch, and by the postzygapophyses on the second vertebra (Fig. 4A). The state of preservation of *Triadobatrachus* does not permit a full understanding of its neck structure. The second vertebra of *Triadobatrachus* is damaged (Roček and Rage 2000, fig. 3), but what remains appears to be quite consistent with the morphology of the same element in *Czatkobatrachus* (Fig. 4A).

Tuberculum interglenoideum. — As most frogs, *Czatkobatrachus* lacks an interglenoid tubercle between the atlantal cotyles, having instead a flat surface perforated by the notochord. However, an anterior median process reported by Báez and Basso (1996, p. 143) in *Notobatrachus* and a nubbin-like process in the same position of *Prosalirus* (Jenkins and Shubin 1998, p. 500 and fig. 3A) may represent remnants of the interglenoid tubercle. The tubercle is present in most crown group salamanders (secondarily lost in some paedomorphic taxa, *e.g.*, batrachosauroids, Estes 1981), in albanerpetontid amphibians (SEE personal observations), in stem-caecilians (Jenkins and Walsh 1993; Evans and Sigogneau-Russell 2001), and in the derived amphibamid *Gerobatrachus* (Anderson *et al.* 2008). It is absent in the Middle Jurassic karaurid *Marmorerpeton* (Evans *et al.* 1988), but has been described as present in the Upper Jurassic *Karaurus* from Kazachstan. Its presence might be a synapomorphy linking caecilians, crown-group salamanders and albanerpetontids (*e.g.*, Feller and Hedges

1998; but see Hay *et al.* 1995), or, given its presence in *Gerobatrachus* (Anderson *et al.* 2008), a character of *Gerobatrachus* and Batrachia (*sensu* Anderson *et al.* 2008). This would require a subsequent reversal in crown-group caecilians, in salientians, and in *Marmorerpeton*. However, the tubercle can also occur in other amphibian lineages (*e.g.*, some microsaurs, Carroll and Gaskill 1978), and it may be of functional significance.

Caudals. — On present evidence, the fusion of the caudal vertebrae to form the urostyle is a derived character of crown-group Anura, although some early taxa retained a single postsacral vertebra in front of the urostyle (*e.g.*, some *Notobatrachus*, Báez and Basso 1996). According to Ritland (1955a), the extant *Ascaphus* also retains a strong tendency for the possession of discrete post-sacral vertebrae. In *Czatkobatrachus* the presence of discrete caudals is considered plesiomorphic, as is their presence in *Triadobatrachus*, but the reduced caudal number they probably share is derived. The widely open notochordal canal in *Czatkobatrachus* caudals implies the persistence of the notochord into the tail.

Transverse processes/ribs. — Developmental studies on living frogs (Blanco and Sanchiz 2000) have shown that the transverse process and small free rib, where present, are part of the same anlagen. Differences between clades reflect different degrees and patterns of ossification. In neobatrachian frogs, the transverse process ossifies as a single unit and fuses to the vertebral body. Three extant families (ascaphids, discoglossids and pipids: Trueb 1973), and virtually all Mesozoic anurans (Rocek 2000, including *Vieraella*, *Notobatrachus*, *Prosalirus*, *Eodiscoglossus*), retain small ribs on the anterior presacrals. In *Triadobatrachus*, all vertebrae, except the atlas (but see Rage and Roček 1989 for different opinion) bear free ribs, and no vertebra has more than a short transverse process to which the rib attaches. This is presumably the primitive salientian condition since it is also found in stem caudates (Evans, unpublished data). *Czatkobatrachus* resembles primitive modern frogs in having short transverse processes that probably contacted free ribs (not yet recognized, but interpreted from the pitted terminal surfaces of the processes) on a few anterior presacrals (ZPAL Ab IV/108–110), but fused ones on posterior vertebrae (ZPAL Ab IV/6, 10, 127, 128, 146) as shown by areas of incomplete fusion in ZPAL AB/IV/6 (Fig. 2A). These processes are directed laterally in some anterior vertebrae and posteriorly in most of the others; they are slender mid-trunk, but become thickened immediately in front of and behind the sacrum. The state of transverse processes/ribs in *Czatkobatrachus* is here considered derived.

Pectoral girdle. — The pectoral girdle of *Czatkobatrachus* has been reconstructed (Borsuk-Białynicka and Evans 2002) as a pair of undivided scapulocoracoid plates ventrally connected in an arciferal manner (Fig. 5C), no clavicle, cleithrum or sternum fragments having been identified. Crown-group frogs, with both arciferal and firmisternal girdles, have a separate scapula and coracoid. This is in contrast to non-lissamphibian temnospondyls (Borsuk-Bialynicka and Evans 2002 and references herein) and to caudates that have a single scapulocoracoid, this state being considered plesiomorphic. Within Anura, more basal clades like Ascaphidae, Discoglossidae and Pipidae display short scapulae, in contrast to neobatrachian frogs where the scapula may be longer and more slender (Trueb 1973), but never to the extent seen in *Czatkobatrachus*. In ascaphids and pipids the scapulae are proximally uncleft while being cleft or bicapitate in almost all other frogs (Trueb 1973). The widely held opinion (*e.g.*, Trueb 1973) that short uncleft scapulae are primitive for frogs has been challenged by the structure of the scapulocoracoid in *Czatkobatrachus*. Its elongate scapular blade is proximally perforated by the supraglenoid foramen. This separates the anterior acromial part from the posterior, glenoid part, and is most probably homologous to the scapular cleft (Borsuk-Białynicka and Evans 2002) or a scapular cleft *in statu nascendi*.

Trueb (1973) stated explicitly that the arciferal type of pectoral girdle was plesiomorphic for salientians, and that firmisterny is derived. Emerson (1983) was more cautious. However, the consistently arciferal structure of the caudate pectoral girdle suggests that this is the plesiomorphic state, and we accept this view. Firmisterny is derived, and is probably better as a shock-absorbing device Although earlier reconstructions of *Triadobatrachus* (Rage and Roček 1989) suggested it had a tripartite pectoral girdle like that of modern frogs, our studies have shown that the pectoral girdle of the Malagasy specimen might be reinterpreted as a single structure (Borsuk-Białynicka and Evans 2002) like that of *Czatkobatrachus*.

Ilium and ilio-sacral joint. — An elongate anteriorly directed ilium is synapomorphic for the Salientia (*Triadobatrachus* included) and is shared by *Czatkobatrachus*, but its contact with the sacrum is probably still plesiomorphic or intermediate. Emerson (1979) was probably the first to realize that the ilia articulate ventral to the sacrum in extant frogs. They do also in *Notobatrachus* (Báez and Basso 1996, fig. 13). As reconstructed herein, the contact in *Czatkobatrachus* occurs between the medial surface of the ilium and the lateral concavity of the sacral process whereas the anteroventral extension of the transverse process props the ilium from the ventral side. However, a posterior extension of the transverse process does overlap the ilium shaft dorsally and may represent a rudiment of the modern configuration.

Puboischiadic plate. — In salamanders, the pubis is unossified and the same is generally true of frogs (Trueb 1973), although Ritland (1955a) reported it as ossified or calcified in *Ascaphus* (calcified according to Trueb 1973). It is also ossified in all pipids (Roček, personal communication 2007). In albanerpetontids (McGowan and Evans 1995) an ossified pubis remains, providing evidence that it was still present in the lissamphibian ancestor (assuming monophyly), although Anderson *et al.* (2008) report it as unossified in the amphibamid *Gerobatrachus* (but this could be due to immaturity). In living frogs, the pubis is restricted to a small unossified region of the ventral pelvic plate between the ilium and ischium. The pelvis of *Czatkobatrachus* thus represents an intermediate stage in which the pubis has been greatly reduced (as in modern frogs) but remains ossified. It is also intermediate in the presence of the perforating canal.

In amniotes and in most non-lissamphibian temnospondyls, the ossified pubis contains a conspicuous foramen for the obturator nerve and its accompanying blood vessels. In salamanders, this nerve supplies a puboischiofemoralis internus muscle on the inner face of the pelvis (Francis 1934) and then sends branches to puboischiofemoralis externus on the outside. The nerve is said to be reduced in salamanders compared to other tetrapods (Noble 1922) and is absent in living frogs (Green 1931; Ritland 1955a), with its role taken over by a branch of the femoral nerve. This change has been linked to metamorphosis, when there is a loss of some spinal nerves (Green 1931). The presence of a homologue of the obturator canal in *Czatkobatrachus* implies retention of the nerve. This would be consistent with the fact that there has been less reduction of the presacral region in *Czatkobatrachus* than in crown group frogs.

Sacro-caudal joint. — According to Trueb (1973) the anuran sacro-urostylar joint is subject to considerable variation. Most crown-group frogs have a bicondylar sacro-urostylar joint, and this was regarded as primitive by Trueb (1973, see also Duellman and Trueb 1986). However, the Jurassic *Prosalirus*, and the extant *Ascaphus* and *Leiopelma*, retain a simple fibrocartilaginous intercentral connection that is identical to those within the presacral column. This condition is considered to be more primitive by Jenkins and Shubin (1998), and is that found in *Czatkobatrachus*. The *Czatkobatrachus* sacrum retains postzygapophyses, as a plesiomorphic character, as does *Notobatrachus* (Báez and Basso 1996). These are absent in *Prosalirus* (Jenkins and Shubin 1998) and in most extant frogs (Trueb 1973; exceptions include some extant pelobatids and discoglossids).

Limb bones. — Both the humerus and femur display a strikingly anuran morphology that may be at least partly size-dependent. Which, if any, of their characters are synapomorphic for *Czatkobatrachus* and crown-group anurans is a question that requires more extensive studies of the out-groups. The large capitate eminence of the anuran humerus is shared not only by caudates and albanerpetontids (SEE personal observations) but also by the Dissorophoidea and by a more-inclusive group of temnospondyls (the Euskelia of Yates and Warren 2000), and is thus plesiomorphic at the level of Lissamphibia. The size and shape of the ventral crest of the humerus is also similar in both anurans and caudates, but salientians lack the dorsal crest of the humerus, that bears an attachment for the humeral retractor (subscapularis muscle) in caudates. The slender elongate salientian-type femur bears a low ventral crest for the attachment of hip muscles (*mm. pectineus*, *gluteus*, *iliofemoralis*, *pyriformis*, *quadratus femoris*, and *obturator externus*; Ritland 1955b) instead of the protruding finger-like trochanter serving the same function in caudates. The development of prominent humeral and femoral crests is probably derived for salamanders, with salientians showing the primitive state.

FUNCTIONAL MORPHOLOGY

General axial characters. — Shortening the axial skeleton limits its capacity for lateral undulation during locomotion and implies that both *Czatkobatrachus* and *Triadobatrachus* had already modified their locomotor strategy towards a gait in which there was a greater dependency on the limbs.

Transverse processes. — Reduction of lateral mobility of the vertebral column in *Czatkobatrachus* is also supported by the fusion and, sometimes, by elongation of transverse processes, which suggest the spine was more stiffened in the horizontal plane than that of *Triadobatrachus*. Enlargement of the peri-sacral transverse processes may be associated with strengthening of the ilio-lumbaris (anteriorly) and of caudal musculature homologous to coccygeo-iliacus and coccygeo-sacralis (posteriorly) (Emerson and De Jongh 1980). These may have provided additional support and stabilisation to the ilio-sacral articulation during locomotion (see also for lumbo-dorsal fascia below).

Caudal vertebrae. — The reduction of the tail in *Triadobatrachus*, and presumably also in *Czatkobatrachus* (see above), shows that these animals had moved away from a primarily undulatory mode of locomotion, for which the tail is of great importance. Despite the absence of the urostyle in both these animals, the juxtaposition of a shortened tail between elongate, anteriorly directed ilia may, according to Jenkins and Shubin (1998), represent a primitive stage in the evolution of the anuran caudopelvic musculature linkage. We concur with this view. The absence of any ridges or tuberosities on the cylindrical terminal caudal elements suggests they were not tightly held together and probably retained some flexibility (but see also the information on transverse processes above).

Elements of the caudopelvic mechanism. — Saltation is, without doubt, the most distinctive feature of crown-group frogs and was present in the earliest known and most primitive anuran taxa (*Prosalirus*, *Vieraella*, *Notobatrachus*). The key finding of Emerson and De Jongh (1980) was that the typical anuran saltation mechanism requires a body divided into two components — anterior (head, forelimbs, presacral column and sacrum) and posterior (pelvis, urostyle and hind limbs) separated by a joint (sacro-urostylar) that permitted dorsoventral flexion and extension. In jumping, the sacro-urostylar joint extends to bring the sacrum, presacral series and head into line with the urostyle and the long axis of the ilia.

Sacro-caudal joint. — In extant frogs a loss of sacral postzygapophyses and the development of a bicondylar, uniaxial, joint between the sacral centrum and the urostyle (Jenkins and Shubin 1998) allow for extension-flexion movements in the sacro-urostylic joint. In *Czatkobatrachus*, the retention of both a simple sacro-caudal joint and sacral postzygapophyses do not exclude, but do limit, the potential for dorsoventral excursion of the spine at this joint (Jenkins and Shubin 1998). Modern anurans that lack this capacity also lack true saltation, and have locomotor patterns involving walking, swimming, climbing, or burrowing. This is likely to have been the case for *Czatkobatrachus*.

Ilium. — The presence of an elongate ilium, the shaft of which extends well anterior to the level of the acetabulum, obviously contributed to the stiffening of the posterior body segment. This important element of the frog-type locomotory mechanism had already developed in *Czatkobatrachus* and, to a lesser degree (Fig. 4), in *Triadobatrachus*. The rotation and elongation of the iliac shaft, that occurs prior to metamorphosis in extant frogs (Green 1931), was also one of the first postcranial characters developed in salientian phylogeny. As this iliac elongation evolved well before true saltation, its selective advantage remains obscure, particularly as it now functions in many different locomotory types including jumping, walking, and swimming.

The ilia of *Czatkobatrachus* and *Triadobatrachus* are distinctive in having a hypertrophied dorsal tubercle — dorsal prominence (according to Sanchíz's 1998 terminology). In extant frogs, the dorsal prominence is associated with the origin of the gluteus magnus muscle, a powerful extensor of the hip. The function of hip (and knee) extension in leaping is obvious, but it is less clear why this tubercle should be so enlarged in two taxa that were clearly not saltatory. In most frogs that possess a dorsal prominence, this structure is aligned with the iliac blade and is not protruding. It is, however, hypertrophied in living pipids and some bufonids, apparently in relation to the presence of an accessory tendon of the gluteus magnus muscle that attaches to it (Dunlap 1960; Emerson and Jongh 1980). This tendon is said to be a part of the dorsolumbar fascia and has a role in limiting movement of the urostyle in relation to the pelvic girdle. Both pipids and bufonids are locomotor specialists, swimming or walking respectively. Since they are not related, this is a convergent adaptation. The accessory tendon is not present in either *Ascaphus* or *Leiopelma*, and the same was presumably true of early crown group frogs as the dorsal prominence is not hypertrophied in *Prosalirus* (Jenkins and Shubin 1998), *Vieraella*, or *Notobatrachus* (Báez and Basso 1996). Whether the enlargement of the dorsal prominence of stem-frogs is comparable to that of pipids and bufonids is, of course, impossible to determine but it does suggest the gluteus magnus, or an accessory tendon, had an important role in stem-frog locomotion, perhaps (as in the living taxa) in stabilisation of the pelvis against the sacrum and tail. This could have been important to taxa like *Czatkobatrachus* and *Triadobatrachus* in which the ilio-sacral joint was still very weak (see below).

Ilio-sacral joint. — Emerson (1979, 1982), Emerson and De Jongh (1980), and Jenkins and Shubin (1998) have dealt with this topic in some depth. The ilio-sacral joint of crown-group frogs is not a synchondrosis or an abutting joint as it is in most tetrapods. Instead, the sacral diapophysis lies above the iliac blade, suspending it by means of a specialised ligament system that frequently contains a sesamoid. Emerson (1982) described three principle types of ilio-sacral joint in frogs, ranging from the specialised joint of pipids (her type I) that permits fore-aft sliding between an expanded sacral diapophysis and a long ilium, to the mechanically simplest kind (her type IIB) in which the sacral diapophysis is only slightly dilated and the iliac blade is suspended from it by means of a ligament that runs from the distal end of the sacral rib to the ventral surface of the ilium. This arrangement, found in basal ascaphids and derived ranids (as well as the Jurassic *Prosalirus*, Jenkins and Shubin 1998), is said to maximise dorsoventral rotation of the pelvis on the sacrum and tends to limit movement to this plane. There is a variant of this arrangement (Type IIA) in which distally expanded sacral processes with arcuate distal edges are connected to the ilium by means of a ligament inserting dorsally near the base of the sacrum rib. The difference between types II A and IIB in the position of the ligament origin reflect a difference in mobility, type IIA allowing for a lateral swing of the pelvis on the sacrum. This type, found mostly in walking frogs, tends to increase the range of protraction (and thus stride length), but at the expense of jumping ability (since the body would be less stable in the leap). It could be predicted that early frogs and stem-frogs might have an arrangement intermediate between type IIA and IIB, so that there was both dorso-ventral and lateral movement, permitting walking and imperfect jumping, in the absence of the specialised sacro-urostylar system. This is clearly not the condition in *Triadobatrachus* where the sacral ribs remain separate from the vertebral body and the distal ends are elongated, posteriorly directed processes that have a long abutting contact with the medial side of the ilium (Rage and Roček 1989), much like the arrangement in more basal amphibians. *Czatkobatrachus* has sacral diapophyses that are fused to the vertebral body. Each of them has a widely extended distal end containing a dorsolaterally to laterally facing concavity that probably received the ilium in a lateral (rather than ventral) position. A dorsal ligament furrow, extending medially, well towards the shaft of the sacral process, clearly recalls Emerson's type IIA and suggests lateral mobility rather than jumping. According to Jenkins and Shubin (1998), the ventral position of the ilia with respect to the sacral transverse processes in crown-group frogs positions the pelvis advantageously to transmit vertical thrust to the axial skeleton during jumping. A lateral, rather than ventral, position of the ilia with respect to sacral transverse process, as reconstructed for *Czatkobatrachus*, contributes to the hypothesis that this stem salientian was a walker rather than a jumper.

Musculoskeletal information. — Among the muscles that fire during the initial phase of take-off, and are positively correlated with the height of jump in extant frogs (Emerson and Jongh 1980), only *m. longissimus dorsi* could have functioned in frog style in *Czatkobatrachus*, *i.e.*, to straighten the back, but this is its normal function. The short, rather strong transverse processes show that it was well developed. Two other muscles that contribute to the caudopelvic mechanism in extant frogs, the *mm. coccygeo-sacralis* and *coccygeo-iliacus*, were probably no different in morphology and function from their homologues in other tetrapods, as shown by the lack of a urostyle in *Czatkobatrachus*. The same is probably true of the pyriformis muscle that, in frogs, contributes to posteroventral rotation of the urostyle at take-off. In *Czatkobatrachus* it probably still acted like the caudifemoralis muscle of caudates, to retract the femur and flex what was left of the tail.

Pectoral girdle. — The nature of the arciferal pectoral girdle organization ascribed to *Czatkobatrachus* (Fig. 5C) is difficult to interpret in functional terms. According to Emerson (1983), the ventral cartilages of arciferal frogs rotate in a horizontal plane, but the exact biomechanical significance of this mobility remains obscure. There is no obvious correlation between locomotion type and girdle type, jumping frogs being both arciferal and firmisternal as are the hopping/walking types (Emerson 1983). In *Czatkobatrachus*, the slender proportions of the scapula are somewhat similar to those of some neobatrachians (*Bufo*, *Rana*, and *Rhinoderma*; Trueb 1973, fig. 2-9c, d, e), but also to the early Jurassic frog *Vieraella herbsti* (Báez and Basso1996, figs 6, 7), and contrast with short scapulae of ascaphids, discoglossids and pipids (Trueb 1973, fig. 2-9i, j, g). The shape is also very different from that of *Triadobatrachus* (Rage and Roček 1989). This difference must be interpreted in functional, rather than phylogenetic terms, but the function remains obscure. More conclusive is the structure of the glenoid discussed in detail elsewhere (Borsuk-Białynicka and Evans 2002). In essence, the structure of the glenoid, which is relatively large in vertical diameter, suggests a greater range of dorsoventral mobility for the forelimb than that of outgroup temnospondyl clades where forelimb movement was primarily horizontal. The directly lateral orientation of the glenoid results in a humeral resting position that was perpendicular to the body axis rather than oblique. This lateral orientation of the glenoid differs from the more posterolateral position of outgroup taxa and the more posterior position of crown-group frogs, but is similar to that of caudates. It has been tentatively interpreted as an early adaptation towards maintaining balance, preventing an animal burdened with a heavy head from falling forwards (Borsuk-Białynicka and Evans 2002). Overall, therefore, the scapulocoracoid of *Czatkobatrachus* suggests terrestrial locomotion in which the forelimbs had a role in raising the body off the ground.

Limb bones. — The humerus of *Czatkobatrachus* is slender and elongate, and apparently more strongly ossified than is usual in extant frogs. It has rather elaborate ends that are completely co-ossified with the shaft. The proximal end of the *Czatkobatrachus* humerus may have been more heavily loaded and subjected to a greater degree of stress, perhaps because the body was less balanced (although it was a very light animal). The distal end is also strongly ossified (as is the corresponding ulna joint) but is more closely similar in its morphology to that of extant frogs, except that the antebrachial bones were not fused. The asymmetry of the epicondyles in *Czatkobatrachus* is interesting, given that symmetrical radial and ulnar epicondyles, as found in *Ascaphus* and *Notobatrachus* (Báez and Basso 1996), were thought to be primitive. However, in living frogs the development of the epicondyles, and of the associated medial and lateral crests, can be size and sex dependent (Ritland 1955a). Nonetheless, since the ulnar epicondyle provides the common origin for the flexor muscles of the hand, this movement may have been more important in *Czatkobatrachus*. The significant length and ossification of the olecranon reflects the size of the triceps muscles extending the elbow joint, an important action for anterior body elevation. This process is also well-developed in the amphibamid *Gerobatrachus* (Anderson *et al.* 2008).

Gans and Parsons (1965) suggested that stem-frogs may have waited for prey with the body propped up on the forelimbs, thrusting forward to grab food using the forelimbs as fixed points. The morphology of the *Czatkobatrachus* forelimbs would be consistent with this hypothesis.

According to Jenkins and Shubin (1998), the length of the femur in the earliest recorded crown-group frog, *Prosalirus*, is about 9.9 of that of a dorsal vertebra, with that in *Notobatrachu*s at 8.5, *Bombina* at 8.1, *Bufo* at 7, and *Triadobatrachus* at 4.9 times the dorsal length. In *Czatkobatrachus* , as preserved, this value is around 6.5. *Czatkobatrachus* femur is longer and more slender than that of the Malagasy stem frog, but shorter than in crown-group leapers, although given the significantly longer vertebral centra of *Czatkobatrachus*, the difference is not significant. The humerus of *Czatkobatrachus* is unusually long (83%) in relation to femoral length, by comparison with *Triadobatrachus* (77%), *Bufo marinus* (75%), *Prosalirus* (70.6%), *Notobatrachus* (65%), and *Rana temporaria* (62.5%). Frogs moving primarily by saltation have relatively shorter fore-limbs than those, like *Bufo*, which do not.

CONCLUSIONS

The detailed study of the postcranial remains of the early Triassic genus *Czatkobatrachus* have not altered the original hypotheses (Evans and Borsuk-Białynicka 1998) with respect to the position of this genus in salientian phylogeny (Fig. 11). *Czatkobatrachus* shows a combination of primitive and derived character states that together place it between purported stem-lissamphibians (*e.g.*, *Gerobatrachus*) and crown-group anurans. However, its position with respect to *Triadobatrachus* remains unclear. Many of its characters (humeral morphology, ilio-sacral morphology, scapula shape, the fusion of the transverse processes) appear to position *Czatkobatrachus* above *Triadobatrachus* on the anuran stem, but these differences could relate to function and lifestyle, if *Triadobatrachus* were less terrestrial.

The most obvious derived characters shared by *Czatkobatrachus*, *Triadobatrachus* and the Anura relate to the pelvis (*i.e.*, the anteriorly elongate ilium and, consequently, posterior position of the acetabulum with

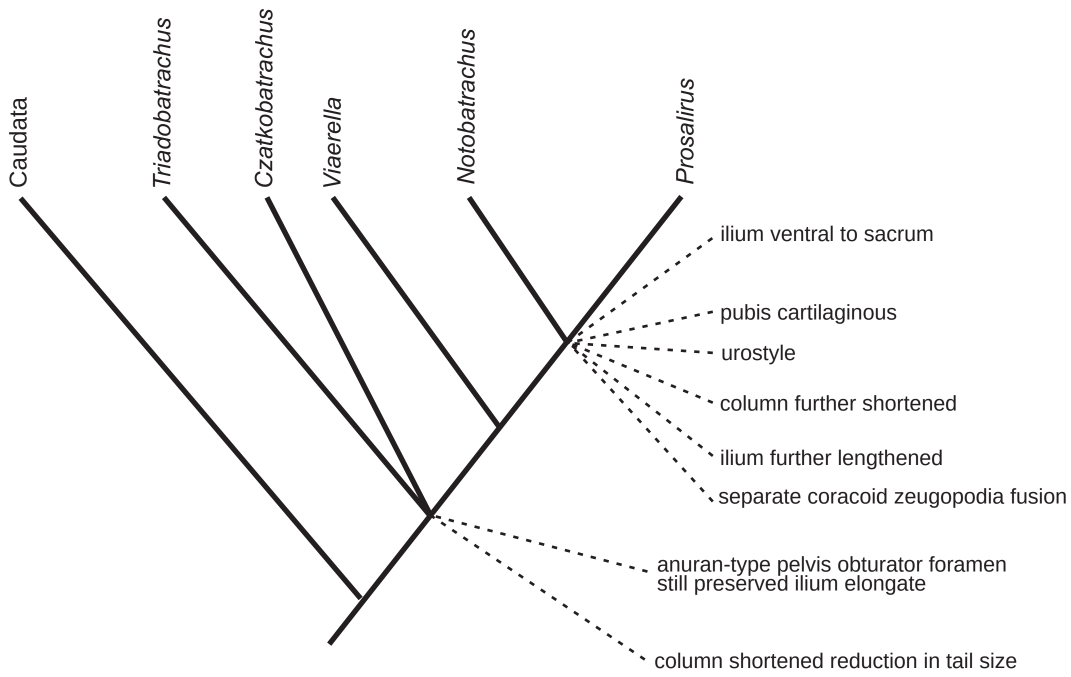

Fig. 11. A possible sequence of character states in salientian phylogeny. Phylogenetic diagram after Evans and Borsuk-Białynicka (1998).

respect to the ilio-sacral joint, and the reduced pubis). The ilium is less elongate than it is in the crown-group frogs but more so than in *Triadobatrachus*.

A shortened presacral column and the reduction in length of the tail, would be further synapomorphies of the Salientia, if our reconstruction, based on vertebra size and structure in *Czatkobatrachus*, is confirmed by the recovery of further articulated material. Similarly, long slender propodials and the loss of the interglenoid tubercle are also putative salientian synapomorphies. The posterior shift of the first spinal nerve, to a position that notches the anterior margin of the neural pedicel of the atlas, is an expression of a lissamphibian evolutionary trend.

Although the material is still limited, we have data on four key regions in the evolution of salientian locomotion: the axial skeleton, the pectoral girdle, the pelvis, and the limb proportions. These suggest *Czatkobatrachus* had taken the following steps:

(1) A shift in locomotor pattern away from lateral undulation toward greater dependence on the limbs (fusion of the ribs to the vertebrae, strong transverse processes, the tail probably reduced in length).

(2) The development of a slender scapula, and a large circular glenoid facing laterad within a basically arciferal pectoral girdle. These characters might be *Czatkobatrachus* autapomorphies related to the importance of the forelimbs in propping up the body, in a stage transitional between caudate-like locomotion and that of anurans. The strongly and fully ossified elbow joint suggests that this was an important part of the same functional complex for this small amphibian.

(3) The development of an anteriorly directed cylindrical iliac shaft, with a large dorsal prominence (associated with gluteus magnus or its stabilising tendon). The orientation of the iliac blade implies that thrust forces from the legs were already being directed anteriorly parallel to the body axis, even if the animal was not yet leaping. The ilio-sacral joint had been modified from an abutting cartilage covered joint into a primarily suspensory one, the two components being fastened by a ligament. The ilium was still positioned lateral to the sacral transverse process at the ilio-sacral joint, but was stabilised both dorsally and ventrally by parts of the sacral diapophysis. However, the posterodorsal convexity might represent a rudiment of the sacral flange that overlaps the ilium dorsally in crown-group frogs. The combination of a pelvis modified to transmit thrust anteriorly, with a weak ilio-sacral joint and a short but probably flexible tail, would have placed considerable reliance on the soft tissues holding these elements together. This may explain the increased size of the peri-sacral transverse processes and the enlargement of the dorsal prominence of the ilium (for a stabilising tendon of gluteus magnus).

(4) The development of longer, more gracile limbs without strong muscle attachment surfaces. The retention of fore- and hind limbs of similar length is a primitive character, compared to the disparity found in crown-group anurans. However, the elongation of the humeri, by comparison with both *Triadobatrachus* and crown-group frogs, may represent another autapomorphy of *Czatkobatrachus*, reflecting an unusual, transitional, locomotor pattern.

In combination, these features suggest *Czatkobatrachus* was a small agile terrestrial animal that walked, and perhaps hopped, with a stiffened back, and a reduced tail. It thus shows many of the morphological features predicted by Gans and Parsons (1965) for the ancestral stem-frog stage. *Czatkobatrachus* was substantially smaller than *Triadobatrachus*, was longer limbed, and would have been more agile. It was probably also more fully terrestrial, judging by the higher degree of ossification throughout the skeleton (even by comparison with basal crown-group taxa).

The reconstructed palaeoenvironment for *Czatkobatrachus* (Borsuk-Białynicka *et al.* 1999; Cook and Trueman 2009) was a small non-permanent water body (or group of such water bodies), surrounded locally by vegetation (oasis), but in a rather arid environment. This is precisely the environment envisaged by Hecht (1962) and Gans and Parsons (1965) for the stem-group frog stage. Food, in the form of insects, is likely to have been concentrated in the vegetation around the water, providing a focus for small vertebrates.

Together *Triadobatrachus* and *Czatkobatrachus* demonstrate that the evolution of the pelvis (elongate anteriorly directed blades, reduced pubis) and some aspects of the ilio-sacral joint (loosening of the ilio-sacral contact, development of a suspensory system), preceded the evolution of those features uniquely associated with saltation (the urostyle, fusion and elongation of the antebrachial and tibiofibular bones, a separate coracoid element and more parasagittal position of the fore-limb for jumping). The saltatory functional complex had evolved by the Early Jurassic (*Prosalirus* Shubin *et* Jenkins, 1995), but further Triassic material is needed in order to determine the sequence of intermediate steps. These may, in turn, shed light on the peculiar functional complex presented by *Czatkobatrachus*, as would the recovery of more of its Permian antecedents (*Gerobatrachus* being an important recent addition). Since very few localities of appropriate age yield articulated specimens, microvertebrate localities like Czatkowice probably offer the best chance of filling the void.

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PROCOLOPHONIDS FROM THE EARLY TRIASSIC OF POLAND

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Borsuk-Białynicka, M. and Lubka, M. 2009. Procolophonids from the Early Triassic of Poland. *Palaeontologia Polonica* **65**, 107–144.

Early Triassic disarticulated bones from karst deposits at Czatkowice 1, southern Poland, are assigned to a procolophonine species *Procolina teresae* gen. et sp. n. *Procolina teresae* is characterized by a small adult size, unicuspid tooth crowns, and a derived heterodont dentition. Unicuspid tooth condition is here considered a paedomorphic, rather than primitive, state and a possible result of a constrained miniaturization of *P. teresae*. The remaining procolophonid material is described using open nomenclature. The second procolophonid (genus indet. I) differs from *Procolina* in dental formula, slower developmental rate and larger adult size. The rarest procolophonid (genus indet. II) is a tiny form with bicuspid teeth and notochordal centra. The Czatkowice 1 procolophonids display an unusual type of tooth replacement with no resorption pits on the lingual side and an extensive resorption of the bony tissue on the labial side of the jaws. In *Procolina*, the process was probably limited to early stages of ontogeny, but it lasted longer in genus indet. I.

Key words: Parareptilia, Procolophonidae, tooth replacement, Early Triassic, Poland.

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INTRODUCTION

The procolophonid material described herein comes from an Early Triassic bone breccia discovered in the late 1970's at the locality of Czatkowice 1 near Kraków, southern Poland (Paszkowski and Wieczorek 1982, Paszkowski 2009). The age of the locality has recently been determined as early Late Olenkian (Shishkin and Sulej 2009).

Aside from procolophonids, the assemblage includes a basal archosauriform *Osmolskina czatkowicensis* (Borsuk-Białynicka and Evans 2003; 2009a) similar to *Euparkeria* in size, a small prolacertiform-grade reptile (Borsuk-Białynicka and Evans 2009b), two basal lepidosauromorphs (Evans and Borsuk-Białynicka 2009a), including a basal kuehneosaurid (Evans 2009), a prefrog *Czatkobatrachus polonicus* of *Triadobatrachus* grade (Evans and Borsuk-Białynicka 1998, 2009b), as well as some small temnospondyls (Shishkin and Sulej 2009) and fish (Borsuk-Białynicka *et al.* 2003).

The procolophonids (Procolophonidae Seeley, 1888) represent the most basal lineage of amniotes from the Czatkowice 1 assemblage (Borsuk-Białynicka *et al.* 1999). They originated in the Late Permian possibly in Gondwana (Modesto *et al.* 2002) and invaded the Early Triassic environments of Europe just after the P/T extinction event. As early herbivores they radiated intensively at this time, and are considered to be of biostratigraphical importance. The fast rate of evolution during the Triassic gave an array of possible index taxa (Spencer and Benton 2000). The Czatkowice 1 material includes numerous specimens of different individual age, and thus has a potential to shed some light on various developmental problems, tooth replacement phenomena included.

The objective of the present paper is to give an account of the procolophonid material from the Czatkowice 1 locality. *Procolina teresae* gen. et sp. n. is the dominant and best represented taxon in this material. The main goal of the present paper is to determine the modal type of morphology and the possible variability range of this species. The remaining procolophonid material is left in open nomenclature until new, more complete material will allow more precise identification.

The material from the Czatkowice 1 fissure filling is housed in the Institute of Paleobiology and the Museum of the Earth, both Polish Academy of Sciences.

Institutional abbreviations. — BPI, Bernard Price Institute for Palaeontological Research, Johannesburg, Republic of South Africa; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MUZ, The Museum of the Earth, Polish Academy of Sciences, Warsaw, Poland; PIN Institute of Paleontology, Russian Academy of Sciences, Moscow, Russia; ZPAL, Institute of Paleobiology Polish Academy of Sciences, Warsaw, Poland.

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GEOLOGICAL SETTING

Discovered in 1978, the bone breccia of Czatkowice 1 was briefly studied by a team from the Institute of Geology of the Jagiellonian University in Kraków (Poland), and the geological setting was described (Paszkowski and Wieczorek 1982). More detailed data concerning the geology is given by Paszkowski

(2009) and Cook and Trueman (2009). The fissure/cave system of Czatkowice developed in the Early Carboniferous host limestone includes infillings of Early Triassic, Late Triassic and Early Jurassic age. The material coming from the fissure exposure Czatkowice 1, described herein, has been dated subsequently as of late Olenekian age at youngest (Borsuk-Białynicka *et al.* 1999), as late Early Olenekian (Borsuk-Białynicka *et al.* 2003), and finally, as earliest Late Olenekian (Shishkin and Sulej 2009). The latter date is most probable. The deposition of the material of Czatkowice 1 probably occurred in a freshwater oasis within the arid circumequatorial belt of Northern Pangea. According to Paszkowski (2009), at times of heavy rain, flooding and surface run off would have washed animal remains into water pools or directly into the fissure system. According to Cook and Trueman (2009), a redeposition of the material from the lacustrine sediments into the karst fissure system could have occurred, and a short transport was possible.

MATERIALS AND METHODS

Procolophonids constitute the second most abundant component of the Czatkowice 1 vertebrate assemblage. In frequency, they are exceeded only by the archosauriform *Osmolskina czatkowicensis* (Borsuk-Białynicka and Evans 2003, 2009a). The skull material consists mostly of tooth-bearing elements: maxillae, premaxillae, dentaries, but other bones such as palatines, pterygoids, vomers, quadrates as well as jugals and braincase elements (not included in this paper) have also been identified. A huge number of vertebrae completes the procolophonid material recognized to date.

From several hundred procolophonid bones, a subset of the best preserved were chosen for study. They are: 23 dentaries (ZPAL RV/510–517, 683, 716–719, 733, 740, 741, 762–764, 791, 792, 798–802; Appendix 1); 19 maxillae (ZPAL RV/64, 523, 707–712, 717–720, 736–738, 793, 800); 7 premaxillae (ZPAL RV/62, 65, 759, 794–797); 9 vomers (ZPAL RV/518, 519, 685, 714, 729, 750, 760, 761, 986); 5 palatines (ZPAL RV/525–527, 732, 748); 8 pterygoids (ZPAL RV/63, 64, 503, 505, 520–522, 747); 34 vertebrae (ZPAL RV/767–772, 825–842, 845, 846, 849–853, 860, 868–870), quadrates (ZPAL RV/774, 775), and numerous unnumbered specimens. Supplementary fragmentary material has been consulted.

As shown by vertebral material (Lubka 1999), more than one procolophonine taxon of similar body size might be present. This fact, combined with the disarticulated state of preservation of the material, causes serious problems with the assignment of particular bones. Allowing for ontogenetic variation, the dental formula has proved helpful in associating the tooth-bearing elements, and comparative studies.

The main weakness of the procolophonid material described hitherto is the lack of criteria for tooth homology. Given the gradual transition from incisiform to molariform teeth, and the variability in the rate of this transition, a tooth formula composed of incisiform and molariform number is quite arbitrary. In this account only one tooth, the dominant one, in each the upper and the lower tooth row, will be regarded as a molariform tooth. In the maxilla it is situated directly lateral to the posterior part of the facet for the palatine (Fig. 4), and approximately below the accessory foramen for the superior alveolar nerve (here referred to as a posterior maxillary foramen, Fig. 3C, see also Appendix 1). In the mandible, the dominant molariform is implanted above the posterior inferior alveolar foramen (Fig. 9, arrows), which opens on the lingual side of the dentary approximately above the Meckelian groove. All the teeth posterior to the molariform tooth will be referred to as accessory teeth, all anterior teeth will be considered premolariforms, of which some are incisiforms. The accessory teeth are located over the coronoid facet (Fig. 9), which provides an additional homology criterion. According to our observations, these foramina are fairly stable in position within the Procolophoninae at least.

This account should be considered preliminary. The huge amount of bone material includes many tiny specimens that may illustrate the early phases of ontogeny, but are very fragile and badly damaged. We concentrate on the better preserved specimens that exceed a certain minimum in size. The small size of the procolophonid tooth-bearing elements (Appendices 1, 2) along with the unicuspid condition of the teeth could suggest that only juveniles have been preserved. Indeed, all the specimens from Czatkowice 1 material roughly correspond in length to juveniles recognized by Li (1983, Group 1) in *Eumetabolodon bathycephalus.* The juveniles of Li's Group 1 bear unicuspid teeth that are replaced by bicuspid ones later in ontogeny. As stated elsewhere (Borsuk-Białynicka *et al.* 1999), the Czatkowice 1 material may be biased towards small, *i.e.*, possibly juvenile, elements. However, this probably does not concern the procolo-

Table 1. Estimated dimensions (in mm) of *Procolina teresae* gen. et sp. n. bones on the basis of skeletal bone proportions in *Tichvinskia vjatkensis* (measurements based on illustrations in Ivakhnenko 1979).

Measurements — Taxa / Cat. no	*Tichvinskia vjatkensis* PIN 954/1	*Procolina teresae* estimated size	*Procolina teresae* actual size	Number of specimens
Dentary tooth row length (dtl)	14.3	–	7.0–11.5	17
Mandible length	32	15–25		
Skull total length	32	15–25.7	–	
Maximum frontal length	13.5	4.7–7.43	–	
Vomer length	8.5	2.97–4.9	ca. 4.5	10
Palatine length	8.5	2.97–4.9	ca. 4	10
Pterygoid length to basipterygoid joint	8	2.8–4.7	ca. 4	10
Quadrate articular condyle width	3.3	1.6–2.7	1.8–2.6	9
Presacral vertebra length	4.5	2.1–3.6	1.5–7.0	83*
Total vertebral column length	177	62–101.8	–	
Antero-posterior diameter of ilium neck	ca. 5	2.4–3.8	1.9–2.9, 4.9	5

* based on Lubka (1999).

phonids, of which the largest fragments do not reach the size of the majority of specimens preserved in Czatkowice 1 breccia (mostly those belonging to *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003). A decisive argument comes from the vertebral column (neural arches fused with the centra) that points to small adult size of the main species *Procolina teresae*. On this hypothesis, the largest, most common and best preserved specimens have been considered at least subadult and regarded as taxonomically valid material.

The skull elements, other than tooth bearing bones, have been associated with jaws on the basis of frequency and size as predicted on the basis of bone proportions known from complete skeletons (Table 1), especially the *Tichvinskia* skeleton illustrated by Ivakhnenko (1979).

The index of the dentary tooth row (dtl, Table 1) to total skull length of *Tichvinskia* has been used as a basis for these estimations. In *Tichvinskia* this index amounts to 0.45 whereas the mandible almost equals the skull in length. However, it must be kept in mind that the proportions can vary both taxonomically and in ontogeny (Colbert and Kitching 1975). The index is 0.3 in *Procolophon trigoniceps*, and the mandible is only 0.75 of the skull length (Carroll and Lindsay 1985, fig. 1).

Terminology used in the present paper is mostly based on Oelrich (1956). In some instances, where exact reference to procolophonid anatomy is necessary, Ivakhnenko's (1979) terminology has been followed. In the illustrations, all the teeth are numbered according to the dental formula.

SYSTEMATIC BACKGROUND

The procolophonids are most often included in the Parareptilia (Fig. 1), or a roughly corresponding group Procolophonomorpha (Lee 1995). Parareptilia is a taxon erected by Olson (1947), intended to include a number of extinct amniotes once referred to as anapsid reptiles, but widely confined to groups now considered stem-amniotes such as Seymouriamorpha and Diadectomorpha. The term was successively abandoned and then resurrected by Ivakhnenko (1983a) and Gauthier *et al.* (1988) with a different concept of its composition, and of the interrelationships of the included taxa. In spite of many particular problems as yet unresolved, a universal consensus (Fig. 1A, B) exists about the fairly close relationship of procolophonids with pareiasaurs, and their affiliation within the Parareptilia, which are the sauropsid sister-group of a clade including Diapsida (Fig. 1C) (Laurin and Reisz 1995). According to Lee (1995), Owenettidae (*Owenetta* and *Barasaurus*) constitute the sister-group of the Procolophonidae (see also Reisz and Scott 2002), and the Nycti-

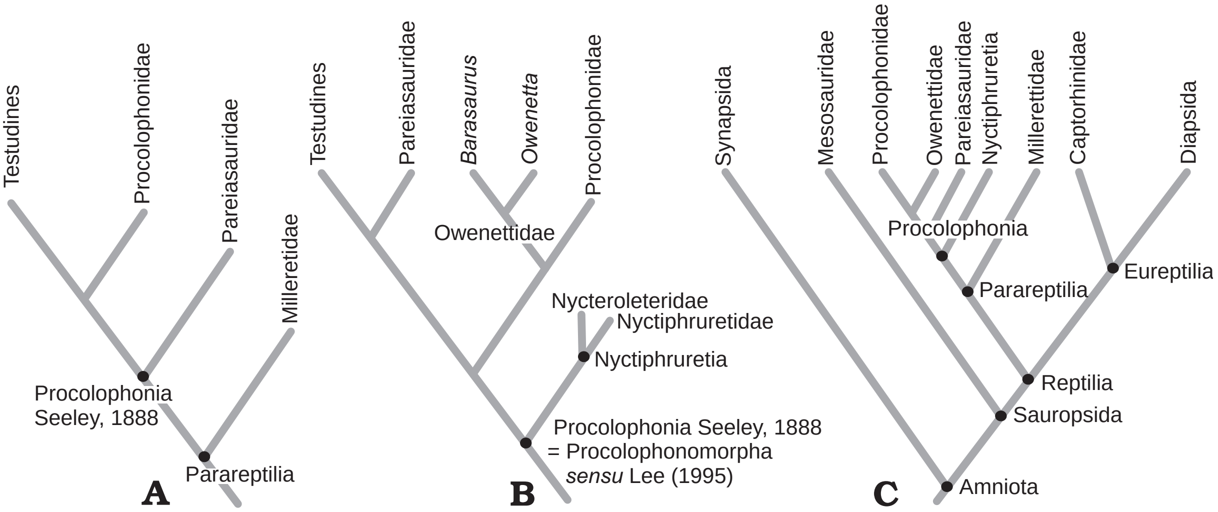

Fig. 1. **A**. **B**. Relationships within the Parareptilia. **A**. Simplified cladogram by Laurin and Reisz (1995). **B**. According to Lee (1995). **C**. Position of the Procolophonidae within the Amniota according to Laurin and Reisz (1995).

phruretia (*Nyctiphruretus* and *Nycteroleter*) are a sister group of both Procolophonidae and a group including Pareiasauria and Testudinata (Fig. 1B) (but see DeBraga and Rieppel 1997 for completely different view of a chelonian position). Lee (1995) has, thus, substantiated long held but less precise opinions (*e.g.*, Romer 1956) about the relationships within this primitive sauropsidan lineage.

The procolophonids are small parareptiles reaching up to 50 cm in body length, with a heavy skull, elongated orbits including a space for the adductor musculature, and a durophagous, heterodont dentition. A new feeding strategy that appeared in their ancestors in the Late Permian resulted in the development of several lineages of omnivorous to vegetarian taxa (Gow 1978) in the Triassic, most of them in the Early Triassic of Eastern Europe (Ivakhnenko 1979) and South Africa (Modesto *et al.* 2002). Ivakhnenko's (1979) subdivision of the Procolophonidae into three subfamilies: Spondylolestinae, Procolophoninae, and Leptopleuroninae, is currently used for the sake of order within this diversity, but the first two subfamilies are probably paraphyletic (Spencer and Benton 2000; Modesto *et al.* 2002). The Spondylolestinae encompass genera with relatively weakly differentiated and numerous (more than 10 on each jaw), mostly unicuspid teeth. Ten or fewer differentiated teeth on the jaws, and molariform teeth usually with complex crowns are typical of the Procolophoninae. In spite of their unicuspid teeth, the procolophonids from Czatkowice 1 certainly belong to the second subfamily on the basis of their shortened and highly heterodont dentition. The Leptopleuroninae are a specialized, most probably monophyletic group, mostly from the Late Triassic of Euramerica (Ivakhnenko 1979, Sues *et al.* 2000 and references therein) and China (Chow and Sun 1960).

SYSTEMATIC PALEONTOLOGY

Subclass **Parareptilia** Olson, 1947

Order **Procolophonia** Seeley, 1888

Family **Procolophonidae** Seeley, 1888

Subfamily **Procolophoninae** Seeley, 1888 emend. Ivakhnenko, 1979

Genus ***Procolina*** gen. n.

Type species: *Procolina teresae* gen. et sp. n.

Derivation of the name: From abbreviated family name.

Diagnosis. — As for the species.

Procolina teresae sp. n.

Holotype: Right maxilla ZPAL RV/711 (Fig. 3A, C).

Type horizon: Early Late Olenekian.

Type locality: Czatkowice 1, southern Poland.

Derivation of the name: In honour of Prof. Teresa Maryańska who transfered her procolophonid material to us, and helped us with her experience.

Material. — Many disarticulated premaxillae, maxillae, dentaries, palatal bones and quadrates, vertebrae referred to as type B1 vertebrae by Lubka (1999), and numerous bone fragments.

Diagnosis. — Very small representative of the Procolophoninae. Size below the minimum of other East European procolophonids. Estimated adult skull length about 25 mm. Vertebral centra fused early with neural arches. Heterodonty combined with unicuspid crowns. Modal dental formula: 3 in premaxilla, 3-4.1.1. in maxilla, 5.1.2. in dentary. The vomer bears usually 5–6 large teeth. One of them is anteromedial in position, the other are organized in a single lateral row. The posteromedial part of the vomer is toothless. Palatine without teeth. Pterygoid ventrally concave; no teeth on the transverse flange. Very strong, indented premaxilla-maxillary joint.

Range. — Early Late Olenekian.

SKULL BONES

Premaxilla. — The premaxilla has a robust body and three processes, the anterior, nasal process, the palatal process, and the posterior process (Figs 2B, C, 3A). The anterior process has a large base and a tall, arched ascending process. The top is anteroposteriorly flattened (Fig. 3A). Medially, it contributes to the symphysial surface along with the flat medial surface of the palatal process (Fig. 2E). The palatal process is a broadly triangular shelf pierced by a circular foramen praepalatinum (Figs 2, 8) for branches of the ethmoidal nerve (Ivakhnenko 1979, pp. 28, 29; Carroll and Lindsay 1985) and subnarial branches of the maxillary artery (Oelrich 1956). When articulated with their counterparts the palatal processes give a strongly tapering horizontal outline to the anterior end of the snout (Fig. 8). Medially, they form a common posterior projection that is dorsally overlapped by the vomers. On both sides, this projection is bordered by a U-shaped incision (Figs 2, 8). Directly anterior to it, the dorsal surface of the process is penetrated by numerous small vascular foramina (Fig. $2C_2$). It could have supported the anterior part of the cartilaginous nasal capsule. On each premaxilla, the vomerine facet is triangular with its longest side following the symphysial border of the bone (Fig. $2C_2$). The facet is divided into two parts by a longitudinal step that matches a concavity on the anterior process of the vomer (Fig. $5A_2$, arrow).

The posterolateral process of the main body extends directly posteriorly, and slightly above the level of the palatal process (Fig. 3A). Its end tapers posteriorly to enter a triangular incision of the medial surface of the maxilla (Fig. 3E) situated just above the anteriormost maxillary tooth. Laterally, the posterior process of the premaxilla bears an elongated, triangular maxillary facet that reaches forward beyond the anterior edge of the last premaxillary tooth (Fig. 3A). By means of this articulation, the premaxilla was strongly fastened to the maxilla.

Apart from the general size, ontogenetic variation involves the size of the nerve foramen, the degree of anterior protrusion of the base of the nasal process, and, probably the proportions of the body. The predominant tooth number is three. The degree of tooth wear is variable, the wear facets facing posteromedially.

Maxilla. — The maxilla is roughly triangular in side view (Figs 3E, 4A). The anterior border is concave and passes gradually into the premaxillary process, the posterior border slopes posteroventrally in a straight line. The nasal process reaches approximately 1/3 the entire length of the bone in depth. It ascends dorsally rather than curving dorsomedially, and hence the lateral surface is only slightly convex dorsoventrally. It is straight longitudinally except for the posterior region where it becomes slightly concave due to the posterolateral orientation of the jugal process. The premaxillary process extends straight forwards, but its anterodorsal portion is inclined medially to produce an oblique shelf (Fig. 3B). In *Procolina* the shelf underlies the naris and differs from the maxillary depression (*sensu* Carroll and Lindsay 1985) in position. Whether it could be homologous with the maxillary depression of *Contritosaurus*, *Tichvinskia*, and *Pareiasuchus* figured by Ivakhnenko (1979) and interpreted as housing a nasal gland, is obscure. Neither is the maxillary depression homologous with the narial shelf (Laurin and Reisz 1995) in contrast to a supposition by Pineiro *et al.* (2004). The narial shelf of Laurin and Reisz (1995) is a thickened portion of the nasal above the external

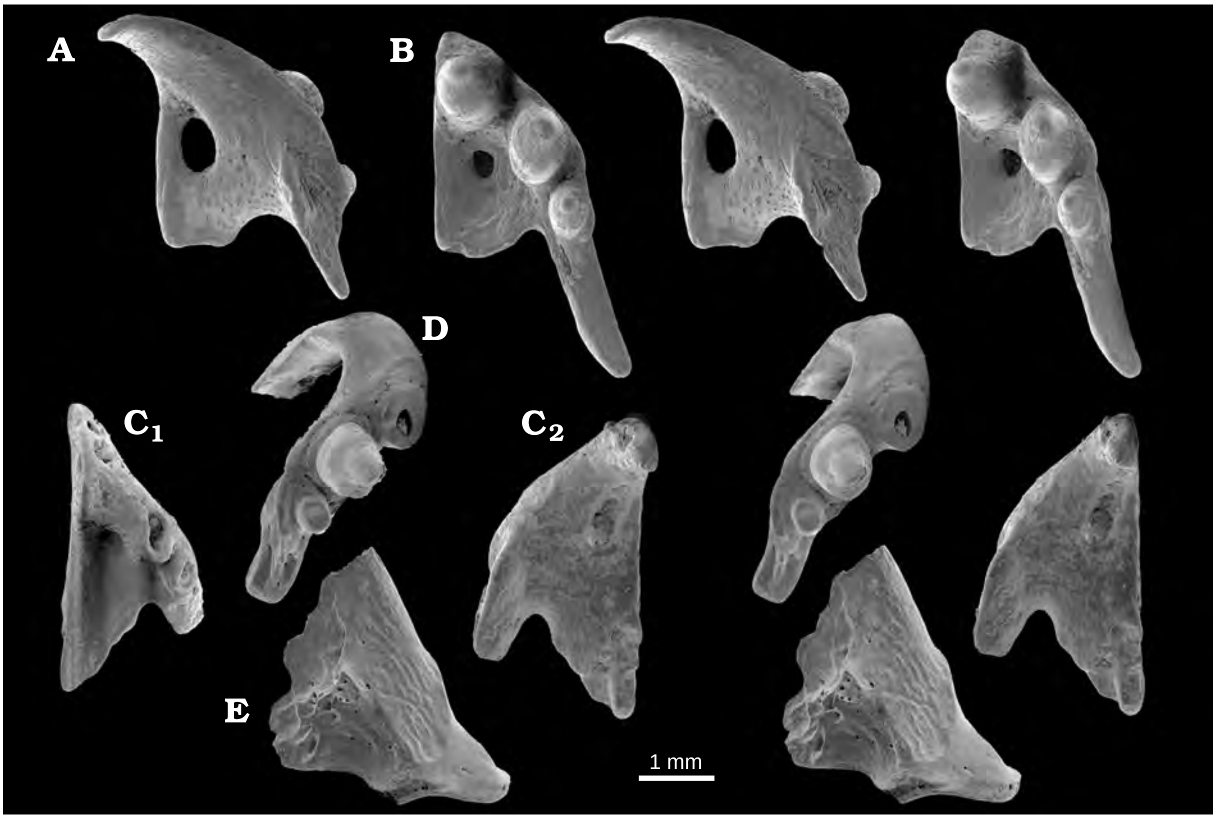

Fig. 2. *Procolina teresae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**–**D**. Premaxillae. **A**. Right bone ZPAL RV/794, in dorsolateral view. **B**. Left bone ZPAL RV/797, in ventral view. **C**. Left bone ZPAL RV/795, in anteroventral (C_1) and dorsal (C_2) views. **D**. Right bone ZPAL RV/796 with palatal process broken off, in ventrolateral view. **E**. Left quadrate ZPAL RV/774, in anterlateral view. SEM micrographs; all but C_1 stereo-pairs.

naris. The phylogenetic importance of this character is not understood. A large foramen for the superior alveolar canal of Ivakhnenko (1979), or anterior maxillary foramen of Oelrich (1956), carrying the maxillary artery and superior alveolar nerve, opens on the labial surface at the base of the premaxillary process. An additional, smaller neurovascular foramen or slit, referred to herein as a posterior maxillary foramen (Fig. 3), earlier reported by Li (1983), opens above the largest molariform tooth.

The medial surface of the nasal process should have broadly overlapped the nasal, lacrimal and jugal, as shown by numerous oblique ridges or folds extending on corresponding facets (Fig. 4A). The premaxillary process bears an elongated, triangular facet that matches the maxillary facet of the lateral face of the premaxilla (Figs 3E, 4A). Corresponding to the size of the molariform teeth, the tooth-bearing shelf is very broad and protrudes strongly medially above the second quarter of the length of the maxilla from the rear, while narrowing towards the ends, quite abruptly so posterior to this region.

The medially protruding part bears a complicated facet for the palatine (Fig. 4A). The exact articulation is far from clear, but the central eminence of the palatine border must have been received by one of the concavities in the maxillary border, which gave entry to anastomosing arterial and nervous branches (Oelrich 1956, p. 26) coming from the transverse furrow on the dorsal surface of the palatine (see below). The latter neurovascular branches probably continued anteriorly in a furrow sending small branches into the thickness of the bone through several tiny foramina. Above the palatine facet, the medial surface of the maxilla is excavated by a conspicuous, sinuous and dorsally open furrow probably carrying the superior alveolar nerve and maxillary artery. Anteriorly, it leads to the posterior entrance of the canal that exits through the anterior maxillary foramen (Fig. 3) onto the lateral face of the maxilla. The furrow narrows posteriorly, and is pierced by the posterior maxillary foramen (Fig. 3E), which opens on the lateral face of the maxilla above the largest tooth. Still more posterior, a more lateral longitudinal furrow accommodated the jugal.

The outline of the maxilla is rather consistent. The variability concerns mainly the dentition (see below). Compared to the best known maxilla of *Tichvinskia*, the maxilla of *Procolina* is more clearly triangular in

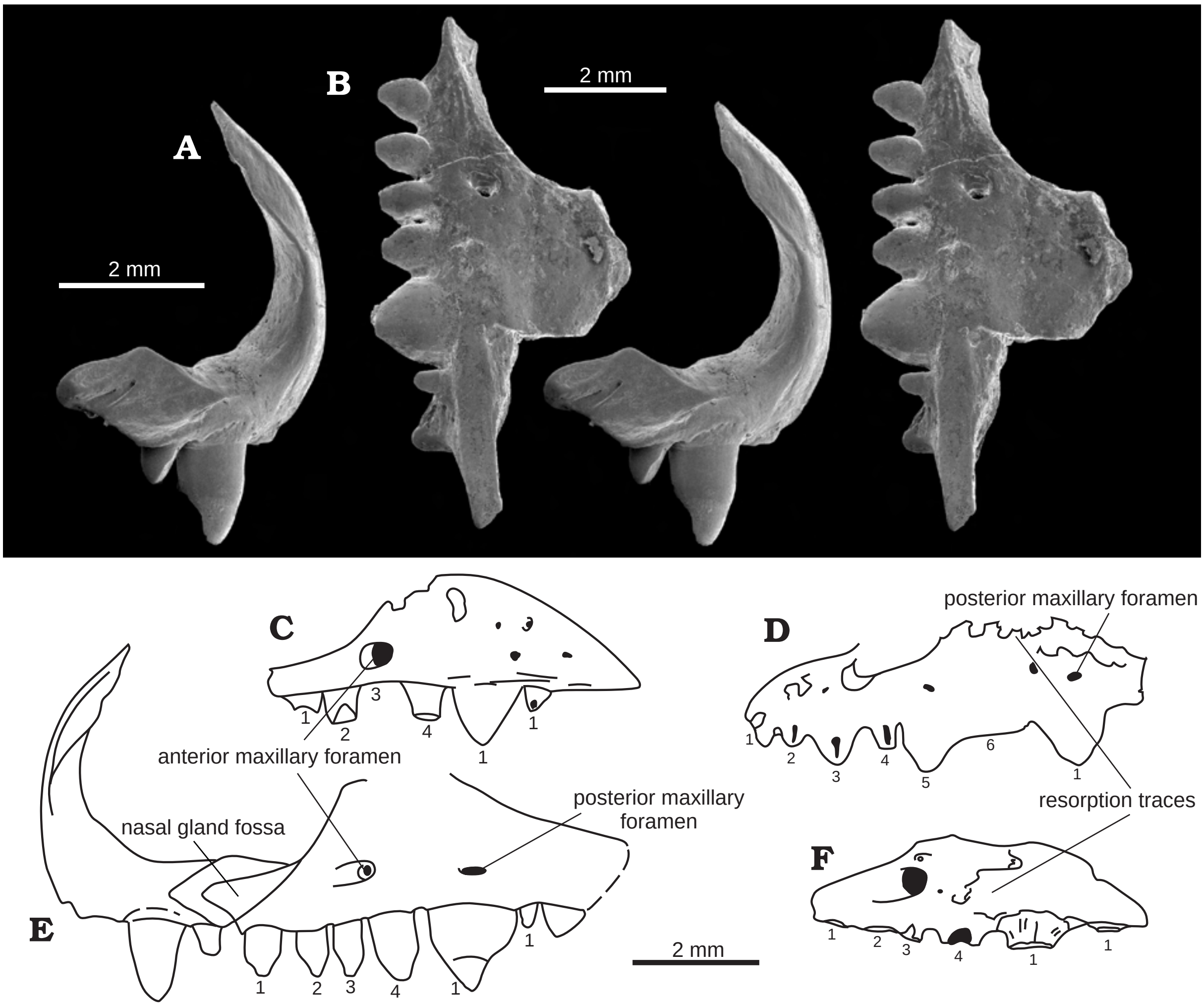

Fig. 3. **A**–**C**, **E**, **F**. *Procolina teresae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Right premaxilla ZPAL RV/796. **B**. Right maxilla ZPAL RV/711. **C**. Juvenile right maxilla ZPAL RV/735 (reversed). **E**. Left maxilla ZPAL RV/711 combined with the premaxilla ZPAL RV/796. **F**. Juvenile left maxilla ZPAL RV/742. **D**. Procolophonidae gen. indet., Early Triassic of Czatkowice 1, Poland. Juvenile left maxilla (reversed) ZPAL RV/734. Left lateral view. A, B, SEM stereo-pairs.

outline, and much shorter (the index of maximum length to maximum depth is 3, rather than 4 as in *Tichvinskia*), with the anterior slope relatively longer and the posterior end relatively deeper than in *Tichvinskia*. In *Procolophon* the maxilla displays a roughly ovoid outline, only slightly deeper in front. It bears more teeth than in *Procolina*, and the teeth are smaller relative to maxillary depth than they are in *Tichvinskia* and much more so than in *Procolina*.

The premaxilla-maxilla joint with two long processes, one of each bone, entering counter concavities, is much more intimate than it is in most Lepidosauria (while recalling a basal lepidosauromorph *Marmoretta*, Waldman and Evans 1994). In view of the fairly consistent type of procolophonid dentition the type of contact might be expected to be consistent too. However, it appears dramatically different in *Tichvinskia vjatkensis* in which a straight rather than V-shaped suture is shown (Ivakhnenko 1979, fig. 26). The *Tichvinskia* pattern is shared by *Nyctiphruretus* and *Contritosaurus* (Ivakhnenko 1979, fig. 26), and is thus probably plesiomorphic for procolophonines. In articulated skulls of *Procolophon trigoniceps*, as illustrated by Carroll and Lindsay (1985, figs 5, 7), this region is rather obscure, but is most probably similar to that of *Tichvinskia*. The extremely strong premaxilla-maxilla joint might be a unique character of *Procolina* or some more derived group of procolophonines, probably of "kapoids" (see Discussion).

Vomer. — The vomer is a subovoid bone with a flattened medial surface, a pointed antero-medial premaxillary process, and a posterior process that is dorsoventrally deep and projects laterally (Figs 4C, 5). The ventral surface usually bears five undifferentiated unicuspid teeth of which the two anterior ones make up a

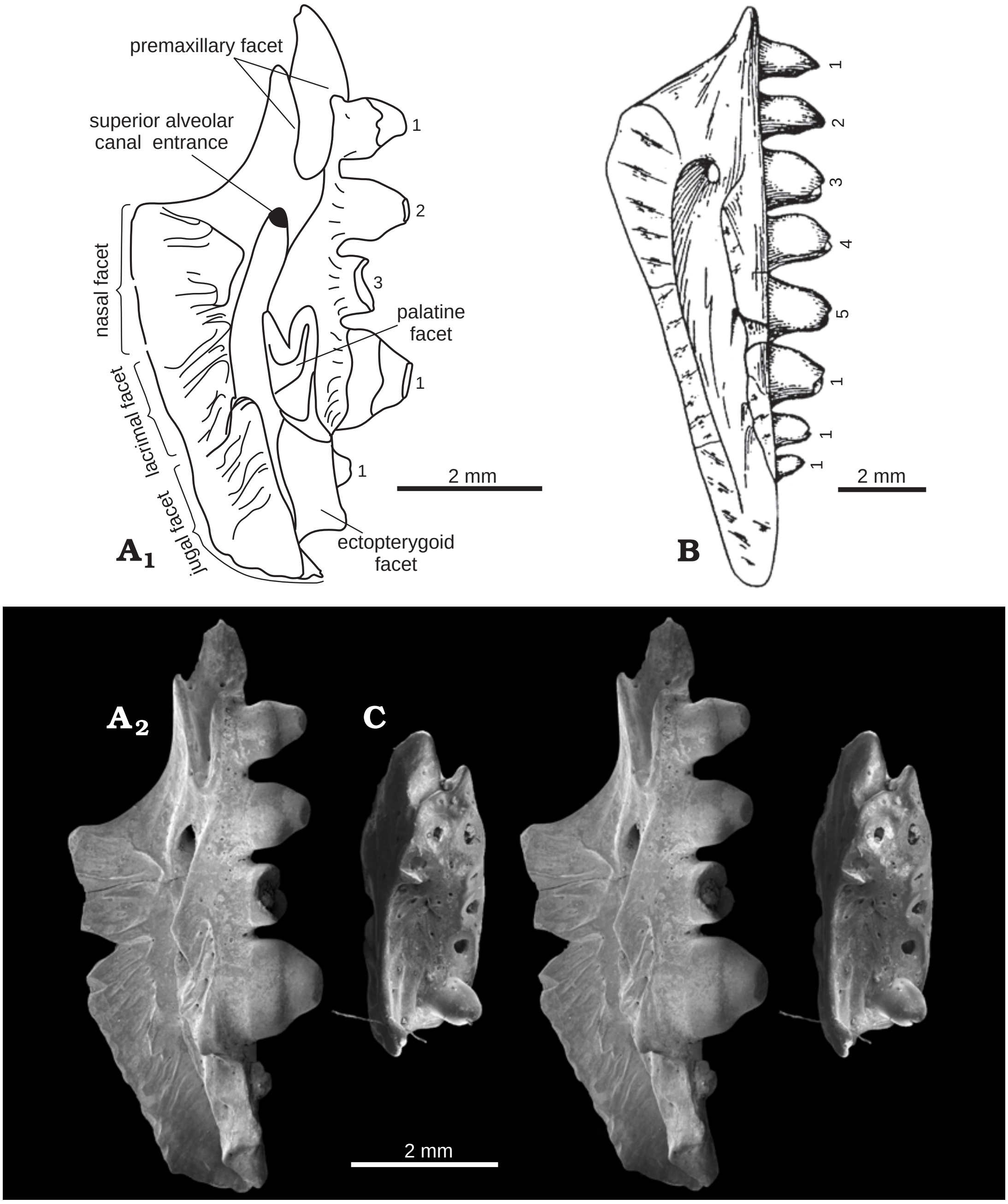

Fig. 4. **A**, **C**. *Procolina teresae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Left maxilla ZPAL RV/710, in medial view. **C**. Juvenile left vomer ZPAL RV/986, in ventral view. **B**. *Tichvinskia vjatkensis* Tchudinov *et* Vjushkov, 1956, right maxilla, reversed (after Ivakhnenko 1979, fig. 10B). A_2, C, SEM stereo-pairs.

transversely set pair, and the remaining three follow the lateral tooth (Fig. $5A_2$). Surrounded by the teeth, the ventral surface of the bone is concave and bears some neurovascular foramina. The premaxillary process is pyramidal and has an anteriorly ascending position (Fig. $5A_1$). Ventrally, it bears an elongated concave premaxillary facet that slopes ventro-laterally (Fig. $5A_2$, A_3, arrows) and matches the longitudinal step of vomerine facet of the premaxilla (see above). The posteromedial border of the bone is rarely preserved (Fig. 4C), but the posterolateral process seems to extend further posterior than the body of the bone itself, in which case it would match a deep subquadrangular medial incision on the palatine (Fig. 6B). The dorsal surface of the bone is concave (Fig. $5A_1$), and bears complicated palatine facets. When articulated the paired vomers produce an elongated posterior incision to receive the medial processes of the pterygoids (Fig. 8). The symphysial surface of the bone is heavily sculptured (Fig. 5B) with oblique posteroventral furrows, and penetrated by vascular canals. In the posterior one third it bears a distinct facet, probably for the pterygoid.

The described vomer is referred to Procolophonidae on the basis of its dentition that closely corresponds to that of the anterior parts of the jaws in relative size and morphology.Vomers of this type are among the most common procolophonid bones, and correspond to *Procolina teresae* in frequency and absolute size. This type is reminiscent of the procolophonin vomers illustrated by Ivakhnenko (1979, fig. 3) except for the lack of a medial row of denticles. It also differs from the vomer of *Tichvinskia* in relatively larger size of the teeth. In *Procolophon trigoniceps* (Carroll and Lindsay 1985, fig. 10), the vomerine teeth are still smaller than in *Tichvinskia* and more numerous. A comparison with outgroups (*Contritosaurus*, Nyctiphruretidae; Ivakhnenko 1979) shows that a reduced number and increased size of vomerine denticles, as well as the disappearance of the sagittal row of denticles are all derived character-states in procolophonids.

Variability of the vomer mainly concerns the dental formula. It is unordered and seems to reflect phases and anomalies of the tooth replacement process. The normal tooth count of 2 + 3 may occur in both juveniles and adults. We assume that growth of the bone was normally accompanied by a replacement of smaller teeth by larger ones, probably involving fusion of two or more very early tooth buds into one. However, this process must have been easily disturbed, as demonstrated by specimens having small replacements forced between the functional teeth (ZPAL RV/761) or implanted medial to the main tooth row (ZPAL RV/729) (Fig. 5B).

Palatine. — Only one type of procolophonid palatine has been identified in the material. It is exemplified by specimens ZPAL R-IV/525–527 (Fig. 6A–C) and many fragments. All of them have exactly the same roughly triangular outline with many corrugations and bear no palatal denticles. Oriented after the data from articulated specimens published thus far (Ivakhnenko 1979, figs 3, 4; Carroll and Lindsay 1985, fig. 6), they have the acute apex directed anteriorly, and lack the elongated appearance of the palatines of diapsid reptiles.

The ventral surface of the bone (Fig. 6A) is strongly concave with the axis oriented parasagittally, towards the choana. A tongue-like process protrudes anterodorsally and slightly above the choanal border. It is accompanied by several smaller tubercles situated medial and posterior to it, that together make up a complicated facet facing anterodorsally that may have received the prefrontal (Fig. $6B_1$). Lateral to it, a sinuous facet was destined for the maxilla (ventrally) and most probably for the lacrimal (dorsally). It consists of two tubera separated by a U-shaped infraorbital incision situated directly at the lateral exit of the transversal furrow on the dorsal surface. Posteriorly, the maxillary facet passes into the ectopterygoid one, which probably merged with the ectopterygoid facet of the pterygoid. The posteromedial border was overlapped ventrally by the pterygoid, as demonstrated by a partly preserved shelf-like facet (Fig. $6A_2$). A deep excavation of the anteromedial border must have accommodated the posterior process of the vomer (Fig. $6B_1$).

The dorsal surface of the palatine (Fig. 6B) is saddle-shaped, concave longitudinally and convex transversely. A conspicuous groove extends from the medial border of the bone just posterior to the vomer facet to the already mentioned U-shaped infraorbital incision. According to Carroll and Lindsay (1985), the foramen could have carried a portion of the maxillary branch of the Vth nerve and palatine artery and/or vein. According to Ivakhnenko (1979) it contained an anastomosing branch between the palatine artery and the maxillary artery.

Common reptilian, in particular lepidosauromorph, features such as a suborbital fenestra with a U-shaped incision between the main palatine body and the posterolateral corner of the maxillary process, were absent or very limited. The entire margins of the bone were in contact with neighboring elements except for the choanal incision and passages for arteries and nerves. A small posterior portion of the palatine is probably broken off (ZPAL RV/526, Fig. 6).

Both Ivakhnenko (1979) and Carroll and Lindsay (1985) report the presence of palatine denticles in the Procolophoninae. According to Ivakhnenko (1979), they also occur in *Contritosaurus* while disappearing only in Late Triassic *Hypsognathus*, a specialized representatives of the Leptopleuroninae. The lack of palatine denticles in *Procolina* is here regarded as derived.

Pterygoid. — The pterygoid of *Procolina* displays broad proportions with largely expanded palatal wing and large quadrate process. The ventral surface of the palatal wing (Fig. $7B_2$, C) is strongly concave between a medial margin that is thick and truncate, and a lateral one that is sharp. The concavity passes gently through the neck onto the medial side of the quadrate process. The palatal wing is not separated from the neck by any crest. The dorsal surface of the palatal wing is convex transversely (Fig. 6A), and concave longitudinally. It is very smooth and bears no vascular traces. The quadrate process bears a deep excavation bordered by protruding ridges (possible sites of insertions of the protractor pterygoidei and levator pterygoidei muscles). The medial border of the palatal wing is never completely preserved to demonstrate either the kind of articulation with the

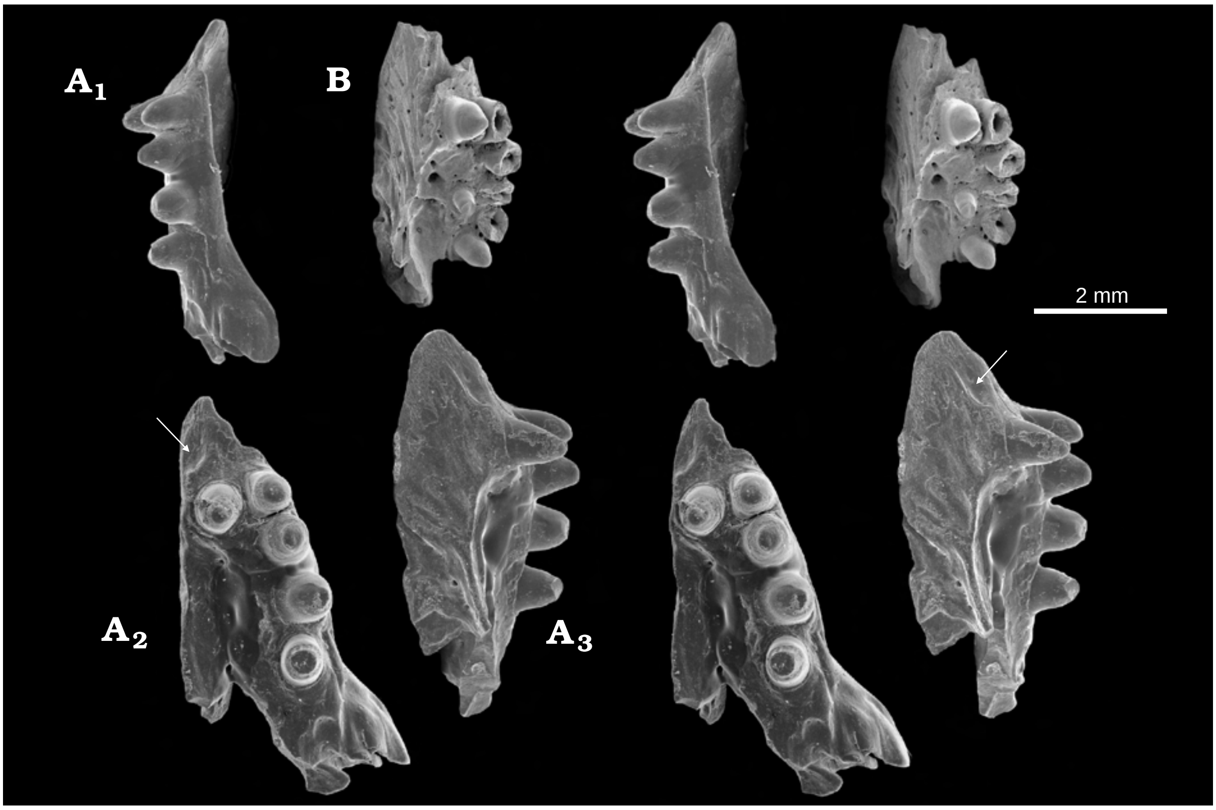

Fig. 5. *Procolina teresae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Left vomer ZPAL RV/714, in lateral (A_1), medial (A_2), and ventral (A_3) views. **B**. Left vomer ZPAL RV/729, in medio-ventral view. The arrows indicates premaxillary facet. SEM stereo-pairs.

vomer or any possible articulation with the contralateral pterygoid. The preserved fragment of the medial border bears one row of denticles (Fig. 7B_2, E), but there are no teeth on the ectopterygoid process (Fig. 7B_2, C).

In a number of specimens, the thick ectopterygoid process is present intact. On this process, the palatine facet (Fig. 7B_2, C) presents a shelf-like offset almost half as large as the entire palatal wing and is medially delimited by an incision. The ectopterygoid facet extends on both ventral and dorsal surface of the thick lateral end of the process. The medial side of the neck is deeply excavated for the basipterygoid articulation, which lacks a bordering knob and is notable in being widely open ventrally (Fig. 7C). In life, the basipterygoid fossa must have faced more or less medially to articulate with the basipterygoid processes, and this implies a medioventral orientation of the excavated surface of the quadrate process.

Quadrate. — The quadrate is represented by at least 9 specimens, each of them with a well ossified distal condyle and a poorly ossified proximal end (Figs 2E, 7D). The articular condyle, which is weakly divided into medial and lateral portions, is much shorter anteroposteriorly than in transverse dimension. Dorsally it passes into an elongated stem. The stem narrows proximally when viewed in posterior view, but anteromedially it extends into a triangular flange that expands proximally (Fig. 2E). The unfinished proximal border of the flange bears a step-wise shelf, probably for the pterygoid articulation. The distal end of the bone protrudes laterally and bears an articular surface for the quadratojugal, which is circular and faces laterodorsally. A concave lateral margin of the quadrate contributed to the quadrate foramen.

The quadrate of *Procolina* does not differ from that of *Procolophon trigoniceps* (Carroll and Lindsay 1985), but the bone is difficult to illustrate and its articulations with the neighboring bones are complicated, so that a detailed comparison is impossible.

Dentary. — The dentary is a fairly massive bone, the depth of the ramus under the molariform tooth (dd) being about a quarter of the length of the tooth row length (dtl; Appendix 1), while expanding dorsally at the level of the posterior teeth (Figs 9, 10). The labial surface is smooth and slightly convex dorsoventrally. A row of irregular mental foramina, for branches of the inferior alveolar nerve, extends on the anterior portion of the dentary at about mid-depth.

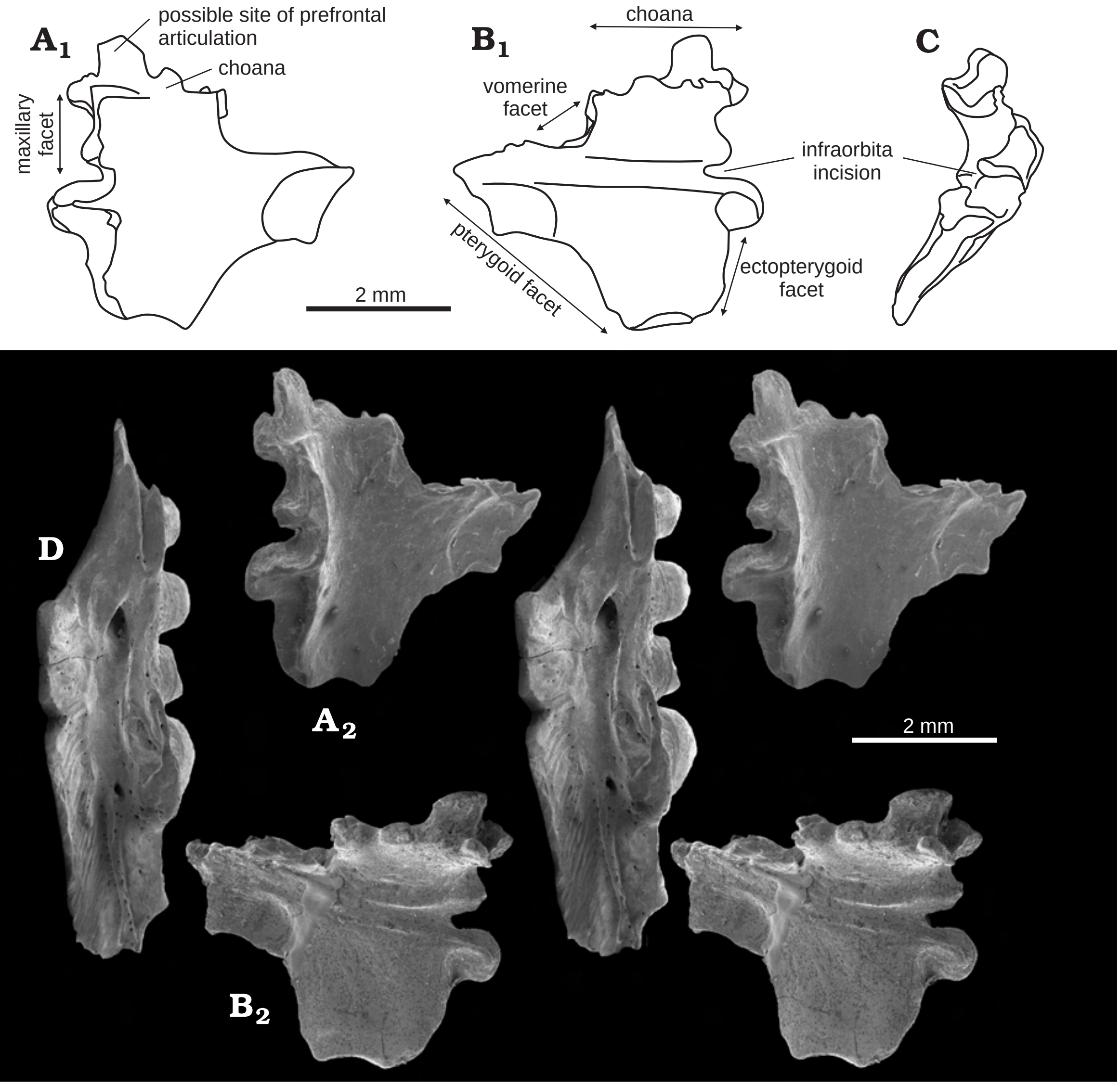

Fig. 6. *Procolina teresae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**–**C**. Right palatine ZPAL RV/526, in ventral (A_1, A_2), dorsal (B_1, B_2 reversed), and lateral (**C**) views. **D**. Left maxilla ZPAL RV/710, in dorso-lingual view. A_2, B_2, D, SEM stereo-pairs.

On the lingual side of the dentary, the irregularly U-shaped symphysis faces anteromedially (Figs 9, 11D$_1$). Its position determines the angle between the mandibular rami as about 60°. The tooth-bearing margin is large and turns medially in the symphysial region. Below the tooth row, a deep dental shelf is slightly flattened for the splenial contact, and bears an elongated coronoid facet posterodorsally (Figs 9, 10A$_2$). As a rule, the posterior rudimentary teeth, referred to herein as accessory teeth, are located above this facet. The dental shelf overhangs the Meckelian fossa. Separated from the fossa by an osseous wall, a dorsal canal carried the inferior alveolar nerve. Its entrance (Fig. 9, indicated by an arrow), situated below the posterior one third of the tooth row, serves as a reference point for the dental formula (see below). The concavity of the Meckelian fossa is ventrally bordered by the thick edge of the dentary, which is lingually flattened for the ventral contact with the splenial. As measured on 13 specimens (Appendix 1), the approximate dimensions show variability range in tooth row length from 6 mm (juvenile) to about 10 mm, with a mean value of about 8 mm and a mean ratio of dentary depth (dd) to the tooth row length of about 1:4.7. These numbers give only a rough indication, because of the small sample on which the measurements can be taken, and the difficulties in taking them exactly. The mandibular proportions given by Ivakhnenko (1979) for procolophonid jaws, and those for mandible to skull length in *Procolophon* (Carroll and Lindsay 1985), allow estimates of mandible length in *Procolina* as about 15 to 25 mm, and hence a total skull length of

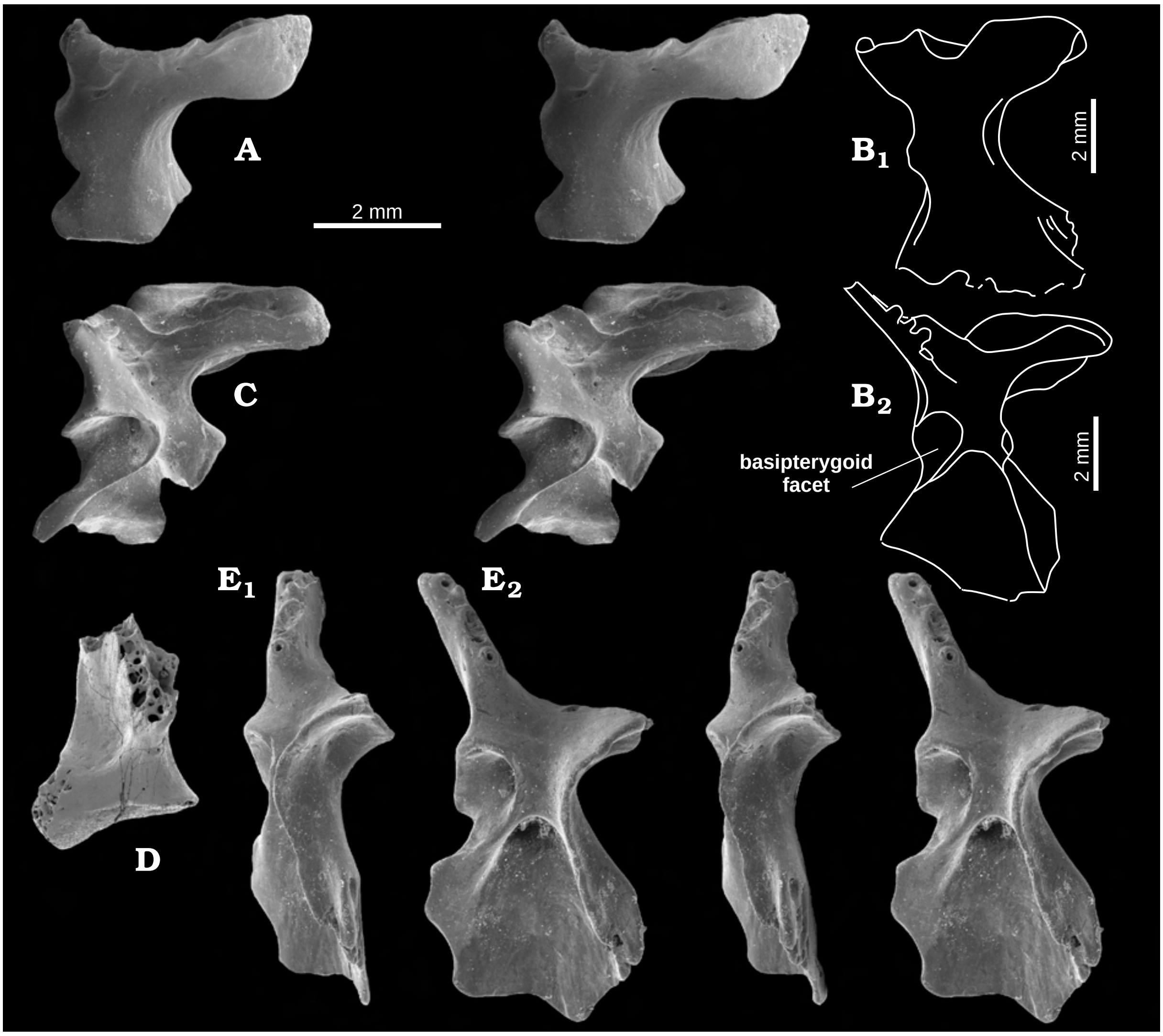

Fig. 7. *Procolina teresae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Right pterygoid ZPAL RV/63, in dorsal view. **B**. Reconstruction of the right pterygoid, in dorsal view (B_1) and the left pterygoid, in ventral view (B_2). **C**. Left pterygoid ZPAL RV/521, in ventral view. **D**. Right quadrate ZPAl RV/756, in anterior view. **E**. Left pterygoid ZPAL RV/505, in lateral (E_1) and medioventral (E_2) views. All but B SEM micrographs; all but B, D stereo-pairs.

about the same or slightly larger. The variability of the dentary is mostly in the dentition and is partly ontogenetic. Other than this, the variability of the posterior outline of the bone is due to different preservation of this fragile part. The juvenile specimen ZPAL RV/515 (Figs 9C, 10A) is noteworthy. This is the only specimen with the posterior part of the dentary preserved, and it is exceptionally long. All remaining specimens have the posteroventral part obliquely broken off. ZPAL RV/515 also differs by having a lateral protrusion of the dental shelf that is separated from the lateral dentary face by an acute bend and is suggestive of a buccal space. Lingually, it bears a surangular facet.

DENTITION

The dentition is heterodont. There is an anteroposterior gradation of tooth size and morphology with the abrupt changes within the posterior portion of the tooth row, where one or two teeth become much bigger, while the posteriormost teeth most often remain rudimentary (herein referred to as accessory teeth, p. 109). Only one dominant tooth in each maxilla and dentary is here regarded as a molariform tooth based on the criteria presented above (p. 109), especially the position of the neurovascular foramina (see Figs 3, 9). In the dentary, the accessory teeth are situated above the coronoid facet.

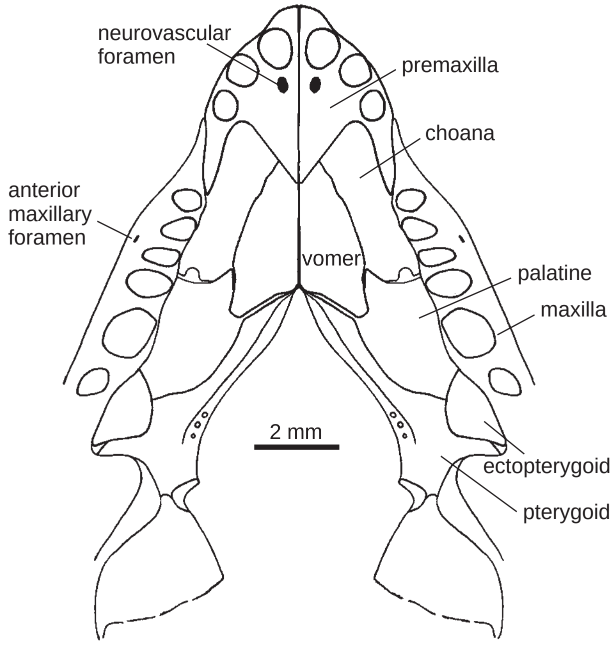

Fig. 8. *Procolina teresae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Reconstruction of palate and jaws, in ventral view.

Tooth shape. — Most specimens display a consistent tooth shape (Figs 10–12) with no trace of bicuspid condition. Incisiform teeth are roughly chisel-like (Fig. 10C$_1$). The outline of their bases, are more or less transversely flattened. Beginning with the premolariform teeth, the crown bases become increasingly more robust toward the rear. They are bulbous, but cylindrical rather than spherical, and are capped with cone-shaped apices of blackish enamel. Wear facets generally face posteromedial on the premaxilla, medial or apical on the maxilla, and apical or posteromedial on the dentary.

Dental formula. — As a whole, the upper (premaxillary + maxillary) tooth row includes 8 or 9 teeth. The premaxilla bears 3 slender and more acute incisor-like teeth referred to as incisiforms. The maxillary tooth row includes 5 or 6 teeth of which the last one is tiny (Fig. 12B, C). The penultimate, usually the biggest, is the molariform. The number of premolariform teeth is subject to a small amount of intraspecific and/or ontogenetic variability. There are either 3 (Figs 4A, 12B) or 4 teeth (Fig. 3E) distributed within the same jaw section anterior to the molariform tooth. Significantly, a maxilla specimen ZPAL R/735 (Fig. 12A), smaller than the average and showing traces of tooth replacement already displays the modal tooth formula 4.1.1. Specimen ZPAL RV/721 bears traces of fusion of tooth buds II and III into one tooth, and probably the same in the case of buds V and VI (Fig. 12B).

The dentary tooth row includes 7 or 8 teeth. The dominant type of mandible matches the morphology of the *Procolina* maxillae. The formula is 5 (rarely 4-6).1.1-2. The degree and rate of molarization along the tooth row are subject to variability, as is the point of transition between the tooth categories. Usually the Vth or VIth dentary teeth are the largest. Which one of them is termed molariform herein is a matter of its position with respect to the posterior alveolar foramen (see p. 7).

Some anteriad shift of the posterior teeth (Appendix 1, Fig. 9E) is evidenced by the differences in relations of the dominant tooth to the posterior alveolar foramen, and to the coronoid facet (see p. 109). There is considerable variability in the size and position of accessory teeth, which may be quite small (Fig. 9C) or equal in size to the molariform tooth (Fig. 10D). Their position varies from posterolabial (Figs 10A, 11D) to directly posterior to the molariform tooth (Fig. 10C). Only in one instance, is there a trace of tooth replacement in a form of small cavities posterolingual to the tooth sites (Fig. 10A$_3$).

Among 21 adequately preserved dentaries (Appendix 1), 15 assigned to *Procolina teresae* display a normal formula 5.1.1-2. Allowing for some amount of variability, the normal formula occurs in the other six, in which a putative formula is 6.1.1 or 4.1.1. They seem to be ontogenetic variants. For example in ZPAL RV/524 (Fig. 9D, Appendix 1) the seventh (instead of the sixth) tooth dominates the dentition. This is considered an overgrown first accessory tooth, because it is located over the anterior part of the coronoid facet, as usual for accessory teeth. The posterior alveolar foramen is located under the anterior part of the sixth tooth. This tooth is thus regarded as the main molariform tooth.

Specimen ZPAL RV/683 (Fig. 9E), considered adult, has just four rather robust premolariform teeth, and the molariform tooth is shifted to a slightly more anterior position. En empty space posterior to premolariforms suggests that one tooth is missing, possibly lost by replacement. This specimen, here considered a variant of *Procolina teresae*, is another example of the cranialword shift of the teeth in ontogeny.

ZPAL RV/510 and 516 (Figs 11A and 9B, respectively) are considered as juveniles of *Procolina teresae*. They already display a normal formula, which varies only by one premolar tooth, from 5.1.0 in ZPAL RV/510 to 6.1.1 in ZPAL RV/516. The posterior alveolar foramen is always close to the dominant tooth.

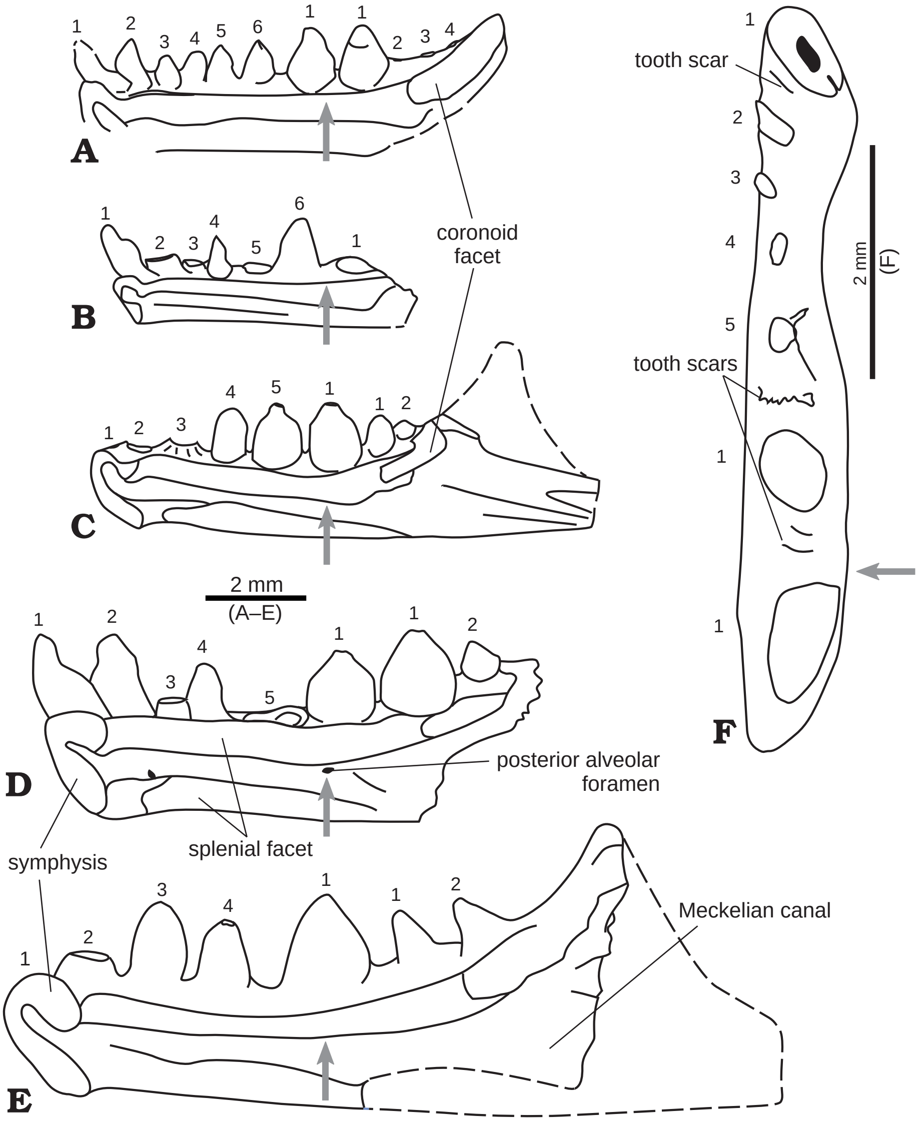

Fig. 9. Right dentaries from the Early Triassic of Czatkowice 1, Poland, in medial view. **A**, **F**. Procolophonidae gen. indet. I: ZPAL RV/733 (**A**) and ZPAL RV/989 (**F**). **B**, **C**–**E**. *Procolina teresae* gen. et sp. n.: ZPAL RV/516 (**B**), ZPAL RV/515 (**C**), ZPAL RV/524 (**D**), and ZPAL RV/683 (**E**). The arrow indicates the position of the posterior alveolar foramen.

Ontogeny. — There are virtually no traces of tooth or jaw resorption on the lingual side. Instead many maxillae specimens demonstrate perforations of the lateral tooth wall, and less solid, resorbed bone surface (Figs 12D, 13B). In larger specimens of *Procolina* (dtl 8.6 mm on average), the bony tissue becomes more compact. Some teeth are perforated apically (Figs 11A, 12A). In ZPALRV/739 the entire dentition is shed, except for the circular tooth bases (Fig. 13A$_2$). The dental formula is rather stable in ontogeny. It is 5.1.1-2 in dentaries (dtl 7.6 on average) and 3-4.1.1 in the maxillae. Tooth replacement affects mostly the premolar section.

VERTEBRAL COLUMN

The better ossified procolophonid vertebrae (Fig. 19A, H) of the Czatkowice 1 material are here associated with the better ossified skull material assigned to *Procolina teresae*. *Procolina teresae* seems to have the spines placed more anteriorly than do other Czatkowice 1 procolophonids, which results in the posterior fossa being more exposed (Fig. 19A$_2$, B$_2$), but these differences might be subjective. It also have less swollen bases of the neural spines. Vertebrae representing all regions of the vertebral column of *Procolina teresae* are known. However, the atlas-axis complex elements and well-preserved sacrals are very rare (respectively ZPAL RV/825, 826 and ZPAL RV/835–838). On the basis of overall morphology we were able to distinguish seven cervical vertebrae (Fig. 16A, ZPAL RV/825–830 and Fig. 16C, the first from the left, ZPAL RV/831). The seventh and probably eighth vertebrae (ZPAL RV/831 and 832) seem to be transitional to the dorsal series. Dorsals (Fig. 16C three on the right, ZPAL RV/845, 833, 834) are proportionally slightly shorter than the cervicals and longer than the sacrals. Three sacrals (Fig. 18), each with distinctive sacral ribs have been tentatively assigned to *Procolina teresae*. Anterior caudals have well-developed pleurapophyses. All centra (pleurocentra) are amphicoelous and reach up to 7 mm in length (Table 1), but usually less than this.

Atlas-axis complex. — The cuboid atlantal centrum is fused with axial intercentrum (Fig. 17A). Dorsally and posteriorly the element is concave. The anterior surface is well ossified and slightly heterocoelous. On the lateral side, immediately dorsal to the axial intercentrum, there is a deep excavation. The articular facet for the atlantal neural arch is located in the anterior and dorsal part and faces dorsolaterally. Ventrally the atlantal centrum is obscured by the axial intercentrum.

The axial intercentrum (Fig. 17A) is triangular in lateral view. It is placed ventral and somewhat posterior to the atlantal centrum and attaches to the latter by its anterodorsal face. The ventral surface is smooth and convex, while the posterodorsal surface is concave.

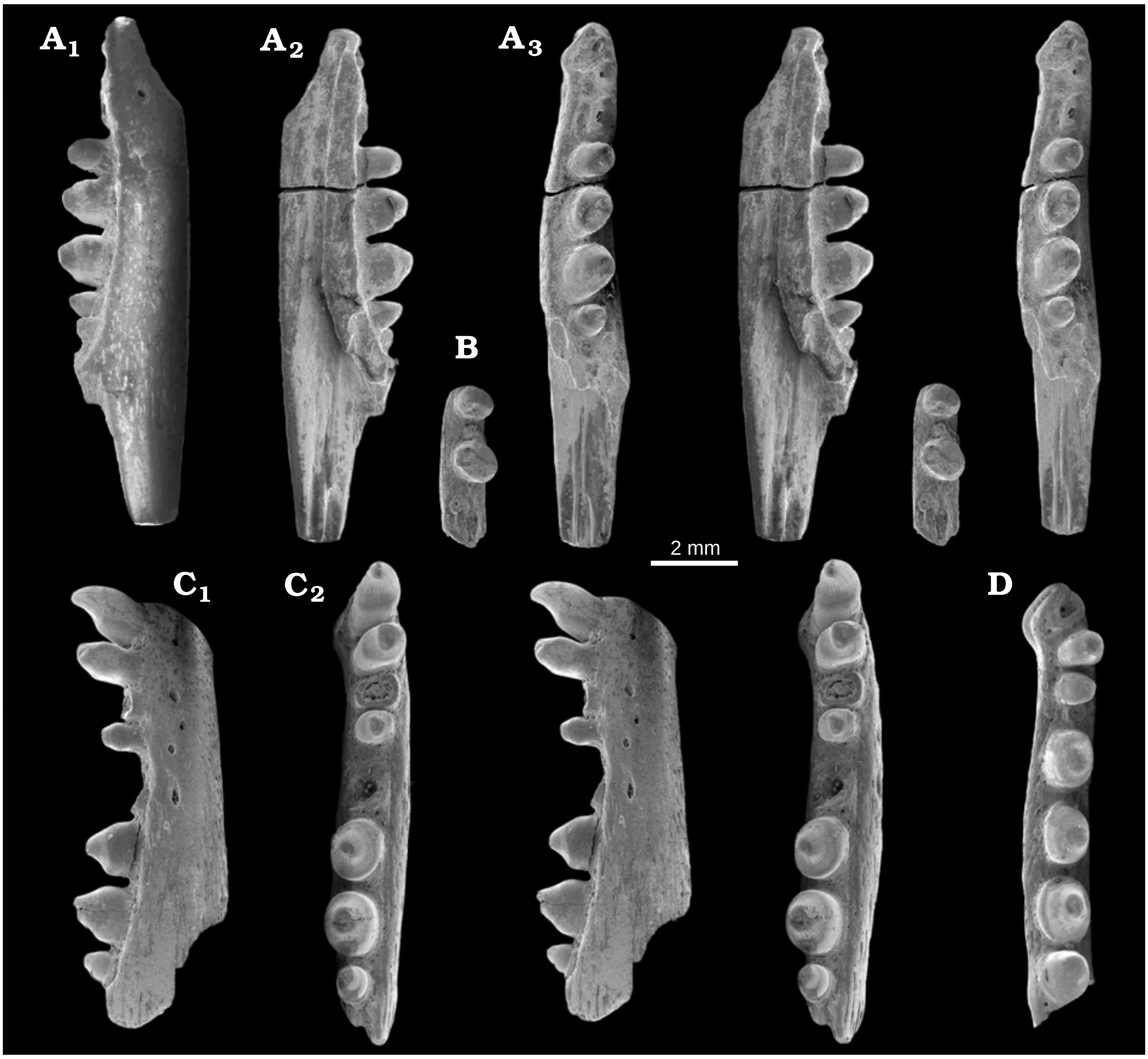

Fig. 10. **A**, **C**, **D**. *Procolina teresae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Right dentaries: ZPAL RV /515 (**A**), ZPAL RV/524 (C), and ZPAL RV /799 (**D**). **B**. Procolophonidae gen. indet. II, Early Triassic Czatkowice 1, Poland. The only fragment with bicuspid dentition ZPAL RV/507. Labial (A_1, C_1), lingual (A_2), and occlusal (A_3, B, C_2, D) views. SEM micrographs; all but A_1, D stereo-pairs.

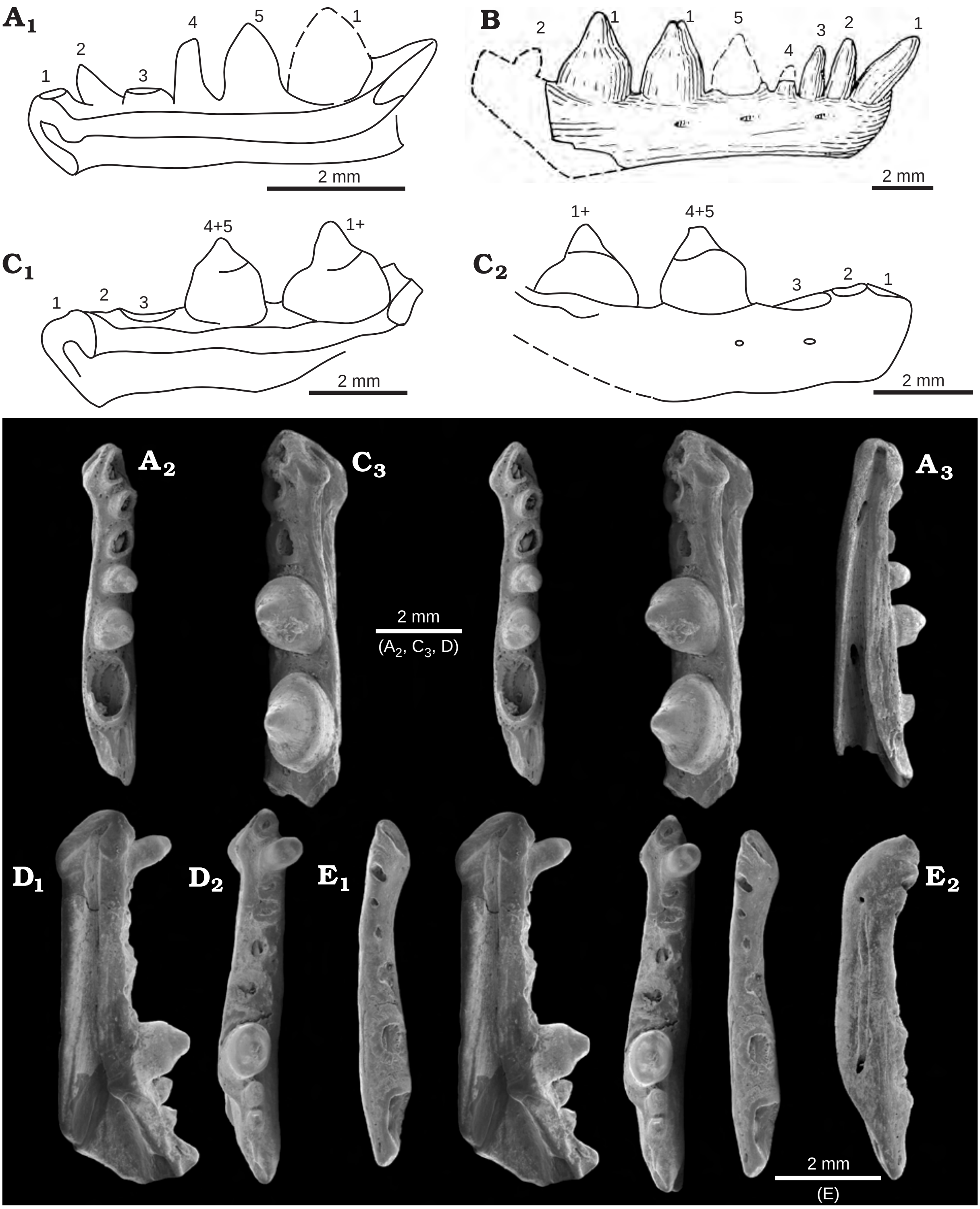

Fig. 11. Procolophonids from the Early Triassic of Czatkowice 1, Poland. **A**, **D**. *Procolina teresae* gen. et sp. n. Right dentaries: ZPAL RV /510 (**A**) and ZPAL RV/513 (**D**). **B**. *Burtensia burtensis* (Otschev, 1958), left dentary. **C**. Procolophoninae gen. indet. III ZPAL RV /716. **E**. Procolophoninae gen. indet. I ZPAL RV /989. Lingual (A_1, A_3, C_1, D_1), labial (B, E_2,), and occlusal (A_2, C_3, D_2, E) views. A_2, A_3,C_3, D_1, D_2, E_1, E_2, SEM micrographs; all but A_3, E_2 stereo-pairs.

The axis centrum (Fig. 17B) resembles other anterior cervicals (especially vertebrae three and four) in overall morphology. It is trapezoidal in lateral view and triangular in cranial view. Broad, shallow concavities are seen on the lateral sides, separated by a ventral sagittal ridge, and the long axis of the centrum extends obliquely (see below). On the anterior part of the centrum, immediately ventral to the raised surface indicating the posi-

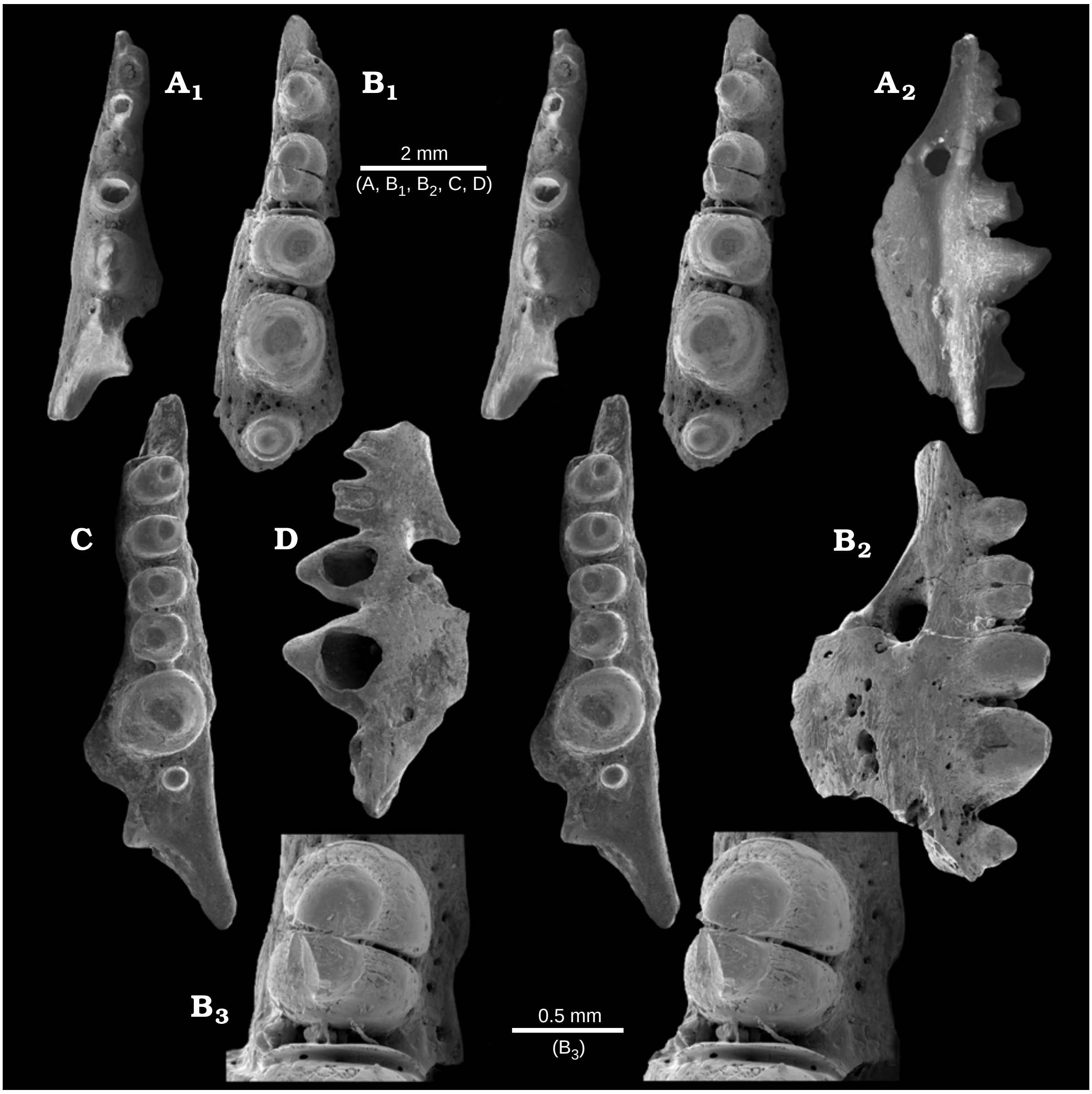

Fig. 12. *Procolina teresae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**, **B**. Right maxillae: ZPAL RV/735 (**A**) and ZPAL RV/721 (**B**). **C**, **D**. Left maxillae: ZPAL RV/711 (**C**) and ZPAL RV/738 (**D**). Occlusal (A_1, B_1, B_3, C) and lateral (A_2, B_2, D) views, fused premolariforms II and III (B_3). SEM micrographs; all but A_2, B_2, D stereo-pairs.

tion of the fully fused neurocentral suture, there is a diapophysis, developed as a small bump. There are no signs of the parapophyses on the axial centrum. The paired subtriangular excavations are located on the caudal side of the arch, at the place where the bases of the postzygapophyses and the neural spine meet.

The axial arch bears a neural spine of distinctive shape. In lateral view, the spine is low with a horizontal dorsal edge (Fig. 17B). A prominent triangular cranial projection is present in the anterior part of the spine. It protrudes cranially to both the prezygapophyses and the anterior margin of centrum. The anterior and posterior ends of the spine are thickened and correspond to the insertion (anteriorly) and origin (posteriorly) of the supraspinal ligaments that connect the apices of succeeding spines. A shallow and extensive concavity on the lateral side of the spine is interpreted as the insertion of the *obliquus capitis magnus* muscle.

The postzygapophyses are similar to those of succeeding cervical vertebrae. In caudal view, their articular facets have a slight slope toward the midline. More or less pronounced mammillary processes for the origin of the semispinalis tendon are located on the dorsal side of the postzygapophyses. In contrast to the dorsals, but similar to the other anterior cervicals, the postzygapophysial bases of the axis are not swollen.

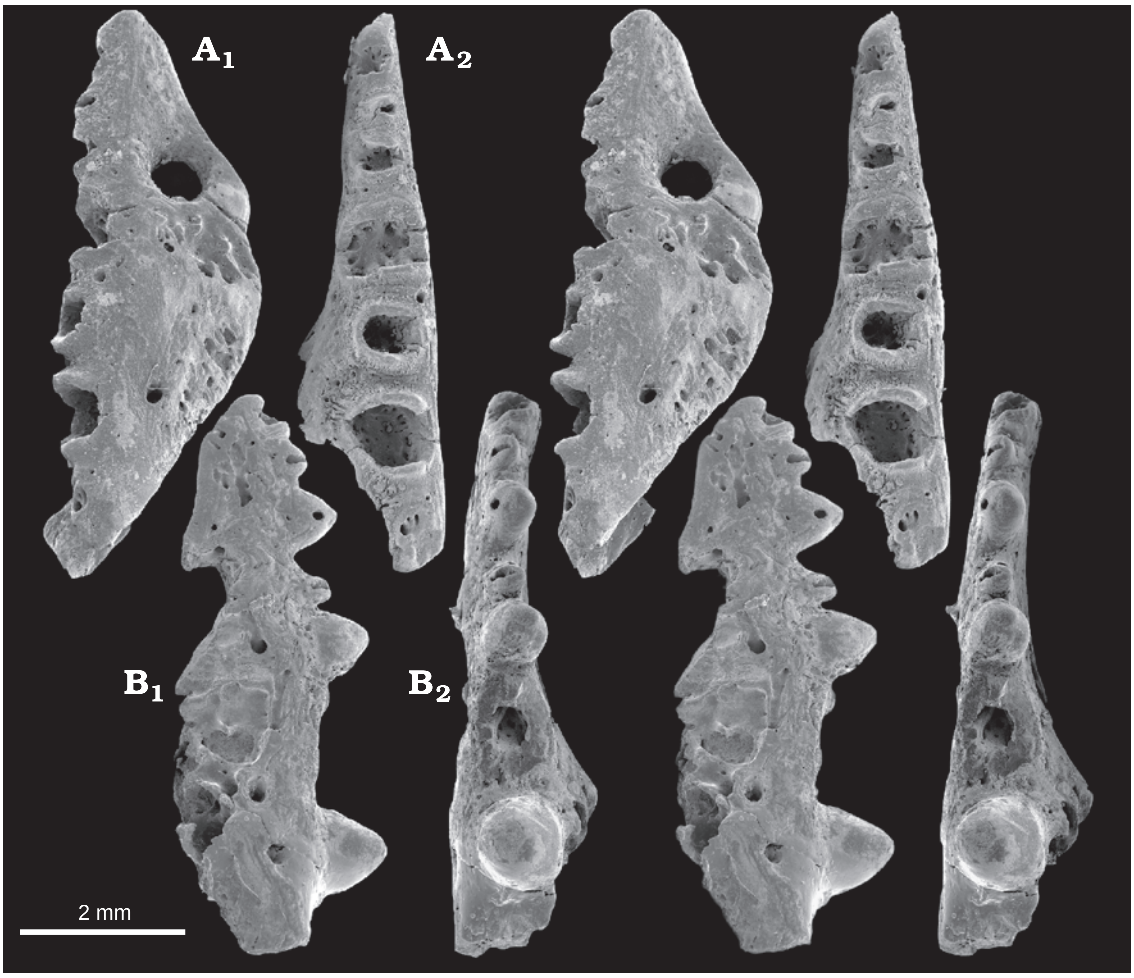

Fig. 13. Procolophonids from the Early Triassic of Czatkowice 1, Poland. Procolophonidae gen. indet. I. **A**. Left maxilla ZPAL RV/739. **B**. Right maxilla ZPAL RV/734. Lateral (A_1, B_1) and occlusal (A_2, B_2) views. SEM stereo-pairs.

As distinct from all other postatlantal vertebrae, the axial prezygapophysial articular facets lie directly on the neural arch walls and are oriented dorsolaterally at an angle of about 45° to the horizontal plane (on other vertebrae, they face dorsomedially).

Postaxial column. — The centra are holochordal, but they bear scars where they were perforated by the notochordal canal. Both the cranial and caudal articular surfaces of the centra are poorly ossified and hardly ever preserved in the Czatkowice 1 material. As preserved, the centra are trapezoidal in longitudinal section (Fig. 17C, D), because the ventral face of the centrum is slightly shorter than the dorsal one, thus suggesting the presence of intercentra in the presacral and caudal parts of the vertebral column. In the sacral series, intercentra must have been much smaller or absent, as indicated by the smaller ventral incisions between adjacent sacral centra.

One very characteristic feature of the cervical centra is that their long axes extend obliquely. This impression is strengthened by the fact that posterior faces of the anterior cervical centra projects somewhat more ventrally then the anterior ones.

In all vertebrae, on the dorsal surface of the centrum, there is a shallow hour glass shaped concavity (Fig. 19I), often divided longitudinally by a medial ridge. This differentiates vertebrae of *Procolina* from those of *Osmolskina* (Borsuk-Białynicka and Sennikov 2009) from the same assemblage, where the dorsal concavity is very deep, nearly reaching its ventral side.

On the lateral side, just below the neurocentral suture, there is a distinct concavity separated from the other side ventrally by a blunt sagittal ridge. Those excavations make the centra appear somewhat triangular in cranial and caudal views. They are most prominent on typical dorsals. On sacrals, they are compressed as

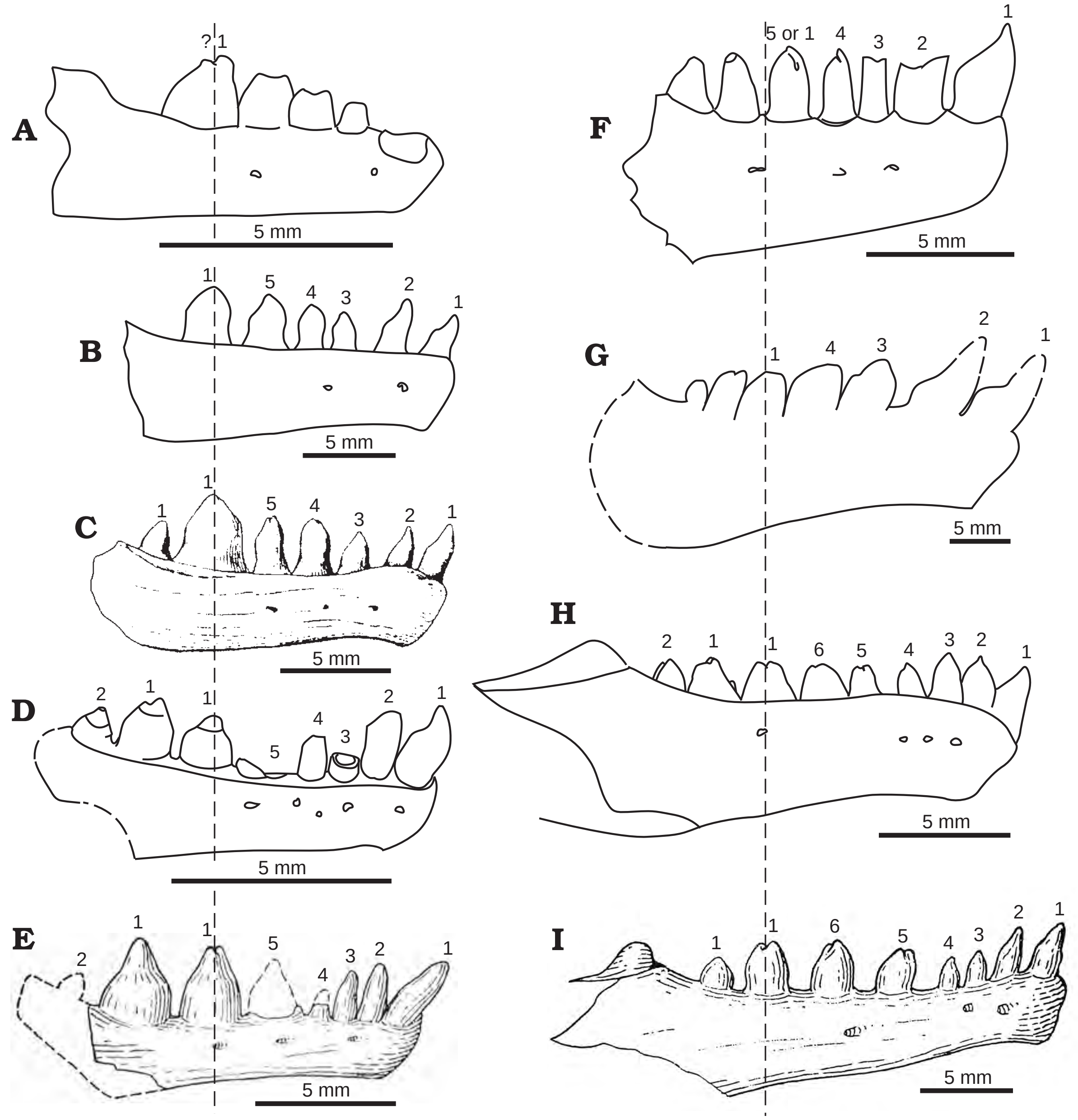

Fig. 14. Procolophonid dentaries in lateral view. **A**. *Kapes bentoni* Spencer *et* Storrs, 2002. **B**. *Kapes majmesculae* (Otschev, 1968). **C**. *Kapes amaenus* Ivakhnenko, 1975. **D**. *Procolina teresae* gen. et sp. n. **E**. *Burtensia burtensis* (Otschev, 1958). **F**. *Lestanshoria massiva* Novikov, 1991. **G**. *Orenburgia bruma* Ivakhnenko, 1983b. **H**. *Tichvinskia vjatkensis* Tchudinov *et* Vjushkov, 1956. **I**. *Timanophon raridentatus* Novikov, 1991. Vertical dashed lines denote the position of the molariform tooth. A after Spencer and Storrs (2002); B after Spencer and Benton (2000); C after Ivakhnenko (1975); F, I after Novikov (1994); G, H after Ivakhnenko (1979).

the massive bases of the sacral ribs push their dorsal borders ventrally. They are also reduced on anterior caudals, where pleurapophyses are located ventrally at the neurocentral suture. The ventromedial ridge has a smouth rounded surface on the dorsals, but forms a blunt keel on cervicals and is somewhat flattened on sacrals.

The third (first postaxial) vertebra has proportionally the longest centrum (Figs 16A, $17C_1$) comparable to the axial one, and centrum length decreases posteriorly to the seventh vertebra (Fig. 16C, first from the left), which has the proportions of a typical dorsal. All dorsals (Fig. 16C three vertebrae on the right) share the same centrum length, which is also retained in the anterior caudals, but sacrals are somewhat shorter.

The neurocentral suture is fully closed in all but the smallest specimens. Where visible it has the shape of a flattened W. It extends nearly horizontally from the anterodorsal border of the centrum, at one third of the

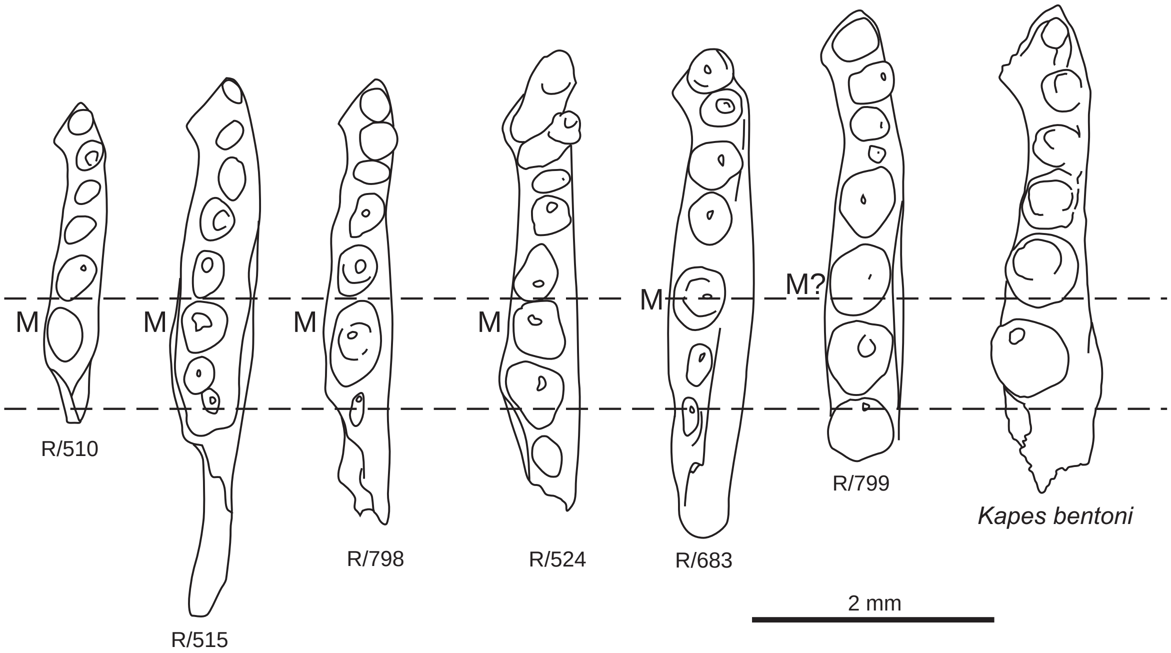

Fig. 15. *Procolina teresae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland, compared to *Kapes bentoni* Spencer *et* Storrs, 2002. Dentaries in occlusal view. The upper dashed-line denotes the level of the posterior alveolar foramen, the lower dashed-line denotes the level of the posterior limit of tooth row in the juvenile ZPALRV/510. Catalogue numbers are shortened. M denotes the position of the molariform tooth. The position of ZPAL RV/799, and that of *Kapes bentoni* are conjectural. No accessory teeth occur in the juvenile ZPAL RV/510. The figure illustrates individual variability of the tooth replacement in accessory part of the dentition.

centrum length it extends steeply posterodorsally and then posteroventrally to form a triangular projection, and then, posteriorly and slightly dorsally, to the posterior border of the centrum.

Neural arch and spine. — Pedicels of the presacral neural arches project vertically from the centrum to support a flat roof. All those elements — with the centrum ventrally — surround a subrectangular to oval neural canal, which is well-developed in cervicals and dorsals, but is constricted in sacrals (Fig. 18) by mediolaterally expanded neural arch pedicels that form the bases for stout sacral ribs. All arches are firmly connected to matching centra as the neurocentral suture closes and fuses in adults. In dorsal view the arch is constricted midway along its length and expands at the bases of the pre- and postzygapophyses.

Neural spines of all postaxial vertebrae are very low and terminate in a somewhat roughened surface for ligament and probably for semispinalis and spinalis muscle insertions. Generally the spines are rectangular in lateral view. Their long axes extend obliquely in cervicals, and the dorsal surfaces of the spines extend anteroventrally. The long axes and, consequently, the dorsal faces, become horizontal in the dorsal series. The spines have the longest bases on anterior cervicals and become increasingly shorter posteriorly. On the seventh vertebra the spine is well-developed with a short base and a roughened end, interpreted here as the insertion of interspinal ligaments. On the dorsals, sacrals and anterior caudals, the spines have a common morphology: they are low with a horizontal dorsal edge and display moderately long bases that start where the prezygapophyses unite. On sacrals they are proportionally smaller. In a few larger (old) specimens the distal end of the spine is rugose, but no lateral or antero-posterior extensions were found on any vertebra.

On the posterior surface of the arch, below the spine and between the postzygapophyses, there is a shallow triangular excavation with prominent scars suggesting a double ligament insertion. (In contrast, the similar ligament excavation is much higher in *Osmolskina*; Borsuk-Białynicka and Sennikov 2009).

Zygapophyses. — The articular facets of the zygapophyses are oval in most specimens, but sometimes may be slightly square or triangular. They slope ventromedially, with the angles displaying some variability. Generally the slope is about 20° to the horizontal plane in anterior cervicals and decreases posteriorly to 10–15° in the dorsals, sacrals and caudals. Zygapophyses are widely spaced on presacral vertebrae, but lie closer to the midline on the caudals.

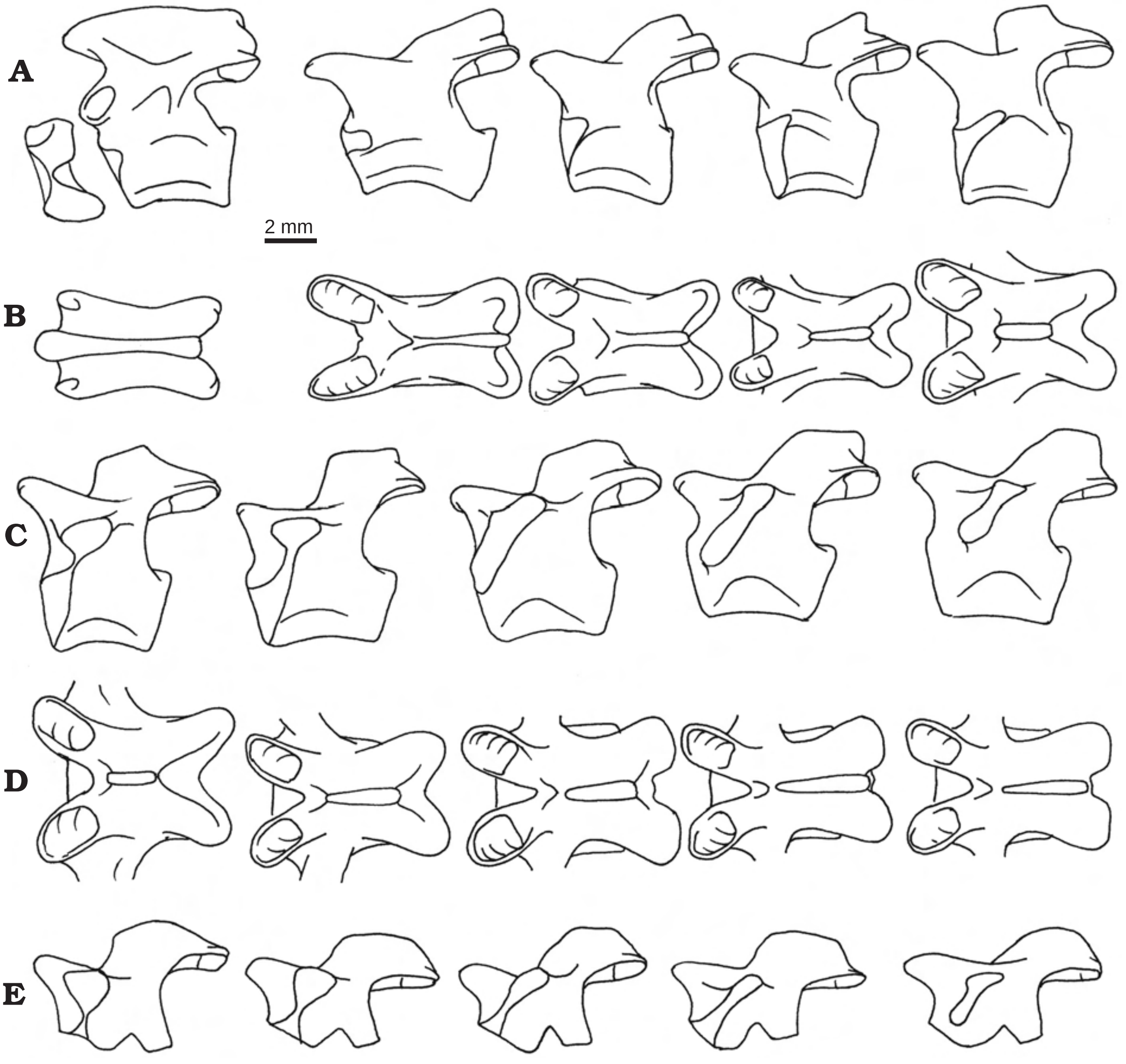

Fig. 16. **A**–**D**. *Procolina teresae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Vertebrae. From left to right: **A**. Atlas centrum + axis intercentrum ZPAL RV/825, and cervicals II–VI ZPAL RV/825–830 respectively, in left lateral view. **B**. Cervicals II–VI, in dorsal view. **C**. Possible sequence of transitional vertebrae VII and VIII ZPAL RV/831, 832, and dorsals ZPAL RV/845, 833, 834, in left lateral view. **D**. The same in dorsal view. **E**. Procolophonidae gen. indet. I: a possible sequence of B2 type neural arches, in left lateral view.

The prezygapophyses extend far cranially (Fig. 16B, D) in all postaxial cervicals to reach the postzygapophyses of the preceding vertebra, separated by the well developed intercentrum. The most distinctive feature of the postzygapophyses is that they are swollen; this condition is most pronounced in dorsals and less so in cervicals. For example, on the third cervical the swelling is hardly visible, but is present, although only slight, on the seventh vertebra.

In many specimens the postzygapophyses bear mammillary processes for muscle tendon attachments. Sometimes they are developed as a conical projection, but in other cases they look only like a small convexity. Their size and form is not dependent on the size or position of vertebra in the column. Moreover, they can be variably developed on the left and right side of the same vertebra.

Diapophysis, parapophysis and sacral ribs. — Unfortunately diapophyses and parapophyses are rarely preserved in a satisfactory state in Czatkowice 1 material, as their distal parts are in most cases abraded.

On the third vertebra (Figs 16A, 17C) the diapophysis is placed on the lateral side of the centrum near the anterior edge and just below neurocentral suture. It is not extended laterally, and the articulation facet for

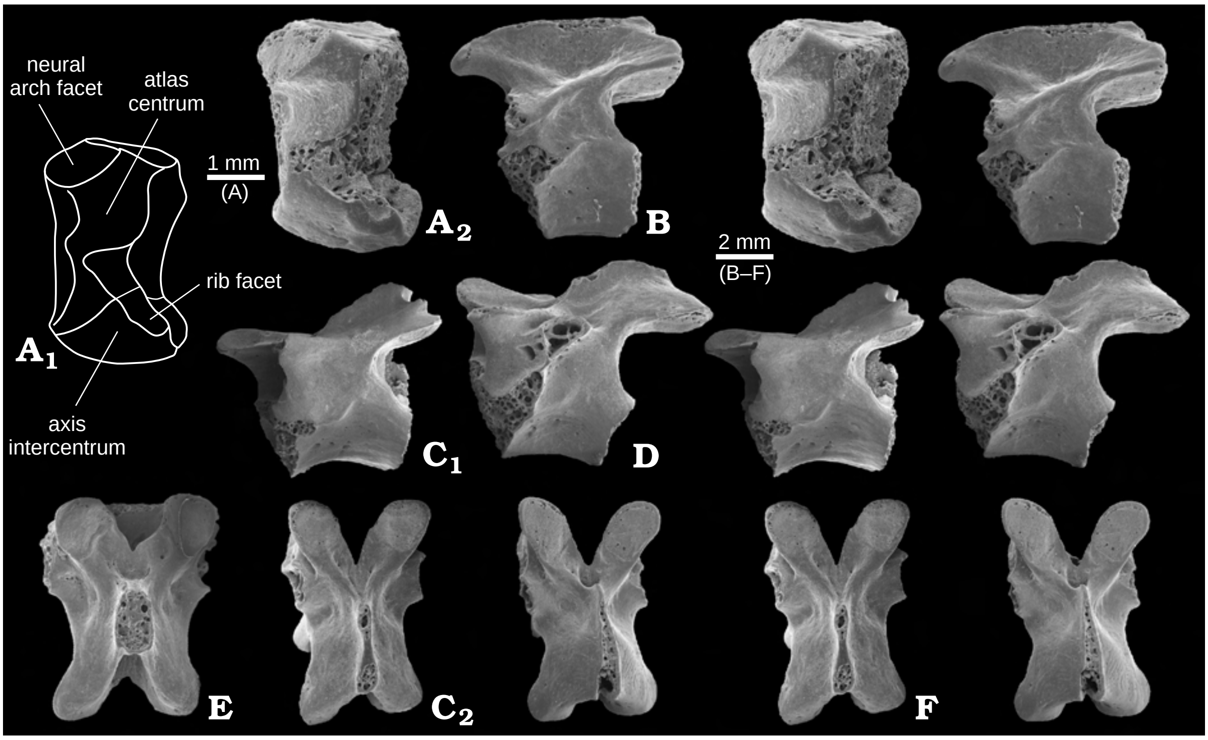

Fig. 17. **A**–**D**. *Procolina teresae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Altas centrum + axis intercentrum ZPAL RV/825. **B**. Axis ZPAL RV/826. **C**. Cervical vertebra III ZPAL RV/827. **D**. Dorsal vertebra ZPAL RV/833. **E**. Anterior dorsal vertebra ZPAL RV/845. **F**. Procolophonidae gen. indet. I ZPAL RV/851. Left lateral (A–D) and dorsal (C_1, E, F) views. All but A SEM micrographs; all but E stereo-pairs.

tuberculum lies on the centrum wall. On vertebrae four to seven (Fig. 16A, C), the diapophysis gradually migrates dorsally and caudally to reach a position on the prezygapophysial base in anterior dorsals (Fig.16 the middle of the row), and becomes increasingly expanded laterally.

There are no signs of parapophyses on the anterior cervical centra, and the capitulum of the rib most probably attached to the well-developed intercentrum. On the posterior cervical vertebrae (fifth and sixth), a small convexity appears on the anterior part of the centrum on the anterodorsal edge of the lateral concavity on the centrum. This is interpreted as the capitular facet. An abraded surface shows the position of the convexity, but the distal part of the latter is always destroyed, so the state of preservation does not allow recognition of the precise point of attachment for the capitulum. It is possible that it still, at least partially, attached to the intercentrum.

In the dorsal series both diapophysis and parapophysis shift dorsally and caudally on successive vertebrae. In a typical dorsal (Fig. 16C three vertebrae on the right), the diapophysis is located on the base of prezygapophysis with its dorsal edge slightly above the line connecting the pre- and postzygapophyses. As a result of this arrangement, a deep sulcus for the soft tissues surrounding the zygapophysial joint forms where prezygapophysial and diapophysial bases meet. The parapophyses are ventral and cranial to the diapophyses and are developed as a lateral projections slightly shorter than the diapophyses. There is a flange under the diapophysis that extends ventrally and cranially to reach the parapophysis on all dorsals. This flange becomes thincker down the column. On typical dorsals the diapophysis and the parapophysis lie so close to each other that they almost unite to form one articular facet for the rib, but there is still a constriction between them in lateral view. Moreover, the capitular facet is placed more medially as the parapophysis becomes slightly shorter. On posterior dorsals (Fig. 16) the diapophysis lies at the midpoint of the vertebral length, and the parapophysis just anteroventral to it. On the lateral side of the neural arch of all dorsals, there is an extensive concavity posterior to the united bases of the diapophysis and parapophysis. This concavity is interpreted as the place where *m. levator* costae originated.

Three sacral vertebrae (Fig. 18) were present in *Procolina teresae*. In all sacrals, the ribs are firmly connected to the transverse processes, and the line between them is indicated by a roughened raised surface. Unfortunately, none of the sacral vertebrae in the collection has the distal part of the sacral rib preserved. The first sacral rib is the stoutest. Its massive base is oval in cross-section and its end is greatly expanded craniocaudally and somewhat dorsoventrally (Fig. $18A_1$, D). The base of the second sacral rib is stout (Fig. $18B_1$, E). As preserved, it does not show much expansion of its end. The massive base of the third sacral rib projects laterally. Its distal part is the slimmest and is curved cranially (Fig. 18C, F).

Well-developed cylindrical pleurapophyses are present on anterior caudal vertebrae. Their bases can be homologized with transverse processes, while much thinner distal parts are probably equivalents of caudal ribs, although no line of fusion is visible. There are no specimens with complete caudal pleurapophyses, so it is not possible to determine if their ends were straight or directed caudally. Lateral projections become increasingly shorter in succeeding vertebrae, to become a small bump in posterior caudals.

Genus indet. I

Material. — Maxillae ZPAL RV/734; ZPAL RV/739; dentary: ZPAL RV/733; vertebrae type B2 (Lubka 1999): ZPAL RV/840–842, 849, 851–853, 860, and numerous unnumbered specimens. All appear to be conspecific with one another, and distinct from *Procolina teresae*. The juvenile mandible ZPAL RV/989 might belong to this taxon.

Jaws. — ZPAL RV/734 (Figs 3D, 13B) is a right maxilla about the size of adult specimens of *Procolina teresae* (6 mm in tooth row length). The tooth formula is 6.1.0. Instead of four premolariforms, which is considered the maximum adult count in *P. teresae*, the maxilla ZPAL RV/734 bears six premolariforms, that alternate in size as do the hatchling teeth in *Sphenodon* (Robinson 1976). The dominant tooth, the VIIth, is implanted posterior to the largest portion of the maxilla, slightly posterior to the usual position. The labial surface and the whole dorsal portion is strongly damaged by the resorption process (Fig. $13B_1$).

ZPAL RV/739 (Fig. 13A) is a left maxilla with the tooth formula 5.1.1 (5.5 mm in estimated dtl). All teeth, but a damaged second one, have been lost. The first, third and fourth teeth left pitted concavities only, the fifth and sixth retain remnants of basal parts of the teeth. The labial surface of the maxilla has a slightly spongy aspect. The molariform tooth is situated posterior to the largest part of the jaw.

ZPAL RV/989 (Figs 9F, 11E) is a very small left dentary (5.3 mm in dtl) displaying juvenile features. Its assignment is problematic. The tooth count is 7, the dominant tooth being situated at the VIIth tooth position posterior to the posterior alveolar canal (Fig. 9, arrow). The teeth are small and widely spaced. Between them, at three intermediate tooth positions, there are scars invaded by bony tissue (Figs 9F, 11E). The scars show that the tooth count was higher at still earlier stages of ontogeny. The fifth tooth position bears scars that probably mark the lingual course of a replacement tooth (Fig. 9F).The inferior alveolar canal is open laterally (Fig. $11E_2$), which indicates the poor ossification of the element.

ZPAL RV/733 (Fig. 9A) is a right fairly long dentary (dtl 8.1) lacking the posteroventral and anteroventral portions. The specimen bears 11 teeth (instead of the modal tooth count 8 of *P. teresae*) and an aberrant dental formula (6.1.4 or 7.1.3). The teeth are comparatively small and only slightly heterodont, with the 6th and the 7th being subequal, the three posterior teeth not fully erupted, and three anterior premolariforms with perforated apices. The tooth apices are more distinctly separated from the main crown than in *P. teresae*. The posterodorsal margin of the dentary is subhorizontal instead of ascending posteriorly. In ZPAL RV/733 the criteria of tooth homology give contradictory signals (Fig. 9A), and the identification of the two teeth dominating the dentition is questionable. This specimen looks like an ontogenetic stage prior to a replacement of smaller teeth by larger ones, associated with a possible anterior shifting of tooth positions. As such, this specimen should be smaller than average, but, it is actually roughly equal in size to the modal specimens of the sample (Appendix 1). It is noteworthy that Gow (1977b) described a similar case of difference in formula and size as a case of intraspecific anomaly within *Procolophon trigoniceps*.

Vertebrae type B2. — The Czatkowice 1 material includes many specimens closely similar to *Procolina teresae*, but in which neurocentral suture is open and neural arch and centrum are separated from each other (Figs 16E, 19G). Neural arches are more inflated at the spine base than in *Procolina*. Dorsal centra are half-cylindrical with only slight lateral concavities and without a ventral medial ridge (Fig. $19B_4$). Possible cervical centra are not oblique and are somewhat dorsoventrally flattened. On the other hand those specimens share some similarities with *Procolina*, such as the shallow hourglass-shaped concavity on the dorsal side (Fig. 19I), scars on the anterior and posterior faces, the shape of neurocentral suture, and amphicoely.

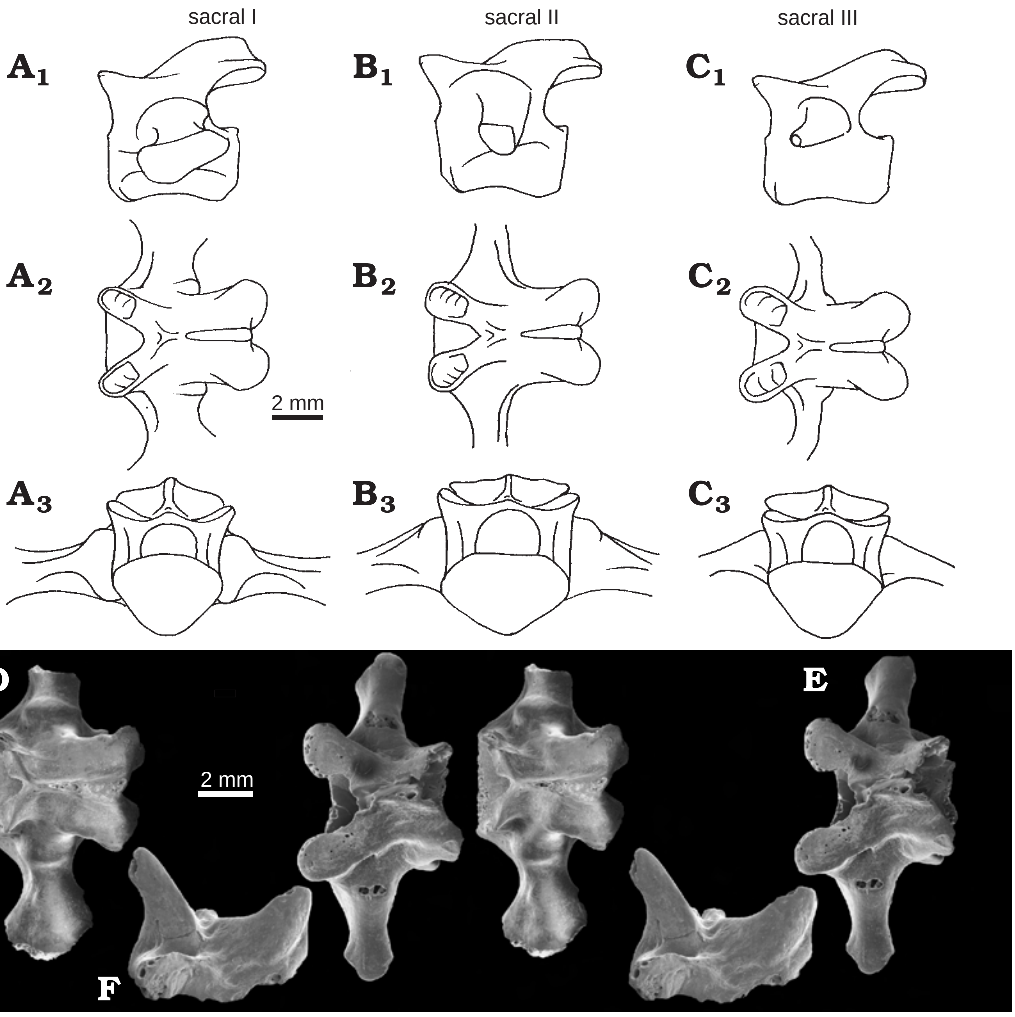

Fig. 18. *Procolina teresae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland, sacral vertebrae. **A**. Sacral I. **B**. Sacral II. **C**. Sacral I–III. **D**. Sacral I ZPAL RV/836. **E**. Sacral II ZPAL RV/835. **F**. Sacral III ZPAL RV/837. Left lateral (A$_1$, B$_1$, C$_1$), dorsal (A$_2$, B$_2$, C$_2$, D–F), and cranial (A$_3$, B$_3$, C$_3$) views. D–F, SEM stereo-pairs.

The isolated neural arches from Czatkowice 1 material excluded from *Procolina teresae* on the basis of relatively late fusion with the centra are similar to those of *Procolina* in shape, except that they are more swollen above the postzygapophyses, more rectangular in dorsal view (Fig. 19B$_2$) and bear relatively more posteriorly located spines (Fig. 16E). However, these differences are distinct only on the anteriormost dorsals. The distal ends of the neural spines are poorly ossified.

Numerous vertebrae of slightly larger size, but smaller than the smallest specimens of *Osmolskina* (Borsuk-Białynicka and Evans 2009), display damage to ventral portions of the centra, which probably indicates weak ossification of this portion. Their attribution is difficult, but they match the weak ossification of the jaws ZPAL RV/733, 734, and 739.

Comments on genus. indet. I. — The maxilla ZPAL RV/734 is considered to be a juvenile on the basis of the premolariform dentition similar to the hatchling dentition of *Sphenodon* (size alternation, Robinson 1976) and the more posterior position of what is probably a prospective molariform tooth. On the other hand, it corresponds in size to adult maxillae of *Procolina teresae*. Specimen ZPAL RV/739 (Fig. 13A) is probably an ontogenetically different specimen of the same taxon that demonstrates what is probably an “instantaneous event” of resorption and replacement of the whole dentition. The most striking feature of both maxillae is an extensive resorption of the labial surface of the bone (Fig. 13A, B). The size of these juveniles shows that the adult size could have exceeded that of *Procolina*.

No mandible can be associated with confidence with ZPAL RV/734, but ZPAL RV/733 (Fig. 9A), more slender than the average, and bearing smaller and more numerous teeth is perhaps a match. Noteworthy is the tooth formula of this specimen, which is either 6.1.4. or 7.1. 3. Except for the formula, this specimen has a much less ascending postmolariform tooth row than *Procolina*, and bears three accessory teeth ready to erupt. How this profile might have changed in ontogeny is obscure, because this region is often damaged.

Described under the genus indet. I, the vertebrae usually have their neural arches completely detached at a size corresponding to that of *Procolina* vertebrae in which the arches are completely fused to the centrum. This implies a longer growth and a corresponding slower developmental rate and larger adult size of the former. In morphological terms, the two forms are distinguished in details (see above).

The jaw and vertebral material described above under the genus indet. I might be conspecific on the basis of shared differences with respect to *Procolina teresae*. These are: more extended period of growth and morphogenesis; possible larger adult size; more intense resorption of the bone during tooth replacement that might correspond with poor co-ossification of vertebral centra and arches.

Genus indet. II

Material. — Dentary fragment ZPAL RV/507; Vertebrae type B3 (Lubka 1999): ZPAL RV/767–772; ZPAL RV/846–870, and several unnumbered vertebrae.

Jaw. — ZPAL RV/507 (Fig. 10B) is a small piece of dentary bearing two decidedly bicuspid teeth, one smaller and one larger. Interestingly, it is still smaller than *Procolina*, and extremely rare.

Vertebrae type B3 (Lubka 1999). — A few dorsal arches, cervical and dorsal centra, and possibly one sacral and one caudal differing significantly from *Procolina* vertebrae represent this taxon in Czatkowice 1 material. The most distinctive features of these vertebrae (Fig. 19C, D–F) are: proportionally small notochordal centra, widely expanded swollen zygapophyses, and neural arch squarer in dorsal view than in type B2; neurocentral sutures are fused, though not always obliterated at much smaller size as in type B2; and the ventral surface of the centra is often poorly ossified.

The centra are amphicoelous and, in contrast to adult *Procolina*, notochordal. They are disproportionately small compared to the neural arch. As in *Procolina*, the anterior and posterior articular facets are not well ossified, and the centra as preserved are trapezoidal in lateral view, with their ventral length smaller than the dorsal one. The prominent excavations on the ventrolateral sides of the centrum, separated by the blunt ventral ridge make it nearly triangular in transverse section (Fig. 19C_3, E). The ridge is similarly developed in all vertebral regions and the small notochordal canal runs through the base of the ridge, which distinguishes these centra from those of *Procolina*. On the dorsal surface of the centrum there is a deep conical excavation, while in *Procolina* this concavity is shallow and hourglass- shaped. In the smallest specimens the arch may be separated from its centrum.

In contrast to *Procolina*, the pedicels of the neural arch are very massive and are somewhat curved to enclose a round neural canal (Fig. 19). In smaller specimens the suture between the two halves of the neural arch is visible on the ventral side of the roof of the arch. It closes in ontogeny from the front to the rear of the arch. The anterior portion of the roof of the arch, located between the prezygapophyses, is embayed. Immediately posterior to this, on the base of neural spine, there is a triangular pit for the elastic ligament insertion. The double origin of the ligament is placed on a vertical plane just below the neural spine and between postzygapophyses on the posterior side of the preceding vertebra.

The neural spine is low with a short base (Fig. 19). It is rhomboidal in lateral and square in dorsal view. The posterior edge of the neural spine base is placed in a line with the posterior edge of the centrum in cervicals, but shifts more caudally in typical dorsals where postzygapophyses reach further caudally. The anterior part of the neural arch lies half way along the centrum length and also shifts caudally in succeeding vertebrae.

The zygapophyses bear oval articular facets and are widely extended laterally so that a square can be circumscribed on the vertebra in dorsal view (the *Procolina* vertebrae are proportionally more expanded craniocaudally). The articular facets are nearly horizontal in cranial and caudal view, as their slope is generally less than 10° on all presacral vertebrae, but can reach up to 20° on sacrals. The zygapophyses of all vertebrae are swollen, but this feature is much better pronounced in postzygapophyses. Buttresses enclose the neural spine base and extend laterally and posteriorly toward the ends of the postzygapophyses. In contrast to *Procolina*, there are no mammillary processes on the zygapophyses.

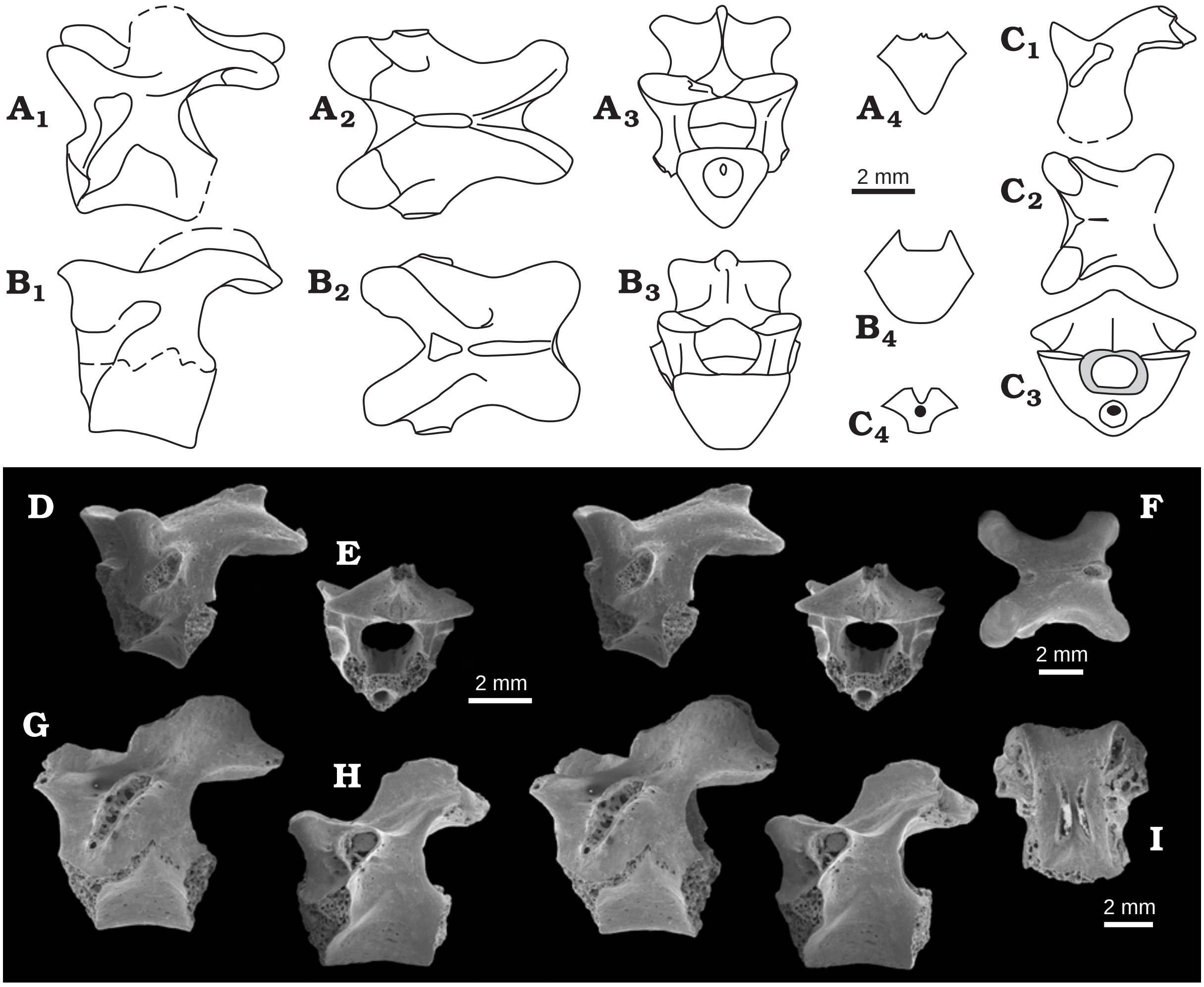

Fig. 19. Procolophonids from the Early Triassic of Czatkowice 1, Poland. Comparison of *Procolina teresae* gen. et sp. n., anterior dorsal type vertebrae (**A**, **H**, **I**) with those of Procolophonidae gen. indet. I (**B**, **G**) and gen. indet. II (**C**–**F**). Left lateral (A_1, B_1, C_1, D, G, H), dorsal (A_2, B_2 C_2, F), anterior (A_3, B_3, C_3), and posterior (E) views. Transversal section of centrum about the mid-length (A_4, B_4, C_4), dorsal view of the centrum without neural arches (I). D–I, SEM micrographs; all but F, I stereo-pairs.

In cervicals, the diapophysis is placed on the anterior part of the centrum, ventral to the prezygapophysis. On succeeding vertebrae it is shifted caudally and dorsally. On dorsals, the diapophysis lies on the base of the prezygapophysis and its dorsal edge can lie above the line connecting the pre- and postzygapophysis, but — in contrast to *Procolina* — no sulcus is formed between the prezygapophysis and diapophysis. While in anterior cervicals there is no capitular facet on the centrum, in posterior cervicals it is located ventral to the diapophysis. A thin low flange extends from the diapophysial to the parapophysial base. In dorsals the diapophysis and parapophysis form a single structure. Its end in lateral view resembles an elongated ellipse with the long axis oriented anteroventrally and posterodorsally. Tubercular and capitular articular facets are separated by a slight constriction. A shallow concavity posterior to the united bases of the diapophysis and parapophysis served as the origin of the levator costae muscle.

In proximal caudals, thin and probably long pleurapophyses are located on the lateral side of the centrum on the neurocentral suture.

Comments. — The dentary ZPAL V/507 is tentatively associated with the vertebrae type B3 on the basis of smaller size and frequency as compared to *Procolina teresae* and the material described under genus indet. I.

Genus indet. III

ZPAL RV/716 is a posteriorly incomplete, fairly large and very thick dentary (Fig. 11C) with a dental formula hardly comparable with *Procolina.* It bears basal parts of three anterior teeth that sink deep into the bone in a manner called protothecodont by Broili and Schroeder (1936), and are followed by two huge, bulbous teeth. The first of these may have replaced two posterior premolariforms, whereas the second one probably replaced the molariform, to which it corresponds topographically, plus possibly the first accessory tooth. It is hardly possible that this is a geriatric specimen of *Procolina teresae* in view of the data on geriatric specimens from Broili and Scheroeder (1936) and Li (1983) that do not differ so much in tooth formula. The specimen differs strikingly in the molariform to dentary depth proportion compared to what is probably the typical adult dentary of *Procolina* (ZPAL RV/799, Fig. 11D) while recalling the holotype of *Burtensia burtensis* except for a much longer premolariform portion of the latter (Fig. 11B).

DISCUSSION

COMPOSITION OF THE PROCOLOPHONID CZATKOWICE 1 FAUNA

In spite of their unicuspid teeth, the procolophonids from Czatkowice 1 certainly belong to the subfamily Procolophoninae Seeley, 1888 emend. Ivakhnenko, 1979 on the basis of their reduced and highly heterodont dentition. On both the cranial and vertebral material the dominant Czatkowice 1 procolophonids fall into two main groups, differing in the state of the bony tissue (skull material), dental formula, and the rate of ossification (vertebral material). The third, much less numerous group of specimens includes tiny notochordal vertebrae of a peculiar morphology and a fragment of bicuspid dentition (Figs 10B, 19C–F). The mandible ZPAL RV/716 is the only specimen representing the fourth taxon.

The first question is whether or not the procolophonid jaws from Czatkowice 1 assigned to *Procolina teresae* and to genus indet. I might represent ontogenetic stages of the same species. The most informative comparative data on procolophonid ontogeny are those given by Broili and Schroeder (1936), Gow (1977a, b) and Li (1983).

Broili and Schroeder (1936) documented a possible ontogenetic sequence of four skulls of the Early Triassic *Procolophon trigoniceps* from South Africa, the largest one differing from the smallest one by about 25% in skull length. The difference in tooth count is by one or by two at most (6 or 7 in the maxilla, 7 to 9 in the dentary), and mostly involves a changing number of accessory teeth. Some variability occurs between left and right sides of the same individual, and partly results from preservation bias. The variability observed by Li (1983) on *Eumetabolodon* material is similar. The tooth count is 5–7 in the maxilla, 6–8 in the dentary, and 9 in the geriatric specimen IVPP V6070, with individual variability overlapping the ontogenetic one. Gow (1977a) reported six consecutive ontogenetic groups of *Procolophon trigoniceps*, the extreme individuals differing by 50% of the skull length, and the tooth count changing from 7 to 9 in the upper tooth row and from 5–8 in the lower one.

In the Czatkowice 1 material, the differences in tooth number between *Procolina teresae* (no more than 6 maxillary and 8 dentary teeth) and the specimens ZPAL RV/739 and 734 excluded from this taxon (p. 130) (8 maxillary and 11 dentary teeth) are of similar range, but the difference in developmental rate (Figs 12, 13) suggests a taxonomic difference. At approximately the same size as the maxilla ZPAL RV/734 (Fig. 13B), *Procolina* type maxilla (ZPAL RV/711, Fig. 12) is more advanced in having more compact tissue around the teeth and jaws, and a more consistent tooth morphology and formula than the former specimen. This is also true of the smaller specimens of *Procolina teresae* (Fig. 12A) reaching only about two thirds or less of the average length, and displaying the typical morphology of the species. In contrast, the maxilla ZPAL RV/739 (Fig. 13A) bears a row of small triangular teeth alternating in size, similar to the hatchling dentition of *Sphenodon* (Robinson 1976). This possible juvenile is larger than those of *Procolina* and shows strong resorption at the labial side. The same intensity of resorption occurs only in very small juveniles of *Procolina*. Specimens of both kinds come from the same samples, and so the differences are unlikely to be preservational artifacts nor due to chemical preparation. In our opinion these differences suggest a different developmental rate and different adult size for the two taxa, which precludes their conspecifity.

This suggestion is supported by the vertebrae from Czatkowice 1 material. Those assigned to *Procolina* are distinguished by small size and a complete obliteration of the sutures between the arches and centra, even in cervicals, which suggests maturity (Brochu 1996). In contrast, the vertebrae described under the genus indet. I of similar size but slightly different morphology are distinguished by fusion lacking (Fig. 17H) or incomplete (Fig. 19G), suggesting a longer growth period and larger adult size.

The conspecifity of the bicuspid tooth ZPAL RV/507 with the tiny vertebrae described under the genus indet. II, based on size and frequency is conjectural and should be tested in the future.

PROCOLOPHONID GENERIC LEVEL TAXONOMY

The fragmentary nature of procolophonid record results in a rather unsatisfactory state of intrafamilial taxonomy of this group. The putative abundance of procolophonid material from Russia (Appendix 2) does not elucidate this problem very much. From about twelve procolophonine genera with 17 species described in the literature (Ivakhnenko 1975, 1979, 1983b, and references therein; Novikov 1991; Novikov and Orlov 1992), Spencer and Benton's (2000) revision left only five genera with eight species, mostly those represented by more complete material (Appendix 2). According to Novikov (1991) and in contrast to Spencer and Benton (2000), we provisionally consider the genus *Samaria* Novikov, 1991, and *Lestanshoria* Novikov, 1991 as valid, for comparative purposes. For the same reason we include the genus *Burtensia* Ivakhnenko, 1975 (see also Ochev 1958).

The jaws and dentition, particularly the lower one, are the only elements shared by all these taxa. They must remain the primary basis of taxonomic conclusions for the time being. The lack of information on intrageneric variability, and the absence of data concerning the position of the reference points are the drawbacks of this material. In this situation, the position of the lower molariform tooth (Fig. 14) was determined approximately on the basis of the dorsal profile of the dentary that tends to ascend in the region of the coronoid facet. The molariform tooth is situated directly anterior to the posterodorsal slope of the dentary border, while the accessory portion of the tooth row begins posterior to the bend. Fig. 14 demonstrates a tentative regionalization of the lower teeth in the East European procolophonid species according to the above rules. Appendix 3 includes the main characteristics of procolophonid genera collected on the basis of the literature and based on the same rules.

The mandibular dental formula 5.1.1-2. is shared by *Procolina*, *Kapes*, *Burtensia* (*B. burtensis* PIN 104/2) (Fig. 14A–E), *Samaria* (*S. concinna*, only known specimen PIN 3362/1), and possibly, by *Lestanshoria massiva* (Fig. 14F). Although its fifth tooth, roughly corresponding to the molariform, hardly exceeds the premolariform and accessory teeth in size, the whole dental formula matches that of *Kapes*. The only known dentary of *Orenburgia bruma* (PIN 4370/3, Fig. 14G) displays a formula of 4.1.2, but a space between teeth II and III suggest the loss of an additional tooth between them, possibly during ontogeny. The genus *Orenburgia* (Fig. 14G) is notable for having tooth crowns that are inclined posteroventrally, low relative to the dentary depth, and progressively decreasing in size with no evident development of a molariform tooth. In our opinion, these features might be generic. According to Spencer and Benton (2000), *Lestanshoria* is probably a subjective junior synonym of *Orenburgia* from which it differs in tooth morphology and gradient (Fig. 14F), but the question remains open.

As stated above, Ivakhnenko's (1979) diagnosis of the subfamily Procolophoninae Seeley, 1888 (or procolophonine procolophonids) includes a maximum tooth count not exceeding 10. The overview of the available information on the procolophonine genera (Appendix 3) reveals the existence of a group in which the number of dentary teeth is still lower and only rarely exceeds 7. Characterized by a fairly consistent dental formula, this group, including *Kapes*, *Burtensia*, *Samaria*, *Lestanshoria*, *Orenburgia*, and *Procolina*, is here informally referred to as the "kapoids". Within the "kapoids" the variability involves relative tooth size, gradient of tooth enlargment and bicuspid condition, as well as the implantation details (in terms of the angulation of tooth crowns with respect to the jaw).

In contrast to the "kapoids", *Tichvinskia* and *Procolophon* have a slightly higher tooth count that reaches 9 dentary teeth in total including 6 or 7 premolariforms. Their teeth are probably smaller with respect to jaw depth, and less heterodont (in terms of crown depth). Possibly, *Timanophon* (Fig. 14I), with 8 widely spaced dentary teeth, may represent the same evolutionary grade, although it display a derived bicuspid state of crowns. Given a high tooth count in *Owenetta* and Nyctiphruretia (Ivakhnenko 1979), the *Tichvinskia* and *Procolophon* dentition is plesiomorphic with respect to that of the "kapoids". Whether or not the tooth count range might be synapomorphic is not clear.

A cursory comparison of the skull bones of *Procolina* with those of members of the ingroup Procolophoninae and the outgroups (*Contritosaurus*, Owenettidae and Nyctiphruretia), demonstrates a rather derived structure of *Procolina*. Unfortunately, these characters are poorly known in other "kapoids".

A plesiomorphic dentition of numerous irregular tiny vomerine denticles of *Nyctiphruretus* type (Ivakhnenko 1979, fig. 1) changes into larger and less numerous teeth arranged in regular rows such as those present in *Contritosaurus simus* (Ivakhnenko 1979, fig. 2), and, further on, to one lateral and one rudimentary medial row, present in *Tichvinskia* (Ivakhnenko 1979, fig. 3), and *Procolophon* (Gow 1977a, fig. 2). A relatively flat pterygoid of *Nyctiphruretus* type (Ivakhnenko 1979, fig. 1) bears teeth in anteriorly divergent rows including one on the transverse flange. In the procolophonids, the transverse flange lacks a dentition, and the bone is strongly concave ventrally, mainly on account of the strongly protruding transverse flange (Ivakhnenko 1979, p. 28). *Procolina teresae* has a vomer and palatine of the derived procolophonine type, both being more derived than usual in Procolophoninae, the vomer in the absence of medial denticles, and the palatine in a complete lack of dentition. A strongly interdigitating premaxilla-maxilla articulation of *Procolina* is much more specialized than simple and feeble joints illustrated by Ivakhnenko (1979, fig. 1) in *Tichvinskia* and in *Procolophon* (Carroll and Lindsay 1985, figs 1, 5). We suggest their exclusion from the "kapoids" (see Fig. 1C). The latter view is in agreement with a position of the *Tichvinskia* resulting from the phylogenetic analysis by Modesto *et al.* (2002).

What we informally call "kapoids" might be equivalent only to the genus *Kapes* with several species, or to several closely related genera, but a formal decision concerning this matter requires further, more complete material.

Bicuspid teeth are currently considered as synapomorphic of all Procolophoninae known to date from Russia (Ivakhnenko 1979; Novikov 1991), and for *Kapes bentoni* from the British Triassic (probably Anisian; Spencer and Storrs 2002). However, data on variability of this character is scarce. In the emended diagnosis of *Kapes* by Spencer and Storrs (2002), the transversal broadening of upper teeth, associated with the bicuspid condition, is certainly overestimated. According to the original diagnosis by Ivakhnenko (1975), it is poorly expressed in the type species, *Kapes amaenus*, at least in the lower dentition.

Given both the advanced shortening of the tooth row and its heterodonty in *Procolina teresae*, the unicuspid condition of the teeth is unexpected. It is unique among procolophonines, and this suggests it could represent an ontogenetic stage in the development of the bicuspidity (see above). However, *Procolina* is here considered a small, possibly miniaturized animal on the basis of the presence of a whole array of ontogenetic stages, and on the size of the completely cossified vertebrae (Brochu 1996). The unicuspid condition may be thus paedomorphic rather than juvenile. We thus consider *Procolina teresae* as a paedomorphic "kapoid". Its assignment to the genus *Kapes* is possible, but this determination should be preceded by the revision of the whole "kapoid" group.

CZATKOWICE 1 PROCOLOPHONID TOOTH REPLACEMENT

In conformity with the earlier evidence, most procolophonid jaws from Czatkowice 1 bear a robust dentition that is strongly fused to the dentigerous margins. They display a quasi-acrodont appearance in that they are implanted apically, instead of lingually, and are tightly fused to the bone. However, on detailed inspection, the crown bases are deeply embedded into the bone in a protothecodont manner. This implantation is probably a procolophonid standard as shown by the literature, among others by Gow (1977a) and Spencer and Storrs (2002). Given this intimate contact, tooth replacement was somewhat of a problem, and was evidently rather variable within the group. Gow (1977a) and Li (1983) considered the process to have been very quick and contingent, and they reported no lingual replacement pores. In contrast, Sues *et al.* (2000) described a typically odd-even alternating pattern of replacement in *Hypsognathus fenneri*, a Late Triassic representative of the most derived procolophonid group. They also reported resorption pits lingual to the functional teeth of *Hypsognathus*, as typical in most reptiles.

In the Czatkowice 1 procolophonid material, gaps that are more likely to be due to replacement than to post mortem loss do occur, but neither *Procolina* nor genus indet. material display resorption pits on the lingual side of the crown bases or tooth-bearing bones (*e.g.*, in some durophagous reptiles *Dracaena guianensis* or some dinosaurs; Edmund 1960, figs 18, 48). A regular replacement of functional teeth by the tooth buds developed on the lingual side of the jaws is typical of both synapsids and diapsids (Edmund 1960, 1969), but not of earlier representatives of Amniota (Captorhinidae; Bolt and DeMar 1975) which may have multiple rows of functional teeth. In the procolophonids, the multiple tooth rows are rare (*e.g.*, in *Thelegnathus contritus*, Gow 1977b), and not found in the Czatkowice 1 material. The lack of replacement perforations in juveniles of *Procolina* and in genus indet. I suggests an instantaneous replacement. The buds must have matured within a thick lingual mucosa to be shifted to the final tooth position only after a total resorption of their predecessors as shown by ZPALRV/739 (Fig. $13A_2$). The hypothesis that the single replacement act was quick (Bolt and DeMar 1975; Li 1983, p. 580) is thus supported in this case.

In the Czatkowice 1 procolophonids, the teeth to be shed are perforated apically and/or labially (Figs 3C, D, F, $12B_2$, D, 13A). In the undetermined procolophonid material, and in tiny juveniles of *Procolina*, but less so in the adult *Procolina*, distinct traces of tooth resorption are associated with erosion of the tooth-bearing bones, and thus the whole organism could have been involved in resorption process. Interestingly, the process affected the labial side of jaws and teeth (Figs 12D, B_2, 13).

The labial deterioration of teeth prior to replacement has not been reported hitherto, except for labial grooves that undercut the molariform teeth reported by Ivakhnenko (1974) in *Contritosaurus*, and by Gow (1977b) in *Thelegnathus*. Illustrated by Gow (1977b, fig. 4C), the lower dentition of *Thelegnathus perforatus* BPI 4585 demonstrates the labial perforations of teeth but this is not discussed in the text.

We hypothesise that the temporary deterioration of tooth-bearing bones appeared as a solution to the difficulties with tooth replacement that resulted from the development of tooth permanency. Our material suggests that the expression of this process was subject to variability, possibly at a generic or specific level. If not a manifestation of pathology, a fusion of two or more smaller tooth buds to develop a single larger tooth, demonstrated by the maxilla ZPAL RV/721 (Fig. 12A), might be a process that made for a decrease in the premolariform tooth count. Posterior (Fig. $10C_2$), or posterolabial (Fig. $10A_2$) to the molariform tooth, the development of new accessory teeth, probably paralleled the posterior elongation of the dentary, as already suggested by Gow (1977a) in *Procolophon* and by Li (1983) in *Eumetabolodon.* Associated with the jaw elongation, and the eruption of new accessory teeth, was a certain amount of anterior shift of the molariform tooth, which is best illustrated by the *Procolina* mandibles (Fig. 15). A possible anterior shift of the molariform tooth is also suggested by the young specimens of the procolophonid genus indet. I that display an unusual posterior position of this tooth (Fig. 13). In the maxilla of *Procolina teresae* the number of accessory teeth, and the position of the molariform tooth, are noticeably stable.

In the dentary, the accessory teeth are most often rudimentary, but sometimes the first of them attains the size of the main molariform tooth as does sometimes the posteriormost premolariform. This process results in two or three quasi-molariform teeth instead of one (ZPAL RV/799, Figs 10D, 15), probably in older individuals. In this account, we consider these differences in terms of intraspecific variability.

BIOSTRATIGRAPHICAL COMMENTS

The Procolophonidae are considered a group of a biostratigraphic importance (Novikov 1995; Spencer and Benton 2000). The Russian procolophonids have the advantage of being distributed over a stratigraphic sequence ranging from the Late Permian to the Mid-Triassic (Shishkin *et al.* 2000) with the climax in the Yarenskian (Late Olenekian) when as many as four genera and six species have been listed (Fig. 20 and Spencer and Benton 2000). However, the morphological details used for infrafamilial taxonomy are poorly understood in evolutionary terms, and so the stratigraphical ranges on this taxa are only conjectural. Obviously, an isodont dentition with numerous teeth is plesiomorphic, and is suggestive of not later than the Induan stage, however stratigraphy does not always match phylogeny. The presence of *Tichvinskia* in the Rybinskian horizon (the earliest Olenekian), as the earliest procolophonine species *T. jugensis*, is in accordance with our suggestion that this genus is more primitive than "kapoids" (see also Modesto *et al.* 2002). However, Spencer and Benton (2000) consider this species a *nomen nudum*, *Tichvinskia* actually appearing only in the Yarenskian horizon (Late Olenekian). *Kapes*, as currently understood, appears only in the Yarenskian (Late Olenekian) (unless *Samaria* from the mid–early Olenekian is congeneric), whereas *Orenburgia, Lestanshoria* and *Insulophon*, which seem more derived, are known earlier (from Sludkian and Ustmylian = mid- and late Early Olenekian).

The age of Czatkowice 1 breccia previously determined as the late Early Olenekian (Borsuk-Białynicka *et al.* 2003) mainly on the basis of the presence of the lungfishes, has recently been revised to early Late Olenekian in age on the basis of *Parotosuchus* remains (Shishkin and Sulej 2009). The present study supports the opinion that the Czatkowice 1 procolophonids are derived, and is consistent with the early Late Olenekian (Borsuk-Białynicka *et al.* 1999).

CONCLUSIONS

TAXONOMY

The remains of four different procolophonid taxa may be recognized in the Czatkowice 1 material, but only the dominant one is formally described as a new taxon *Procolina teresae* gen. et sp. n.

Based mainly on the morphological consistency of the dentition and the obliteration of vertebral sutures, the dominant procolophonid material is considered mature, and the small size of *Procolina teresae* is regarded as specific. The heterodont dentition of *Procolina teresae* is derived. Both the unicuspid condition of teeth and small size of *Procolina* are hypothesized to be paedomorphic.

The undetermined procolophonid material falls into three possible taxa, of which the larger one (genus indet. I) differs from *Procolina* in having a slower developmental rate, and slightly larger adult size. Jaws of the size of adult *Procolina* represent an earlier stage of tooth replacement and show a strong resorption of the bony tissue. The vertebrae tentatively associated with these jaws have centra that are not fused with the arches or are separated by distinct sutures. A tiny fragment of jaw with bicuspid teeth probably belongs to the second taxon (genus indet. II) along with the least numerous, very small and morphologically distinct vertebrae. Only one specimen with the dentition heavy and reduced in tooth number represents the third taxon.

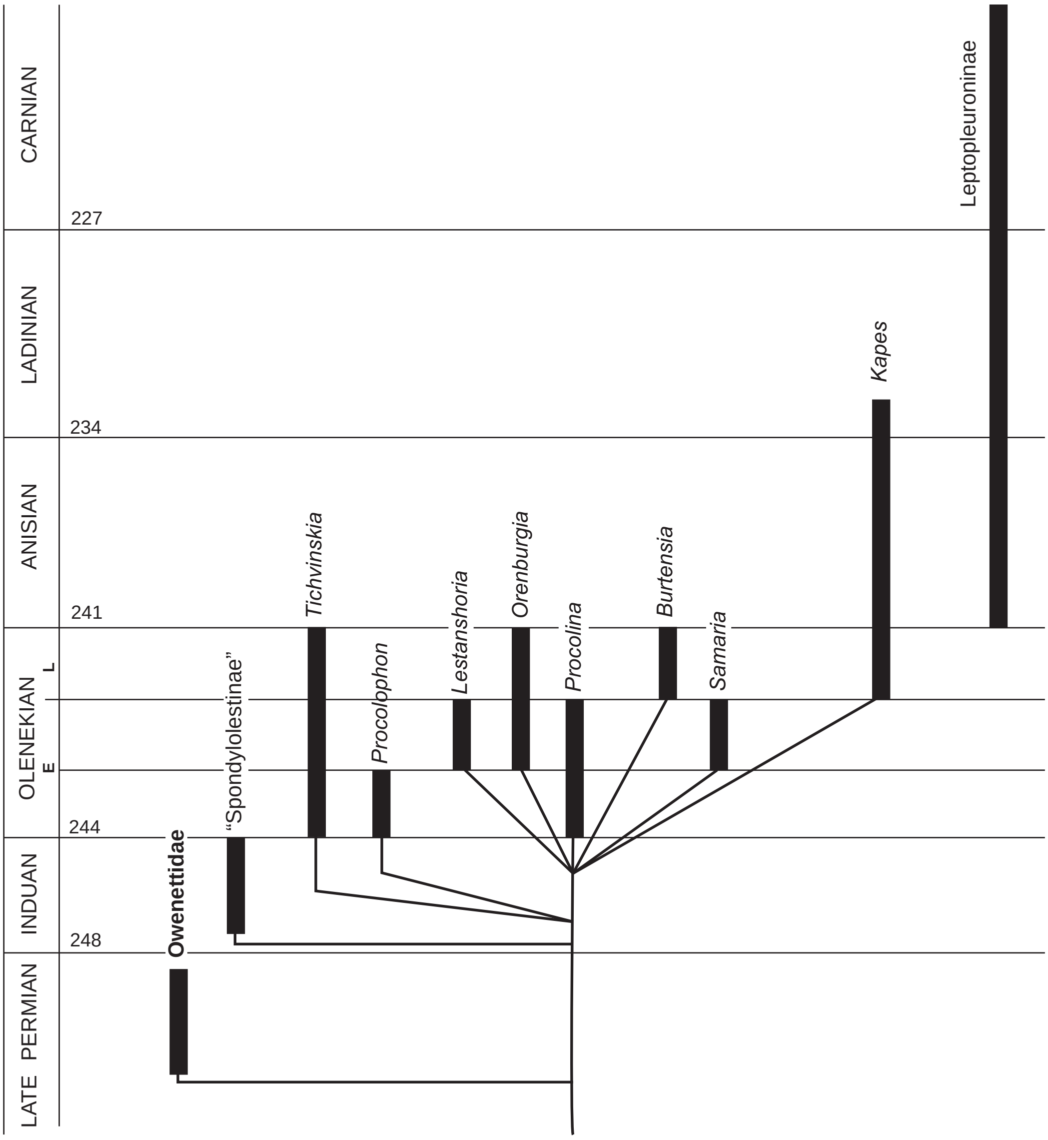

Fig. 20. Possible phylogenetic relationships within the Procolophonidae according to this study combined with a pattern of biochronology based mainly on Spencer and Benton (2000) and Shishkin *et al.* (2000) with *Procolina* included.

Characterized by a fairly consistent dentary tooth formula, 5.1.1-2 , a group of procolophonines including *Kapes*, *Burtensia*, *Samaria*, *Lestanshoria*, *Orenburgia*, and *Procolina* is here informally referred to as "kapoids". Whether a true clade or an evolutionary grade, the "kapoids" appeared in the Early Olenekian (Rybinskian horizon) and radiated in the Olenekian and early Anisian in Europe. *Procolina* fits into this clade, while *Tichvinskia* and *Procolophon* demonstratere plesiomorphic characters.

TOOTH REPLACEMENT PHENOMENA

Neither in *Procolina* nor in gen. indet. material are there resorption pits on the lingual side of the crown bases. Instead, resorption traces probably associated with tooth replacement occur on the labial sides of bones and teeth. In *Procolina*, resorption occurs earlier in ontogeny than in the second procolophonid taxon (genus indet. I).

The temporary deterioration of tooth-bearing bones probably appeared as a solution to the difficulties with tooth replacement that resulted from the development of tooth permanency in terms of implantation.

A supposition that the replacement buds matured in a thick mucosa and were shifted to the final positions after a deterioration of the functional teeth (Bolt and DeMar 1975; Li 1983; Gow 1977b) in a rapid act of replacement is supported.

The lack of a stiff contact between the replacement buds developed in a thick mucosa and the hard tissue is probably what allowed slight horizontal shifts of the tooth positions with respect to the growing jaws.

Some variation in tooth count probably resulted from the replacement of two or more smaller tooth buds by one larger tooth. This was the process that allowed the evolution of a heterodont dentiton from an isodont one. It probably affected early phylogenetic stages and could have been partly retained in ontogeny.

In *Procolina teresae* the dental formula is notably stable beginning in early stages of ontogeny.

BIOSTRATIGRAPHIC IMPLICATIONS

Except for unicuspidity, the morphology of the *Procolina* skull (including vomer, pterygoid and premaxilla-maxilla articulation) corresponds to a derived procolophonine type. It matches Late Olenekian (Borsuk-Białynicka *et al.* 1999; Shishkin and Sulej 2009) rather than Early Olenekian (Borsuk-Białynicka *et al.* 2003) age of the Czatkowice 1 community.

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APPENDIX 1

Variability of dentary and lower dentition features in the Early Triassic procolophonid material from Czatkowice 1. Abbreviations: est., estimated.

Procolina teresae dentaries ZPAL RV/	Tooth formula	Largest tooth position	Ontogenetic age	Posterior alveolar foramen position	Coronoid facet position behind	Dentary tooth row length (dtl)	Figs
510	5.1.0	VI	juvenile	VI	?	7.0	11A
511	5.1.2	VI	?adult	VI	VI	8.0	
513	6.1.2	VII	young adult	VI/VII	VII	7,4	11D
514	5.1.2	VI	young adult	V	VI	7.5	
515	5.1.2	VI	juvenile	VI	VI	7.5	9C, 10A
516	6.1.0?	VII	juvenile	VI/VII	VII	6.5	9B
517	6.1.1	VII	adult	?	VII	8.5	
524	5.1.2	VI, VII	adult	VI	VI	10.5	9D, 10C
683	4.1.2	V	adult	V	VI	9.5	9E
717	5.1.2	VI	adult	VI	VI	7.9	
740	6.1.2	VII	adult.	?	VI	8.0	
741	5.1.1	VI	adult	VI	VI	9.0	
762	5.1.2	VI	adult	?	VI	9.5	
763	5.1.1	VI	adult	VI	?	8.5	
764	5.1.?	VI	adult	VI	VI	est. 8.2	
791	6.1.1	VI	adult	VI/VII	VI	8.9	
792	5.1.1	VI	young adult	?	VI	7.0	
798	5.1.1	VI	adult	VI	VII	7.8	
799	5.1.2	V–VIII	adult	?	?	c. 10.0	
801	5.1.1		adult	VI	VII	8.1	
802	5.1.1	VI	adult	VI	VI	7	
Genus indet.							
989	6.1.0	VII	juvenile	VII	?	6.0	9F, 11E
716	4.1.?	IV, V	adult	IV/V	V	est. 9	11C
733	6.1.4	VII,VIII	juvenile	VII	VII	8.1	9A

APPENDIX 2

The best known procolophonine materials referred to in the present paper. Abbreviations: L., Lower; U., Upper.

Early Triassic procolophonine genera	Stage/horizon	Geographical range	Skull est. length in mm	Material	Holotype/ type species	Included species
Anomaiodon Huene, 1939	U. Olenekian	Germany	32.8	2 skeleton molds	*A. liliensterni*	*A.liliensterni*
Burtensia Ivakhnenko, 1975	U. Olenekian (Fedorovskian)	Russia	26	dentary	SGU 104/2 = PIN 2394/11	*B. burtensis*
Eumetabolodon Li Jinling, 1983	L. Olenekian (Fuguan faunachron)	China	100 45	ca. 20 skull specimens	*E. bathycephalus*	2 species
Insulophon Novikov *et* Orlov, 1992	L. Olenekian (Sludkian)	Russia	23	fragmentary skull and postcranium	WNIGRI 842/10	*I. morachovskayae*
Kapes Ivakhnenko, 1975	U. Olenekian (Yarenskian–Donguzian)	Russia, England	25–35	mainly dentaries	*K. amaenus* PIN 3361/2 L. Olenekian	4 species: *K. amaenus* *K. majmesculae* (incl. *K. serotinus*) ?*K. komiensis* *K. bentoni*
Koiloskiosaurus Huene, 1911	U. Olenekian	Germany	75	fragmentary skeleton	*K. coburgiensis*	*K. coburgiensis*
Lestanshoria Novikov, 1991	u. L. Olenekian	E. Russia	est. 25	dentary only	PIN 4370/4	*L. massiva*
Macrophon Ivakhnenko, 1975 (see *Kapes*)	U. Olenekian	Russia	est. 130	fragmentary maxilla	*M. komiensis* PIN 3361/1	?*Kapes komiensis*
Neoprocolophon Young, 1957	L. Triassic	China	75	partial skull with dentary fragment	*N. asiaticus* LVP 866	*N. asiaticus*
Orenburgia Ivakhnenko, 1975	L. Olenekian (Yarenskian Ustmylian)	Russia	45	fragmentary skull, mandible	*Tichvinskia enigmatica* PIN 1043/1	*O. enigmatica* *O. bruma*
Procolophon Owen, 1876	L. Olenekian	S. Africa	51	several skulls	*P. trigoniceps*	*P. trigoniceps* *P. pricei*
Samaria Novikov, 1991	L. Olenekian (Rybinskian Sludkian)	Russia	est. 33	fragmentary skull with mandible	*Orenburgia concinna* PIN 3362/1	*S. concinna*
Tichvinskia Tchudinov *et* Vjuschkov, 1956	Olenekian	Russia	32	complete skeleton, skulls	*T. vjatkensis* PIN 953/1	?monotypic (*T. jugensis* ?invalid)
Timanophon Novikov, 1991	L. Olenekian (Ustmylian)	Russia	27	skull, mandible fragmentary skeleton	*Burtensia burtensis* PIN 3359/11	monotypic *T. raridentatus*

APPENDIX 3

Comparative data on the procolophonin dentary and lower dentition from the literature. Abbreviations: dd, dentary depth at about the level of the molariform tooth; dtl, dentary tooth row length; est., estimated; md, molariform tooth depth.

Early Triassic Procolophoninae	Dentary teeth formula	Tooth count	Crown shape md/dd %	Dentary tooth row length (dtl) mm	Dentary dtl./dd	Data according to
Burtensia burtensis	5.1.1-2	7–8	bicuspid 125%	13	5.9	Ochev 1958
Kapes amaenus	5.1.1	7	slightly bicuspid 93%	14	2.3–3.1	Ivakhnenko 1975
K. majmesculae	5.1.1		slightly bicuspid 62%	14		
K. bentoni	5.1.1		bicuspid 69–86%	7		Spencer and Benton 2000
Lestanshoria massiva	5.1.1	7	bicuspid 50%	11	2.4	Novikov 1994
Orenburgia bruma	4.1.2	7	bicuspid est. 20–30%	27	2.8	Novikov 1994
Procolina teresae	5.1.1-2	7–8	unicuspid	7.0–11.5	3.6–5.3	
Procolophon trigoniceps	?	8–10 (ca. 15 in juv.)	bicuspid est. 38%	14–18	est. 2.9	Gow 1977a
Samaria concinna	5.1.1	7	bicuspid 66%	12	2.8	Novikov 1991
Tichvinskia vjatkensis	6.1.2	9	bicuspid 50%	14	3.0	Ivakhnenko 1979
Timanophon raridentatus	6.1.1	8	bicuspid	11	3.9	Novikov 1991

AN EARLY KUEHNEOSAURID REPTILE FROM THE EARLY TRIASSIC OF POLAND

SUSAN E. EVANS

Evans, S.E. 2009. An early kuehneosaurid reptile (Reptilia: Diapsida) from the Early Triassic of Poland. *Palaeontologia Polonica* **65**, 145–178.

The Early Triassic locality of Czatkowice, Poland has yielded fish, amphibians, and a series of small reptiles including procolophonians, lepidosauromorphs and archosauromorphs. The lepidosauromorphs are amongst the smallest and rarest components of the assemblage and constitute two new taxa, one of which is described and named here. *Pamelina polonica* shares skull and vertebral characters with the kuehneosaurs, a group of specialised long-ribbed gliders, previously known only from the Late Triassic of Britain and North America. The relationship is confirmed by cladistic analysis. *Pamelina* is the earliest known kuehneosaur and provides new information about the history of this clade. It is less derived post-cranially than any of the Late Triassic taxa, but probably had at least rudimentary gliding or parachuting abilities.

Key words: Reptilia, Kuehneosauridae, Triassic, Poland, gliding, Czatkowice.

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INTRODUCTION

The Neodiapsida of Benton (1985) encompasses a wide range of diapsid lineages, most of which can be assigned to either Archosauromorpha or Lepidosauromorpha (Gauthier *et al.* 1988). Archosauromorpha encompasses a large and successful crown clade (Archosauria) and a series of distinctive stem lineages (*e.g.*, protorosaurs, tanystropheiids, *Prolacerta*, Rhynchosauria, Trilophosauria, Evans 1988; Gauthier *et al.* 1988; Müller 2002, 2004; Modesto and Sues 2004). Crown-group Lepidosauria (Rhynchocephalia and Squamata) also constitutes a large and diverse group but, leaving aside the issue of testudine or sauropterygian affinities (*e.g.*, Rieppel and de Braga 1996; de Braga and Rieppel 1997; Rieppel and Reisz 1999; Müller 2002, 2004; Hill 2005), lepidosauromorph stem taxa are currently limited to the Euramerican Late Triassic Kuehneosauridae (Robinson 1962, 1967a, b; Colbert 1966, 1970), the relictual Mid Jurassic European *Marmoretta* (Evans 1991; Waldman and Evans 1994), and, less certainly, the fragmentary Permo-Triassic South African *Paliguana* and *Saurosternon* (Carroll 1975, 1977). Of these, kuehneosaurs are by far the most specialised.

Kuehneosauridae currently includes three taxa: *Kuehneosaurus latus* (Robinson 1962) and *Kuehneosuchus latissimus* (Robinson 1967a) from the Late Triassic (Norian) fissure deposits of southwest England, and *Icarosaurus siefkeri* (Colbert 1966, 1970) from the Late Triassic (Carnian) Lockatong Formation, Newark Supergroup, of eastern North America. The three genera are characterised by confluent nares, reduced squamosals, and a derived postcranial skeleton. Like the living agamid lizard *Draco* (the "Flying Dragon" of South East Asia), kuehneosaurs had elongated ribs that could be folded back in normal locomotion but opened out to form a "wing" for gliding (*e.g.*, Colbert 1970). When first described, these Triassic reptiles were classified as lizards on the basis of their incomplete lower temporal bars, large quadrates, and small squamosals (Robinson 1962, 1967b; Colbert 1966, 1970; Carroll 1975, 1977; Estes 1983). However, subsequent work has shown that the lower temporal bar was absent in the ancestor of archosauromorphs and lepidosauromorphs (*e.g.*, Müller 2004) and large quadrates characterize lepidosauromorphs generally (*e.g.*, Gauthier *et al.* 1988). Other lizard-like characters were independently acquired (*e.g.*, Evans 1980, 1984, 1988; Gauthier 1984; Gauthier *et al.* 1988), and most authors have relegated kuehneosaurs to the lepidosaurian stem. Moreover, a recent study (Müller 2004) removed kuehneosaurs from Lepidosauromorpha, placing them on the neodiapsid stem as the sister group of the peculiar Late Triassic drepanosaurs (Britain, Italy, North America: Calzavara *et al.* 1980; Pinna 1986; Berman and Reisz 1992; Renesto 1994; Colbert and Olsen 2001; Renesto and Fraser 2003). Until now, however, nothing has been known of early kuehneosaur history.

The Early Triassic karst deposits of Czatkowice 1 (Southern Poland) (Borsuk-Białynicka *et al.* 1999; Paszkowski and Wieczorek 1982) have yielded a microvertebrate assemblage with a range of fish, amphibians (including the stem-frog *Czatkobatrachus*, Evans and Borsuk-Białynicka 1998, 2009a; Borsuk-Białynicka and Evans 2002), and at least seven small reptiles. The reptilian component includes several procolophonians, a very common early archosauriform, *Osmolskina* (Borsuk-Białynicka and Evans 2003, 2009a), and three smaller diapsids. Of the latter, one is a "protorosaur" (Borsuk-Białynicka and Evans 2009b) and the other two are lepidosauromorphs. The smallest lepidosauromorph is described elsewhere (Evans and Borsuk-Białynicka 2009b). The larger lepidosauromorph is described here. Skull, jaw, and postcranial elements support its attribution to the Kuehneosauridae.

Institutional abbreviations. — AMNH, American Museum of Natural History, New York, USA; BMNH, British Museum of Natural History, London, England; TMM, Texas Memorial Museum, Austin, Texas, USA; ZPAL, Institute of Paleobiology Polish Academy of Sciences, Warsaw, Poland.

Acknowledgements. — I am indebted to Magdalena Borsuk-Białynicka of the Institute of Paleobiology, Polish Academy of Sciences, Warsaw, for the invitation to collaborate on the material from Czatkowice 1, for many years of hospitality and discussion at the Institute of Paleobiology in Warsaw, and for her assistance in preparing the plates for this paper. I am also grateful to the team of the Institute of Geology, Jagiellonian University, Kraków, and particularly Józef Wieczorek and Mariusz Paszkowski who discovered, explored and generously transported the bone breccia from Czatkowice to the Museum of the Earth and the Institute of Paleobiology, Polish Academy of Sciences, Warsaw; to the late Halszka

Osmólska (Institute of Paleobiology) and Teresa Maryańska (Museum of the Earth, Warsaw) for access to materials in their care; to Ewa Hara for the acid preparation of the Czatkowice 1 breccia; to Cyprian Kulicki (Institute of Paleobiology) for scanning electron microscope photography; to Jane Pendjiky (University College London) and Aleksandra Hołda-Michalska (Institute of Paleobiology) for assistance with the preparation of the figures. Access to comparative material of *Kuehneosaurus* was provided by Sandra Chapman and Angela Milner (The Natural History Museum, London), Chris Bell (University of Texas, Austin) lent material of *Draco*, and David Dilkes (University of Wisconsin) made helpful comments on an earlier version of the manuscript.

GEOLOGICAL SETTING

The fossil material described in this paper is derived from the Early Triassic cave infilling of Czatkowice 1, Poland, that has been dated as early Olenekian on the basis of dipnoan teeth and procolophonians (Borsuk-Białynicka *et al.* 1999, 2003), or earliest late Olenekian on the basis of temnospondyl material (Shishkin and Sulej 2009). The geology and taphonomy of the locality are discussed elsewhere in this volume and are not repeated here.

MATERIAL AND METHODS

Microvertebrate assemblages are a rich source of small vertebrate remains, but since they consist of disarticulated bones, they present an interpretative challenge. In a multitaxon assemblage the first step is to determine the number of different dentitions — based on tooth morphology (stereomicroscopy and Scanning Electron Microscopy), tooth implantation and tooth number. The same characteristics permit upper and lower jaw components to be associated (and sometimes also parts of the palate), and these, in turn, provide a basis for the attribution of other bones, using evidence from facet morphology, bone texture, overall size (allowing for ontogenetic growth stages) and relative abundance. There is, of course, the possibility of misattribution, but previous work on material of this kind (*e.g.*, Evans 1980, 1981, 1990, 1991; Whiteside 1986) has been validated by the subsequent recovery of articulated specimens of the taxa in question (*e.g.*, Waldman and Evans 1994; Evans and Waldman 1996).

Scanning electron microscopy identified three distinct non-archosauriform and non-procolophonian reptile dentitions from the Czatkowice assemblage and permitted the association of three sets of premaxillae, maxillae and dentaries (Borsuk-Białynicka *et al.* 1999). Subsequent work has attributed these to a “protorosaur” (Borsuk-Białynicka and Evans 2009b), a small derived lepidosauromorph (Evans and Borsuk-Białynicka 2009b), and the kuehneosaur described herein. Most of the other small skeletal elements (cranial and postcranial) also show several distinct morphologies. Procolophonian skull bones can generally be separated from those of diapsids on shape and the absence of fenestral boundaries, in combination with bone type and strong sutural overlaps. For the diapsids, the bones referable to the “protorosaur” (Borsuk-Białynicka and Evans 2009b) could be distinguished by their size range (juvenile up to large adults that overlap with *Osmolskina*) and frequency, as well as internal consistency in terms of bone and sculpture type, and fit. The attribution of the remaining elements to one or other of the lepidosauromorph taxa was based on the criteria described above. For the new taxon described herein, the two most characteristic bones are the premaxilla and the squamosal. These provided a basis for matching the maxilla anteriorly, and the parietal and postorbital bones posteriorly. The frontal must then fit the parietal, and also the postorbital bones and the prefrontal. The prefrontal must articulate between the frontal and the maxilla, and the jugal must fit between the maxilla and postorbital. Many of the skull bones of this reptile are also remarkably fragile, with a thin outer layer of bone surrounding large internal cavities. This provided an additional basis for attribution that also extends to the postcranial skeleton. The Late Triassic *Kuehneosaurus*, although far larger, also has thin bone, paralleling the condition in birds and pterosaurs.

In the descriptive sections that follow, the comparisons focus mainly on the Late Triassic British kuehneosaurs for which good three-dimensional disarticulated bones are available. This material was originally collected by the late Pamela L. Robinson (UCL) but is now in The Natural History Museum, London (prefix BMNH R.). Note, however, that *Kuehneosaurus* (Robinson 1962) and *Kuehneosuchus* (Robinson 1967a) are distinguished from one another primarily on the length of the “wing” ribs, relatively short and massive in *Kuehneosaurus* (1.5 × posterior skull width) but longer and more gracile in *Kuehneosuchus* (up to 5 × posterior skull width) (Robinson 1967a); no differences have been recognised in the skull or major postcranial bones. Thus in the comparative sections reference to *Kuehneosaurus* should be taken to mean *Kuehneosaurus* or *Kuehneosuchus*. Comparisons with *Icarosaurus* are based on personal observation of the type and only specimen (American Museum of Natural History, AMNH 2101), in conjunction with the descriptions of Colbert (1966, 1970).

SYSTEMATIC PALEONTOLOGY

Clade Neodiapsida Benton, 1985
Clade Lepidosauromorpha Gauthier, 1984
Clade Lepidosauriformes Gauthier, Estes, *et* De Queiroz, 1988
Family **Kuehneosauridae** Robinson, 1962

Genus ***Pamelina*** gen. n.

Type species: *Pamelina polonica* sp. n.

Derivation of name: For the late Dr Pamela L. Robinson who described the first kuehneosaur material from Britain.

Diagnosis. — As for type and only species (see below).

Pamelina polonica sp. n.

Derivation of name: From Poland.

Holotype: ZPAL RV/1036, the anterior region of a left maxilla (Figs 1A, 2A) collections of Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Type locality and horizon: Czatkowice 1 Quarry, Kraków region, Poland. Fissure/cave infill dated as Early Triassic (Early Olenekian).

Diagnosis. — Small diapsid reptile resembling Late Triassic kuehneosaurids in having confluent nares framed by specialised premaxillae with posterolateral but not dorsomedial processes; maxilla almost excluded from the narial margin by the posterolateral process of the premaxilla; prefrontal with only a narrow contribution to the preorbital skull wall; loss of the parietal foramen; anterolateral flange on the parietal meeting postorbital to exclude the postfrontal from the margins of the upper temporal fenestra; specialised slender squamosal with a strong posterodorsal process but no anteroventral ramus; no supratemporal bone; mediolaterally compressed amphiplatyan vertebral centra with short slender transverse processes throughout the column; dichocephalous ribs on cervical vertebrae, slender holocephalous ribs on dorsal vertebrae; very lightly built skeleton, bones with internal cavities. *Pamelina* differs from *Kuehneosaurus*, *Kuehneosuchus*, and *Icarosaurus* in lacking teeth on the parasphenoid, and in having more gracile ribs and vertebrae, with short narrow circular transverse processes (unlike the extended processes of Late Triassic taxa) and only limited buttressing on the vertebral body (as against strong buttressing, especially in *Kuehneosaurus*). *Pamelina* also differs from the British kuehneosaurs in lacking three-headed ribs on anterior vertebrae (the condition in *Icarosaurus* is less certain, Colbert 1970, p. 107). *Pamelina* differs from all other known Permian and Mesozoic diapsids in the combination of confluent nares with a reduced squamosal, an incomplete lower temporal arcade, an expanded quadrate, and laterally compressed amphiplatyan vertebrae with long slender transverse processes and extended ribs. The skull of the Triassic *Mecistotrachelos* (Fraser 2007) is poorly known, but the postcranial skeleton of *Pamelina* differs in having relatively short cervical vertebrae.

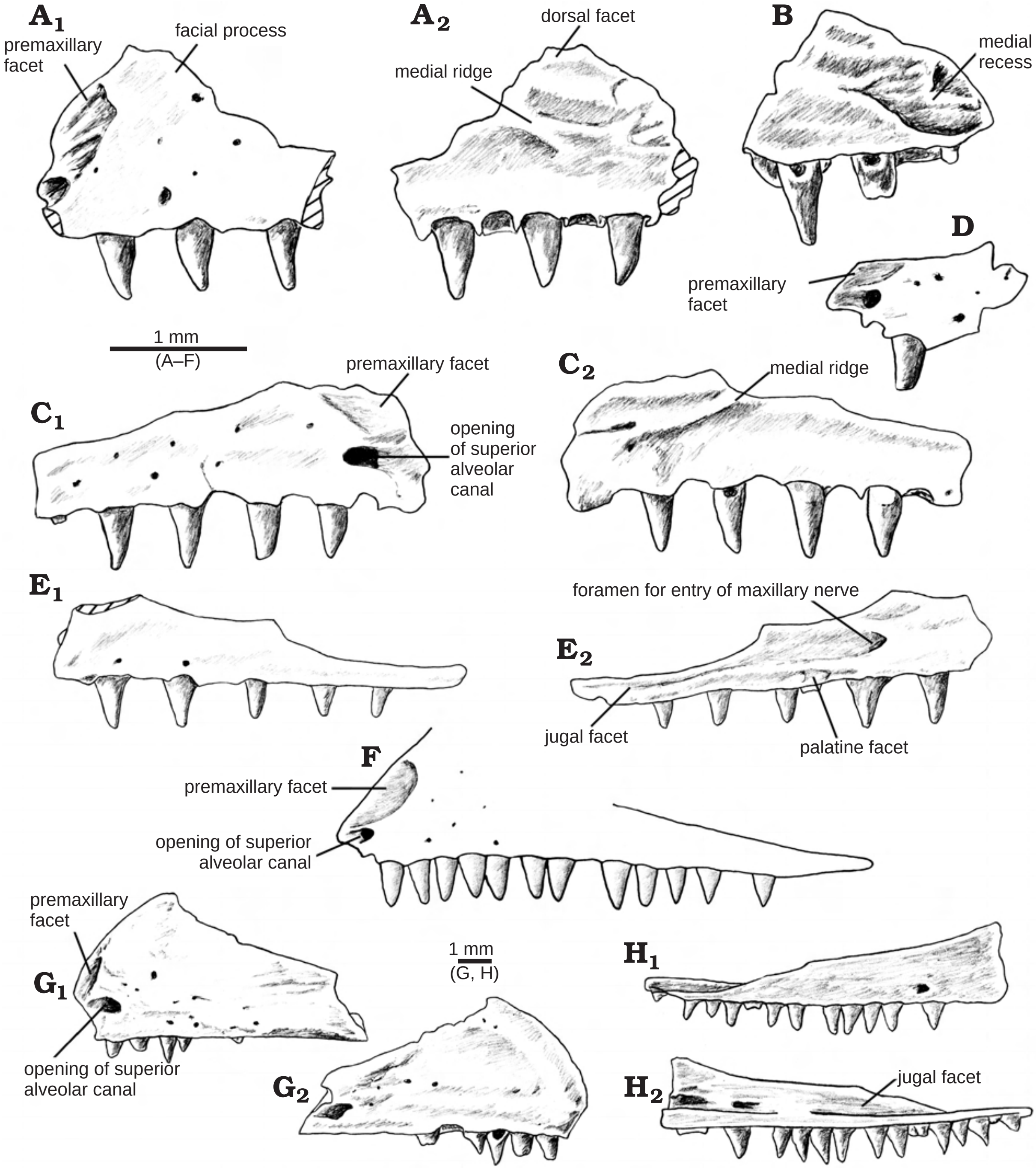

Fig. 1. **A**–**F**. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Holotype left maxilla ZPAL RV/1036, in lateral (A_1) and medial (A_2) views. **B**. Anterior tip of a left maxilla ZPAL RV/1039, in medial view. **C**. Right maxilla ZPAL RV/1034, in lateral (C_1) and medial (C_2) views. **D**. Anterior tip of a left maxilla ZPAL RV/1042, in lateral view. **E**. Orbital process of a left maxilla ZPAL RV/1035, in lateral (E_1) and medial (E_2) views. **F**. Partial reconstruction of *Pamelina* maxilla, in lateral view. **G**, **H**. *Kuehneosaurus*, Late Triassic, Emborough Quarry, England. **G**. Left anterior maxilla BMNH R.12900, in lateral (G_1) and medial (G_2) views. **H**. Orbital process of a right maxilla MBNH R.12903, in lateral (H_1) and medial (H_2) views.

Referred specimens. — ZPAL RV/378, 381, 383–384, 387, 537, 1087 (frontals); ZPAL RV/157, 975–978, 1028 (parietals); ZPAL RV/ 979, 980, 1001, 1002 (prefrontals); ZPAL RV/148, 1003, 1004, 1006, 1007, 1027 (postfrontals); ZPAL RV/806, 1005, 1072, 1077, 1078 (postorbitals); ZPAL RV/1008–1010 (jugals); ZPAL RV/147, 366, 1011–1026 (squamosals); ZPAL RV/1029–1033, 1083 (quadrates); ZPAL RV/1, 6, 1034–1042, 1081 (maxillae); ZPAL RV/146, 151–155, 184, 201, 451, 1043–1045, 1082 (premaxillae); ZPAL RV/1048–1050 (sphenoids); ZPAL RV/142–144, 149, 162, 185, 186, 1046, 1047 (dentaries); ZPAL

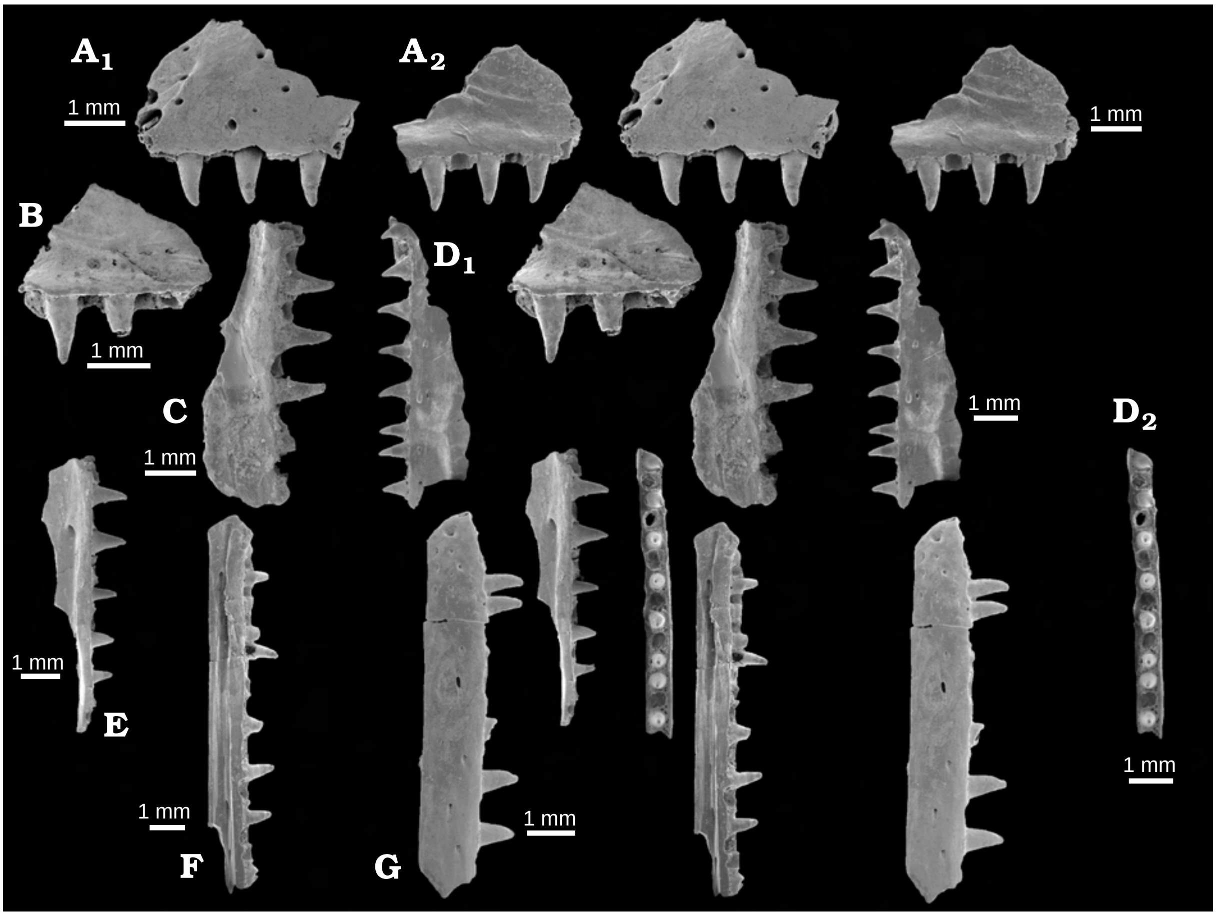

Fig. 2. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Maxilla and dentary. **A**. Holotype left maxilla ZPAL RV/1036, in lateral (A_1) and medial (A_2) views. **B**. Anterior tip of a left maxilla ZPAL RV/ 1039, in medial view. **C**. Midsection of a right maxilla ZPAL RV/1034, in medial view. **D**. Midsection of a left maxilla ZPAL RV/1081, in lateral (D_1) and occlusal (D_2) views. **E**. Orbital process of a left maxilla ZPAL RV/1035, in medial view. **F**. Partial left dentary ZPAL RV/143, in lateral view. **G**. Right partial dentary ZPAL RV/144, in medial view. SEM stero-pairs.

RV/1066, 67 (possible palatines); ZPAL RV/ 613, 617, 627, 1194–1210 (vertebrae); ZPAL RV/1211–1213 (ribs); ZPAL RV/555, 981 (ilia).

DESCRIPTION

SKULL

Introduction. — Using the criteria listed in the Materials and Methods section, the following elements have been attributed to *Pamelina* with a reasonable level of confidence: premaxillae, maxillae, dentaries, frontals, parietals, prefrontals, postfrontals, postorbitals, jugals, and squamosals. The quadrates are referred on the basis that their morphology and size is consistent with that of the squamosal, supported by a close resemblance to those of *Kuehneosaurus*. Other cranial bones (*e.g.*, palatines, sphenoids) are referred more tentatively, but in all cases their basic morphology is consistent with that of *Kuehneosaurus*.

The skull reconstructions in Fig. 3 are based on isolated and incomplete elements from more than one individual. Clearly this has its limitations and should be regarded as providing an estimated, rather than exact, representation of proportions. The key relationships are those between the parietal and squamosal (*e.g.*, ZPAL RV/975 and 147); the frontal, parietal and postfrontal (*e.g.*, ZPAL RV/378, 157 and 978); the frontal and prefrontal (ZPAL RV/381 and 979); the premaxilla and maxilla (ZPAL RV/1044 and 1034); the squamosal and the quadrate (ZPAL RV/147, 1011, 1029); and the length of the maxilla (ZPAL RV/1034, 1035, 1036, and 1038). The ventral edge of the prefrontal lines up roughly with the anterior part of the palatine facet on the maxilla (because it met the anterior edge of the palatine in life) and the ventral condyle of the quadrate gives the outer limit of the lower jaw which, in itself, must run anteriorly on the same line as the maxilla. Without the nasals, the width and length of the skull would ideally be confirmed by palatal elements but this region is poorly known in *Pamelina*. The reconstructions in Fig. 3 were made without reference to *Kuehneosaurus* but, despite differing proportions, the result shows striking similarities, including the very small relative size and posterior position of the squamosal.

Premaxilla. — The premaxilla of *Pamelina* is a distinctive element represented by several good specimens (*e.g.*, ZPAL RV/146, 451, 1043, 1044, 1045, and 1082), and many more fragmentary ones. It is composed of three parts: a shallow, slightly curved alveolar ramus; a posterolateral maxillary process; and an elongate palatal flange (Figs $4A_1$, 5). The narrow alveolar margin bears four or five strong, slightly recurved, teeth set in shallow circular pits (Figs $4A_3$, 5A, C). Starting from a point roughly half way along its lateral edge, the alveolar margin is extended obliquely upwards and backwards (at roughly 45° to the horizontal) by a long laterally compressed blade of bone that fitted against a matching facet on the anterolateral margin of the maxilla and almost excluded it from the border of the external nares (Fig. $4A_2$). In Fig. 3B, the ventral margins of premaxilla and maxilla are shown in alignment, but it is possible that there was a slight anteroventral angulation of the premaxilla in life. Ventromedially, the premaxillae met along a strong anteromedial symphysial surface, but the only remnant of the dorsal nasal process is a slight medial elevation (Figs $4A_4$, $5A_2$, B_2); the nares were thus confluent. Posteromedially, each premaxilla is drawn into a horizontal palatal flange that floored the confluent nares and is separated from the alveolar margin by a narrow choanal embayment (Fig. $4A_3$).

Comparison with Late Triassic kuehneosaurs: The premaxilla of *Pamelina* resembles that of *Kuehneosaurus* (*e.g.*, BMNH R12879, 12880, Fig. 4B) in general shape (confluent nares, posterolateral maxillary process, median flange, five tooth positions), but differs in having a more conspicuous posterior palatine flange (small stub in *Kuehneosaurus*) and a posterolateral process that originates further back, so that the narial opening is wider and more U-shaped (compare Fig. $4A_2$ and B_1). The precise shape of the premaxilla of *Icarosaurus* is uncertain as the bone is overlain by other elements (Colbert 1966, 1970; personal observations).

Maxilla. — No complete maxilla exists for *Pamelina* but it is represented by many anterior and posterior fragments (*e.g.*, ZPAL RV/1034–1042, Figs 1A–F, 2A–D). There were at least 20 tooth positions. The facial process is relatively deep (more than twice the height of the longest tooth) with an almost straight narial margin (*e.g.*, ZPAL RV/1034, 1036) that bears a long narrow premaxillary facet (most sharply defined in large specimens, *e.g.*, ZPAL RV/1036, Figs $1A_1$, $2A_1$). As the facet does not reach the top of the bone, the maxilla clearly entered the narial margin for a short distance dorsally. A large ventrolateral exit foramen for the superior alveolar canal opens into the lower edge of the premaxillary facet and below this, the anterior margin of the maxilla is notched (Fig. 1D). The maxillary teeth, like those of the premaxilla, are attached to the margins of shallow rounded pits and were replaced from the lingual side.

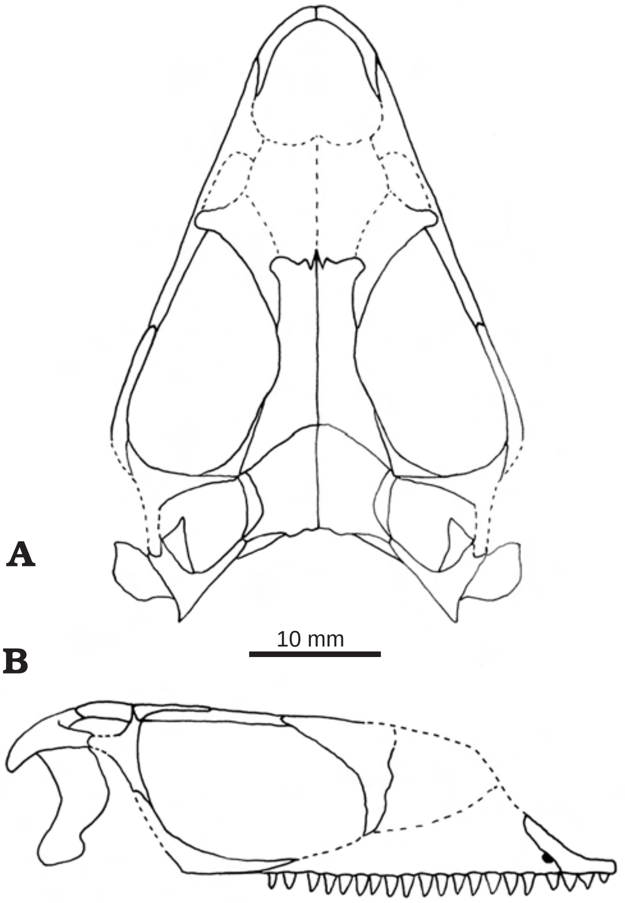

Fig. 3. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Reconstruction of the skull, in dorsal (A) and lateral (B) views.

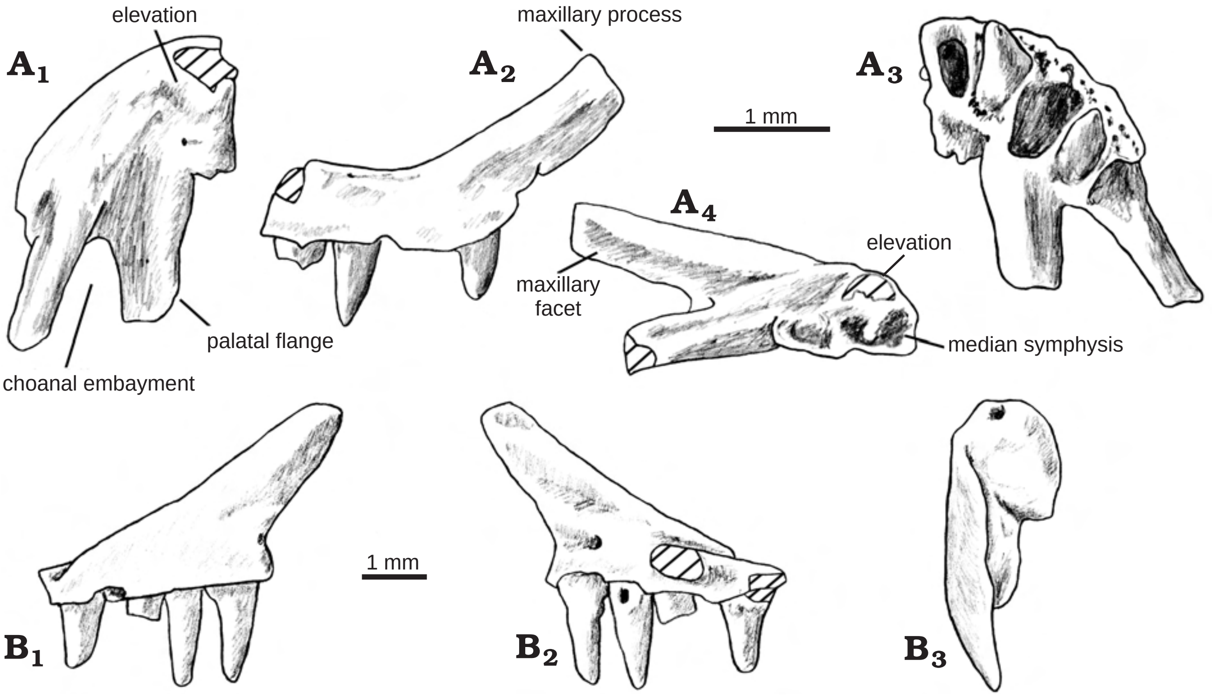

Fig. 4. **A**. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Left premaxilla ZPAL RV1082, in dorsal (A_1), lateral (A_2), ventral (A_3), and medial (A_4) views. **B**. *Kuehneosaurus*, Late Triassic, Emborough Quarry, England. Left premaxilla BMNH R.12880, in lateral (B_1), medial (B_2) and dorsal (B_3) views.

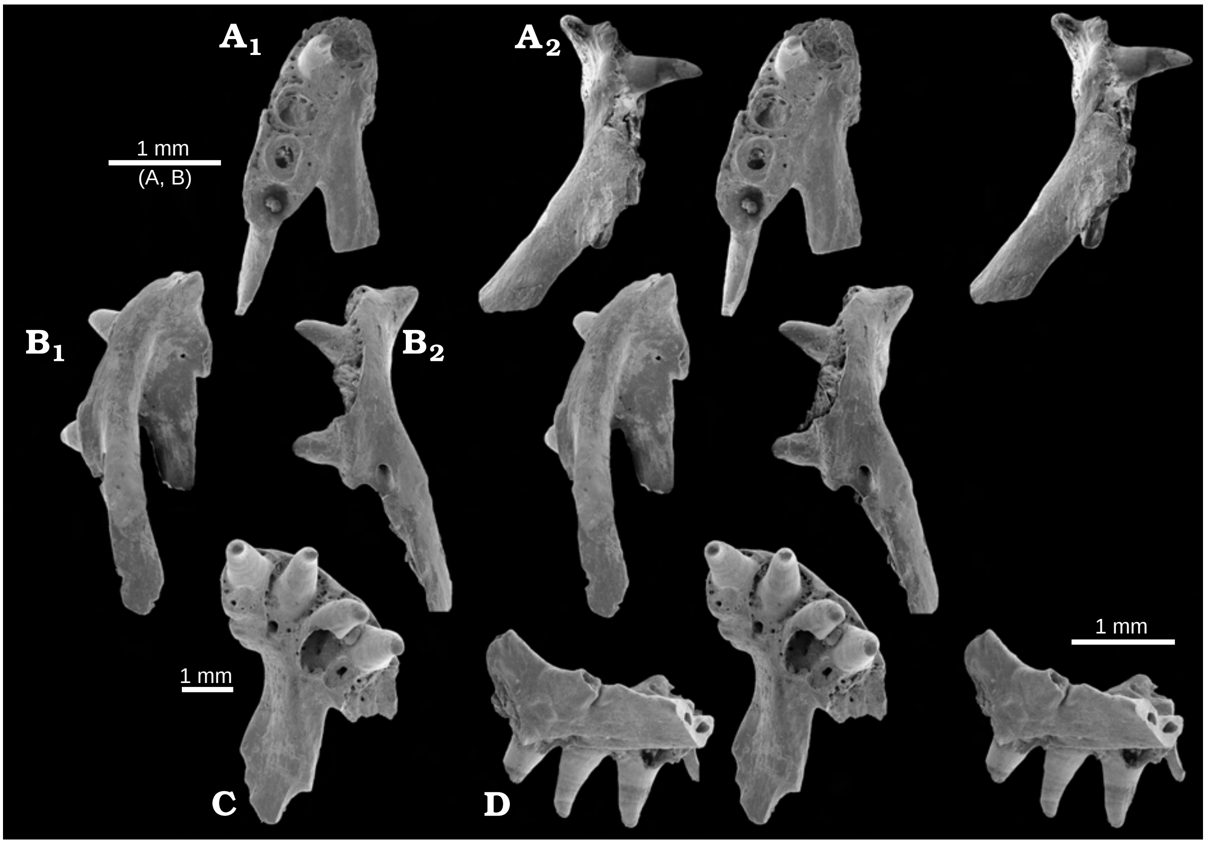

Fig. 5. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Premaxilla. **A**. Right bone ZPAL RV/146, in ventral (A_1) and lateral (A_2) views. **B**. Left bone ZPAL RV/1039, in dorsolateral (B_1) and lateral (B_2) views. **C**. Left bone ZPAL RV/451, in ventral view. **D**. Partial right bone ZPAL RV/1043, in lateral view. SEM stero-pairs.

No specimen preserves the very thin anterodorsal margin of the bone, but a large dorsal facet extending across this region medial to the premaxillary articulation (*e.g.*, ZPAL RV/1034 and 1036) is probably for the nasal. In *Kuehneosaurus*, the large lacrimal reached forward almost to the anterior edge of the facial process, but the posterodorsal part of the maxilla is not preserved in *Pamelina* and the nasal has not been identified, making the relationships of the maxilla, nasal and lacrimal difficult to reconstruct (hence the open area above the maxilla and anterior to the prefrontal in Fig. 3B). The area below the dorsal facet bears anterior and posterior recesses. The posterior recess is separated from the dorsal facet by a conspicuous medial ridge and presumably accommodated part of the nasal apparatus. The anteromedial recess (*e.g.*, ZPAL RV/1039, Fig. 1B) is problematic. It clearly did not accommodate a flange from the premaxilla and the structure of the latter bone renders it unlikely that the vomer met the maxilla anteriorly. The most likely candidate is a septomaxilla, although this suggests a rather larger bone than is present in the modern *Sphenodon* where the attachment is very weak.

The depth of the maxilla decreased towards the articulation with the jugal. The posterior orbital process (*e.g.*, ZPAL RV/1035) is perforated medially by a large foramen carrying the maxillary nerve and blood vessels into the superior alveolar canal. Behind this level, the bone develops a narrow medial facet for the palatine and a posterior jugal facet, supported by a small medial flange.

Comparison with Late Triassic kuehneosaurs: The maxilla of *Pamelina* resembles that of *Kuehneosaurus* (*e.g.*, BMNH R12900, Fig. 1G) in the features of the anterior margin (large superior alveolar foramen open-

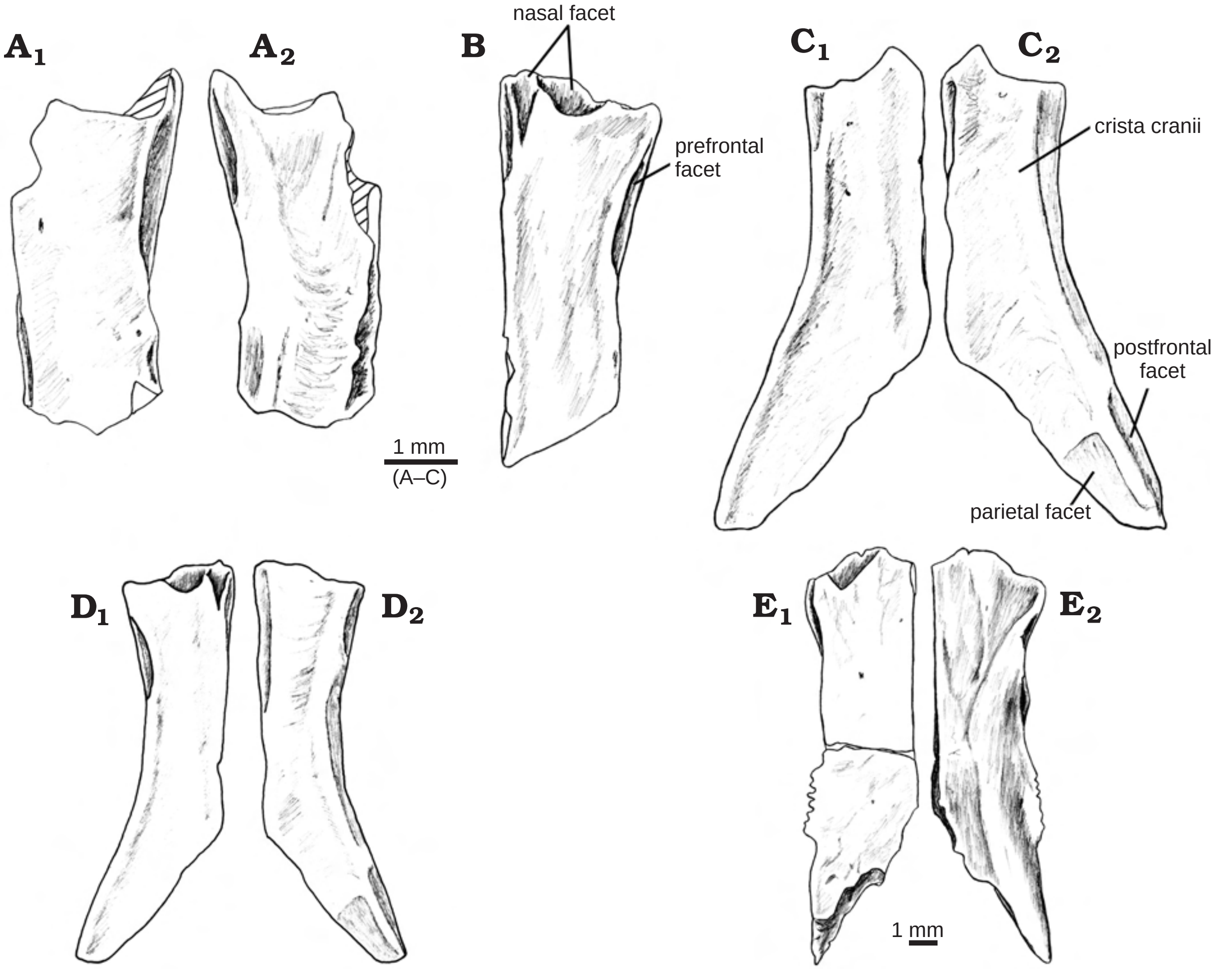

Fig. 6. **A**–**D**. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Anterior part of right frontal ZPAL RV/387, in dorsal (A_1) and ventral (A_2) views. **B**. Anterior part of right frontal ZPAL RV/383, in dorsal view. **C**. Posterior region of a left frontal ZPAL RV/378, in dorsal (C_1) and ventral (C_2) views. **D**. Partial reconstruction of a left frontal, in dorsal (D_1) and ventral (D_2) views; out of scale. **E**. *Kuehneosaurus*, Late Triassic, Emborough Quarry, England. Left frontal BHNH R.12864, in dorsal (E_1) and ventral (E_2) views.

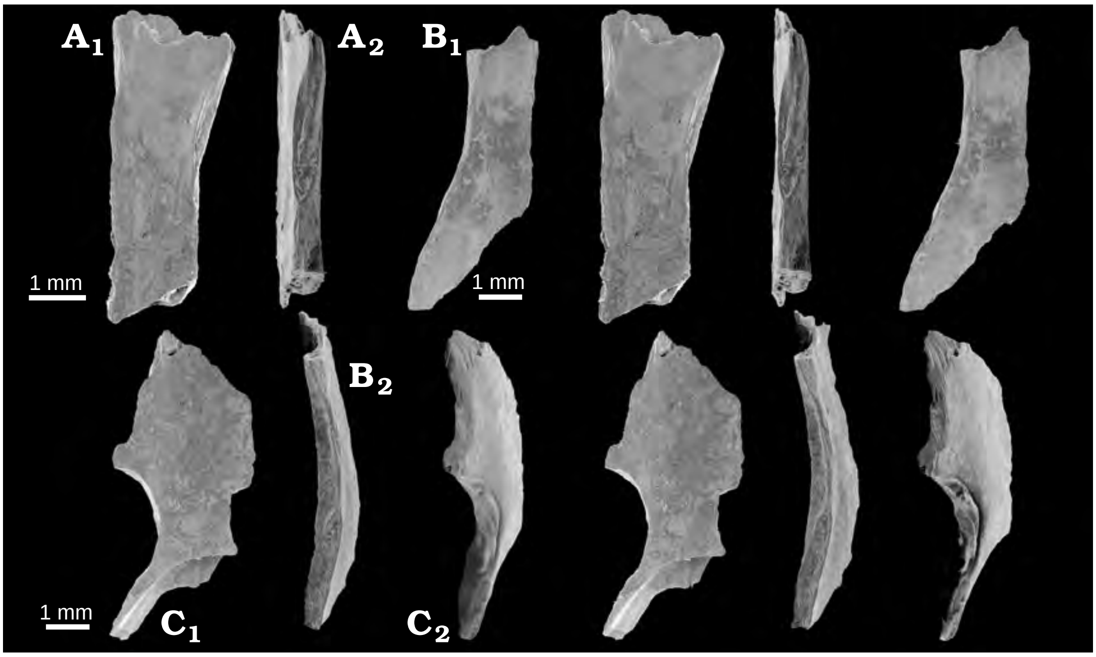

Fig. 7. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Frontal and parietal. **A**. Anterior end of a right frontal ZPAL RV/384, in dorsal (A_1) and lateral (A_2) views. **B**. Posterior region of a left frontal ZPAL RV/378, in dorsal (B_1) and lateral (B_2) views. **C**. Left parietal ZPAL RV/157, in dorsal (C_1) and dorsolateral (C_2) views. SEM stero-pairs.

ing into vertical premaxillary facet; ventral notch; limited entry of maxilla into narial margin), the tooth implantation (sub-thecodont/sub-pleurodont), and the long tapering posterior jugal process with a weakly developed jugal facet (Fig. 1H). *Pamelina* differs in having a more marked medial ridge and the problematic anteromedial recess (absent in *Kuehneosaurus*), and in the pointed anteroventral margin (more rounded in *Kuehneosaurus*, Fig. 1G). In *Icarosaurus*, much of the maxilla is covered by other elements.

Frontal. — All the Czatkowice 1 reptiles had paired frontals of roughly similar shape. Attribution to *Pamelina* has been made on the basis of fit, particularly with the parietal; the absence of dorsal sculpture; and bone texture and density. *Pamelina* frontals (*e.g.*, ZPAL RV/378, 381, 383, 384, and 387) are wider posteriorly than anteriorly, and show a small interorbital constriction and a strongly “U”-shaped posterior margin (Figs 6A–D, 7A, B). They are composed of thin bone that forms a weak shell around a hollow centre, unlike the dense bones of other taxa. There are anterodorsal and posteroventral shelf facets for the nasal and parietal respectively. Ventrally, the frontal is weakly concave posteriorly and a little more strongly so anteriorly. Frontals of *Pamelina* differ from those of the other small diapsids in having very narrow, laterally placed cristae cranii (subolfactory processes) and in being unusually shallow, so that the lateral prefrontal and postfrontal facets have little depth and do not encroach onto the dorsal surface. Medially, the frontals met in a slightly modified butt joint, with a small overlap shelf anteriorly and a weak interdigitation posteriorly.

Comparison with Late Triassic kuehneosaurs: The frontal of *Kuehneosaurus* (*e.g.*, BMNH R12864, Fig. 6E) is thicker overall than that of *Pamelina*, although again it comprises a shell of thin bone around a hollow core. The shape of the nasal and prefrontal facets is closely similar in both taxa (with the prefrontal facet shallow), and in both taxa, the posteromedial margins angle away from the midline to accommodate the anteromedial expansion of the parietal. However, the frontal of *Kuehneosaurus* has a smaller posteroventral facet, a simpler articulation with the nasal (additional medial nasal notch in *Pamelina*, Fig. 6B, D) and much broader lateral borders (cristae cranii), and the interfrontal suture is a simple butt joint (weak interdigitation in *Pamelina*). In *Icarosaurus* the frontals are paired, and relatively thin, but appear to have been proportionally slightly shorter and wider than those of *Pamelina*.

Parietal. — All reptile parietals from Czatkowice are paired. Of the three small diapsid parietal morphotypes, only one (as represented by ZPAL RV/157, 975–978, and 1028) has postparietal processes of the right shape to accommodate the kuehneosaurid type squamosal. The left and right bones overlap medially (right-over-left) with a wide shelf and there is no trace of a parietal foramen. The dorsal surface is flat and

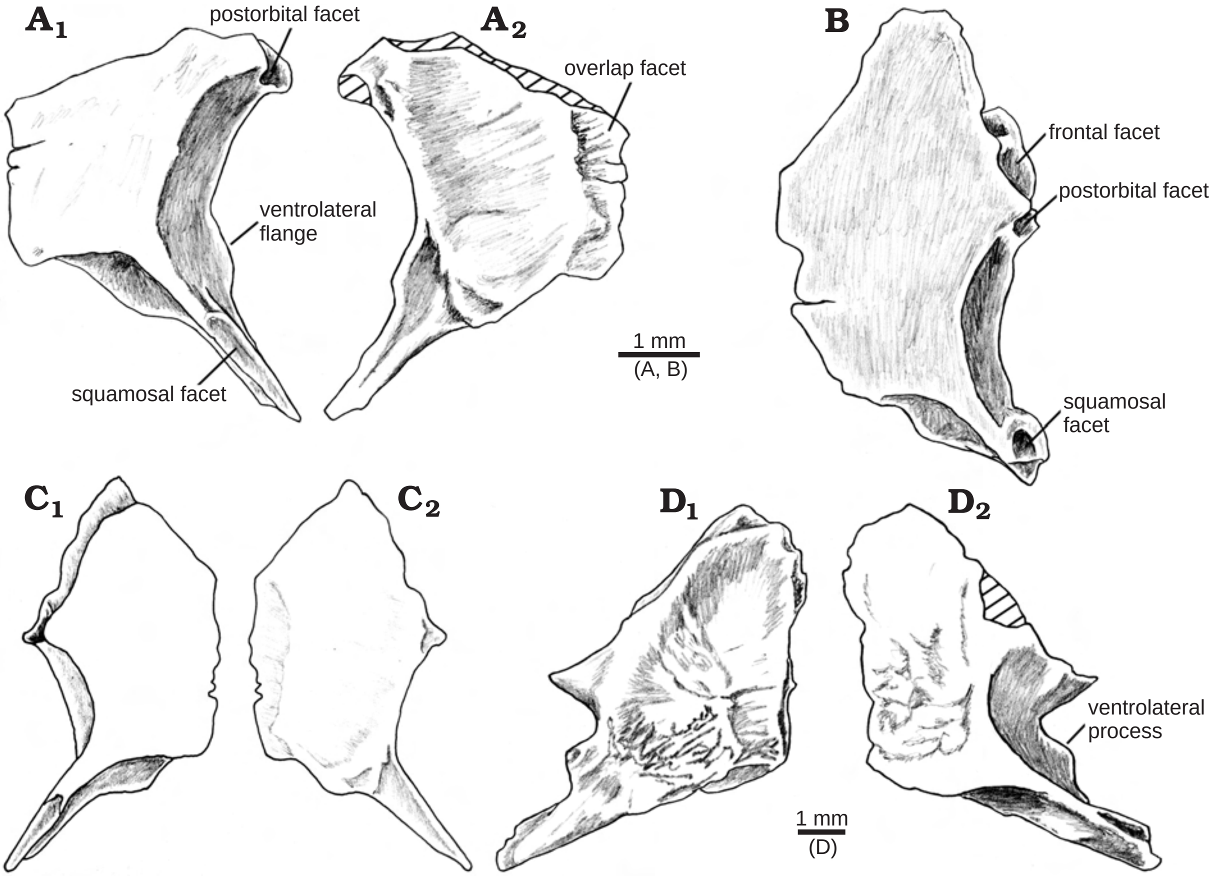

Fig. 8. **A**–**C**. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland, parietal. **A**. Right parietal ZPAL RV/975, in dorsal (A_1) and ventral (A_2) views. **B**. Right parietal ZPAL RV/1028, in dorsal view. **C**. Reconstruction of left parietal, in dorsal (C_1) and ventral (C_2) views, out of scale. **D**. *Kuehneosaurus*, Late Triassic, Emborough Quarry, England. Right parietal BMNH R.12861, in ventral (D_1) and dorsal (D_2) views.

unsculptured (Figs 7C_1, 8A–C); the ventral surface is concave and grooved by cranial blood vessels (Fig. 8A_2, C_2). Overall, the bone is relatively short and broad, with short tapering postparietal processes and smaller anterolateral wings separated by the strongly curved margin of the upper temporal fenestra. This bears a wide, oblique lateral surface for adductor muscle attachment, whereas the posterior border is incised by a deep lateral pocket for epaxial craniocervical muscles.

Anteriorly, the parietals combine to form a rounded median process, the margin of which carries a small slot facet and a larger shelf facet for the frontal. In mature specimens (*e.g.*, ZPAL RV/157, Fig. 7C), the lateral wing also bears an anterior facet for the medial corner of the postfrontal (see below) and a posterolateral facet for the tip of the postorbital. The postparietal process extends posterolaterally at ca. 45° to the long axis of the bone. It is broad at the base and tapers distally. The cross-section is strongly triangular due to the presence of a dorsal crest. The squamosal facet develops on the anterodorsal face of the process, providing a semicylindrical surface around which the concave dorsal process of the squamosal wraps. There is no space for a separate supratemporal.

Comparison with Late Triassic kuehneosaurs: The parietal of *Kuehneosaurus* (*e.g.*, BMNH R12861, Fig. 8D) resembles that of *Pamelina* in having a rounded anterior process; a strong anterolateral wing that meets the posterior process of the frontal, the postfrontal and the postorbital; and a posterior border that is thin medially but expands laterally into large pockets for the epaxial muscles. As exposed on the right side of the skull, the parietal of *Icarosaurus* is similar. *Kuehneosaurus* and *Icarosaurus* differ from *Pamelina* in having a shorter upper temporal fenestra, with the postparietal process directed more laterally than posteriorly, a slightly deeper profile in lateral view, and a more slit-like facet for the squamosal (*Kuehneosaurus*). Half way between the anterolateral wing and the postparietal process in *Kuehneosaurus*, there is a small ventrolateral extension than may have met either the braincase or the tip of the epipterygoid. *Pamelina* has a much weaker

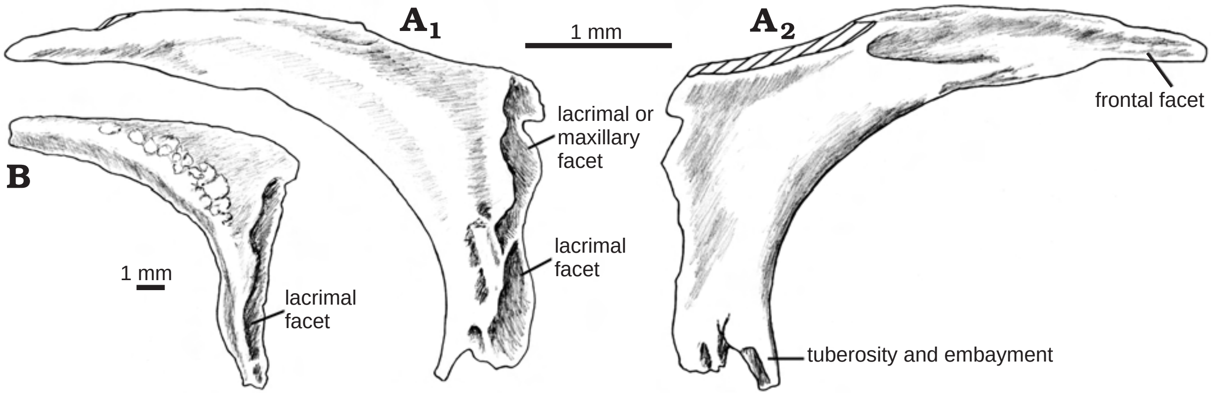

Fig. 9. **A**. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Right prefrontal ZPAL RV 979, in lateral (A_1) and medial (A_2) views. **B**. *Kuehneosaurus*, Late Triassic, Emborough Quarry, England. Right prefrontal BMNH R.12866, in lateral view.

flange in this position. In neither *Kuehneosaurus* nor *Icarosaurus* is the parietal notched by a parietal foramen. Robinson (1962) and Colbert (1966, 1970) reconstructed a foramen at the frontoparietal suture in *Kuehneosaurus* and *Icarosaurus* respectively but the configuration of the bones makes this unlikely and the interpretation seems to have stemmed rather from an expectation that a parietal foramen should be present in what were then regarded as early lizards. A foramen on the frontoparietal margin is a derived character of iguanian lizards and, where present, is typically marked by rounded and slightly raised edges rather than simply a gap between otherwise fully developed bones. The parietal foramen should be coded as absent in Late Triassic kuehneosaurs and in *Pamelina*.

Prefrontal. — Prefrontals are well represented in the Czatkowice assemblage, but most are attributable to archosauromorphs or procolophonians. Of the two rarer types, only one (*e.g.*, ZPAL RV/979, 980, 1001, and 1002) bears a process that would fit against the facet on the *Pamelina* frontal (in being shallow, flat at its tip and then more L-shaped at the anterior point). This prefrontal type (Figs 9A, 10A) is limited to a narrow orbitonasal flange, and a narrow facial strip bordering a deep anterior facet. Only the posterior rim of the facet is ever preserved and it is not clear how much of the thin anterior portion has broken away. The facet is stepped. The lower part at least is interpreted as being for a lacrimal bone that formed much of the preorbital skull wall behind the facial process of the maxilla, but whether the maxilla contacted the prefrontal above the lacrimal is not clear. At the posteroventral edge of the facet there is typically a small low tuberosity or flange of uncertain function. In ZPAL RV/ 979 (Fig. $9A_2$), the lower end of the orbitonasal flange is almost complete and is roughened, presumably for attachment (either directly or through soft tissue) to the palatine. A slight embayment in this margin might be associated with the infraorbital foramen (maxillary nerve).

Comparison with Late Triassic kuehneosaurs: The prefrontal of *Kuehneosaurus* (*e.g.*, BMNH R12866, 12867, Fig. 9B) resembles that of *Pamelina* in general shape (narrow facial portion), but is less rugose in its ventral, palatal portion and more rugose along the orbital rim. As exposed on the holotype, the prefrontal of *Icarosaurus* has a similar form.

Postfrontal. — The postfrontal (*e.g.*, ZPAL RV/1003, 1004, 1006, 1007) is attributed on the basis of fit (to the parietal and frontal), but also resembles other elements in being hollow rather than solid. The bone is the shape of a shallow right-angled triangle, with the hypotenuse forming the orbital margin (Figs 10C, 11A, B_1, B_2). In some specimens (*e.g.*, ZPAL RV/1003) this margin is ornamented by small tubercles (Fig. $11A_1$). The longer of the remaining edges meets the frontal, its anterior tip fitting into a slight recess in that bone. The shorter, posterior edge of the postfrontal bears a grooved facet for the postorbital (Fig. $11A_2$), although the posteromedial corner slotted into the anterolateral parietal recess (Fig. $11B_2$, B_3). When articulated, the postorbital met the tip of the parietal wing to exclude the postfrontal from the margin of the upper temporal fenestra.

Comparison with Late Triassic kuehneosaurs: *Kuehneosaurus*, *Icarosaurus*, and *Pamelina* share a triangular postfrontal that slots into the corner between the rear of the frontal and the anterolateral wing of the parietal. They differ, however, in that *Kuehneosaurus* postfrontal (*e.g.*, BMNH R12868, 12869, Fig. 11C, D)

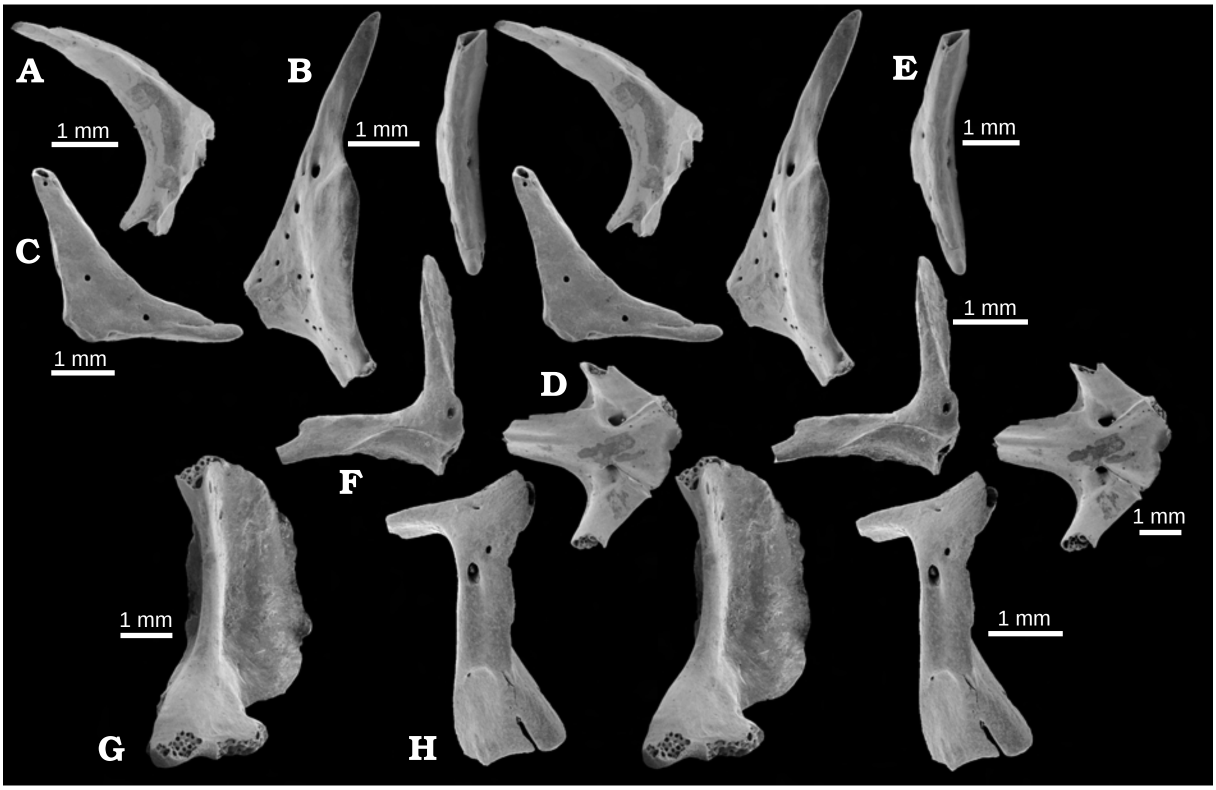

Fig. 10. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Skull bones. **A**. Right prefrontal ZPAL RV/979, stereopairs in posterodorsal view. **B**. Right postorbital ZPAL RV/1077, in lateral view. **C**. Right postfrontal ZPAL RV/1027, in dorsal view. **D**. Sphenoid ZPAL RV/1128, in ventral view. **E**. Right postfrontal ZPAL RV/1027, in orbital view. **F**. Right squamosal ZPAL RV/147, in medial view. **G**. Right quadrate ZPAL RV/1029, in posterolateral view. **H**. Referred left squamosal ZPAL RV/441, in lateral view. SEM stero-pairs.

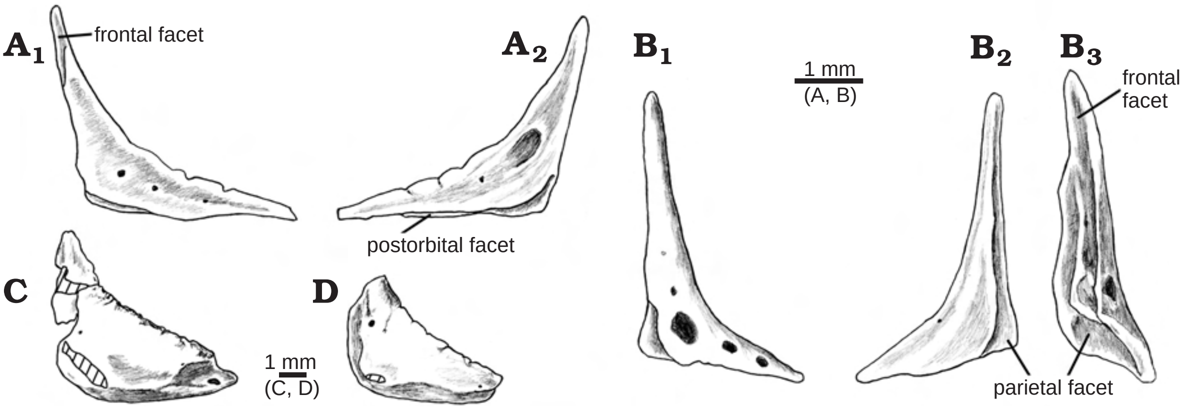

Fig. 11. **A**, **B**. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Right postfrontal ZPAL RV/1003, in dorsal (A_1) and ventral (A_2) views. **B**. Right postfrontal ZPAL RV/1004, in dorsal (B_1), ventral (B_2), and dorsomedial (B_3) views. **C**, **D**. *Kuehneosaurus*, Late Triassic, Emborough Quarry, England. Right postfrontals: BMNH R.12868 (**C**) and BMNH R.12869 (**D**), in dorsal view.

has medial and posterior edges of almost equal length, whereas the medial edge is much longer in *Pamelina* and makes a larger contribution to the orbital margin. As exposed on the right side of the holotype skull, the postfrontal of *Icarosaurus* is more like that of *Pamelina*.

Postorbital. — The postorbital (ZPAL RV/1072, and 1077) is attributed on the basis of fit with the postfrontal and parietal. This element is much rarer than the corresponding postfrontal, probably because it consists of three slender processes stemming from a thicker central orbital region (Figs 10B, 12A–C). The dorsal process extends behind the postfrontal to reach the parietal, as described above. The ventral process is

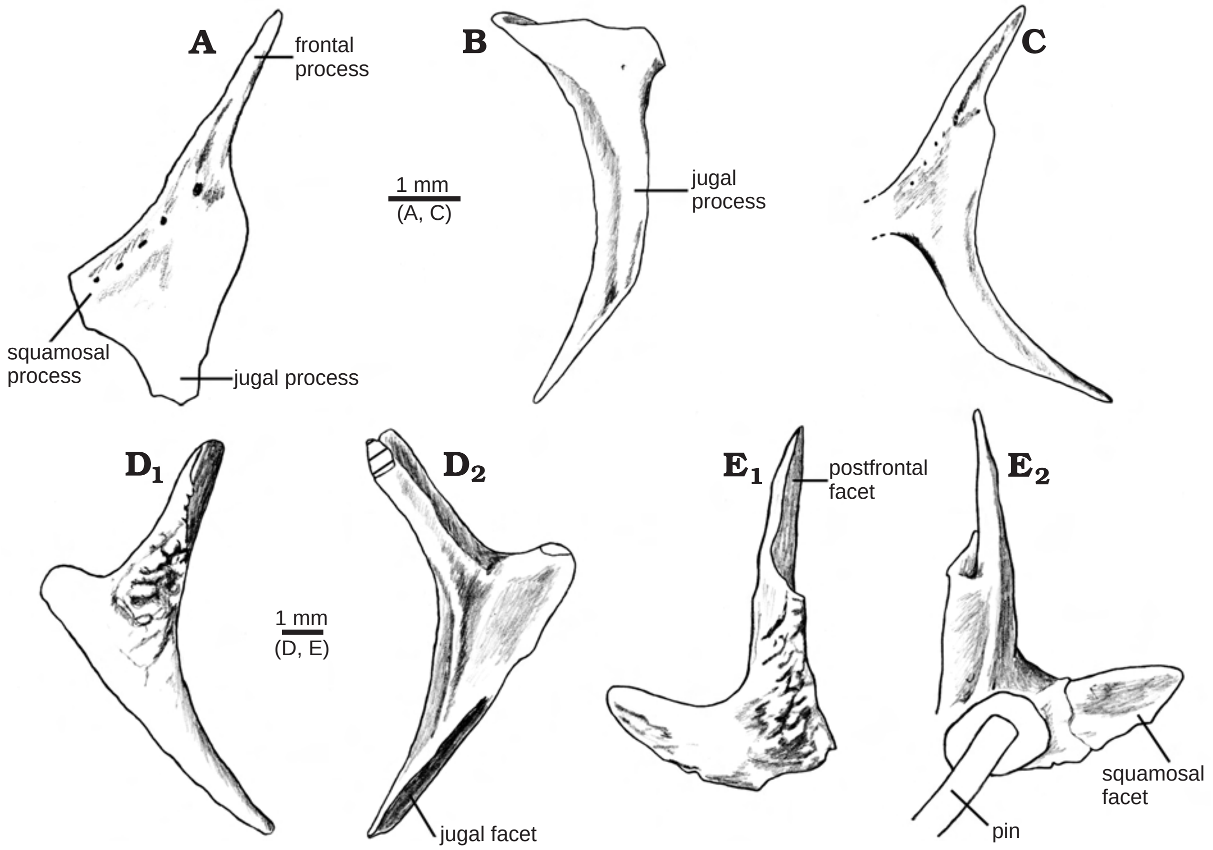

Fig. 12. **A**–**C**. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland, postorbital. **A**. Right postorbital ZPAL RV/1077, in lateral view. **B**. Left postorbital ventral ramus ZPAL RV/ 1072, in lateral view. **C**. Partial reconstruction of right postorbital of *Pamelina*, in dorsolateral view. **D**, **E**. *Kuehneosaurus*, Late Triassic, Emborough Quarry, England. **D**. Right postfrontal BMNH R.12870, in dorsolateral (D_1) and ventromedial (D_2) views. **E**. Right postfrontal BMNH R.12871, in dorsolateral (E_1) and ventromedial (E_2) views (note that the specimen is attached to a museum pin that cannot be removed).

very long and tapers sharply from the central section to form a slender spur (*e.g.*, ZPAL RV/1072) that angles anteroventrally to meet the jugal. The posterior squamosal process is not known.

Comparison with Late Triassic kuehneosaurs: The postorbital is also a rare element for *Kuehneosaurus* (*e.g.*, BMNH R.12870, Fig. 12D, E). It is broadly similar to that of *Pamelina*, but the ventral process appears to have been shorter. The bone is unknown in *Icarosaurus*.

Jugal. — The jugal of *Pamelina* is associated on mainly negative criteria, in that it is a small jugal type that lacks the postulate sculpture found on skull bones of the smaller lepidosauromorph (including its jugal). Several fragmentary specimens are known (*e.g.*, ZPAL RV/1008–1010), but the best is ZPAL RV/1008 (Fig. 13A). The bone is essentially biradiate, with anterior and dorsal processes and, at most, a slight posteroventral angulation. The dorsal process is never complete. The anterior process is long and bears a maxillary facet that is mostly ventromedial in position except when it curves around laterally at the anterior tip. Overall, the facet shape reflects the long, low posterior shelf on the maxilla. The lateral surface bears nutrient foramina; the medial surface is relatively smooth with no obvious articular surface for the ectopterygoid.

Comparison with Late Triassic kuehneosaurs: The main body of the jugal in *Kuehneosaurus* is larger and more triangular than in *Pamelina*, with a stronger posterior angle. In an intact bone (*e.g.*, BMNH R. 12874, Fig. 13B), the maxillary process is long and very slender, with a facet that is first lateral and then medial, but never very large. In *Icarosaurus* the jugal is partially obscured but may have been sickle-shaped, and thus rather more similar to *Pamelina* than to *Kuehneosaurus*.

Squamosal. — The distinctive but fragile squamosal of *Pamelina* is represented by more than 18 elements (*e.g.*, ZPAL RV/147, 336, 1011–1026). The bone is triradiate, with a dorsal parietal process, a posteroventral quadrate process, and an anterior postorbital process (Figs 10F, H, 14A–E). The latter is gen-

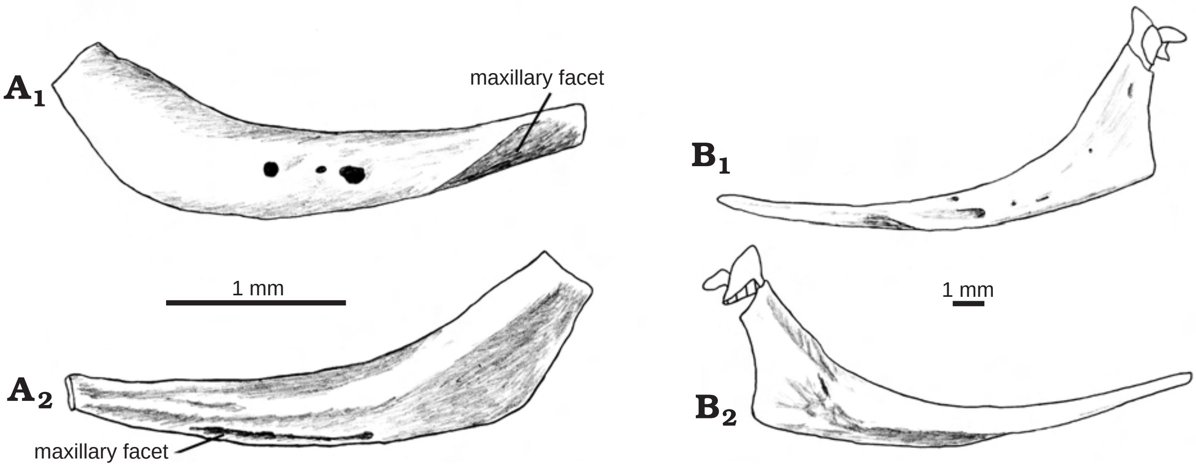

Fig. 13. **A**. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Partial right jugal ZPAL RV/1008, in lateral (A$_1$) and medial (A$_2$) views. **B**. *Kuehneosaurus*, Late Triassic, Emborough Quarry, England. Left jugal BMNH R.12874, in lateral (B$_1$) and medial (B$_2$) views.

erally a slender lamina (short axis vertical, long axis horizontal), with a shallow terminal facet for the postorbital. Its slightly curved ventral border bears an articular cotyle for the quadrate, with the quadrate process overhanging posteriorly and presumably contributing to the frame for the tympanic membrane (Fig. 14C$_2$, D$_2$). The long dorsal parietal process makes an angle of nearly 90° with the body of the bone, and ascends medially and dorsally towards the skull roof (Fig. 14B$_1$, D$_1$). Its posteroventral surface is concave and fits around the anterodorsal surface of the postparietal process (*e.g.*, ZPAL RV/147 fits closely onto parietal ZPAL RV/975), supporting the attribution of both elements to the same taxon. The closeness of fit also precludes the existence of an intervening supratemporal.

ZPAL RV/441 (Fig. 10H) is a problematic element in that has many of the features of *Pamelina* squamosals but is much broader anteriorly. Without more material, it is difficult to know whether this represents pathology, normal variation (*e.g.*, greater maturity), or taxonomic distinction.

Comparison with Late Triassic kuehneosaurs: The squamosals of *Kuehneosaurus* (*e.g.*, BMNH R 12877, Fig. 14F) and *Icarosaurus* have an unusual shape, unlike that of either lizards or traditional diapsids. The squamosal of *Pamelina* is closely similar. *Pamelina* and *Kuehneosaurus* share the absence of an anteroventral process; the shallow, mediolaterally expanded body; the shallow cavity for the head of the quadrate; the small overhanging posteroventral process; the orientation of the long posterodorsal (squamosal process) almost at right angles to the main body of the bone; the groove-like posterior facet for the parietal; the weak facet for the postorbital; and the inferred absence of a free supratemporal. Differences between the Early and Late Triassic taxa are minor. In *Kuehneosaurus* and *Icarosaurus* the bone is somewhat more expanded mediolaterally.

Quadrate. — Of the diapsid quadrates preserved in the Czatkowice assemblage, those of the archosaur *Osmolskina* and the "protorosaur" are the largest and the most common, but there are two smaller morphotypes, both with a lateral conch. ZPAL RV/1029 (Figs 10G, 15A) is representative of the larger of these two morphotypes. It differs from that of the "protorosaur" in being less robust and in having a more distinct lateral conch, a smaller ventrolateral notch, a weaker medial pterygoid facet, a very thin posterior pillar, and no discernable quadratojugal facet. The latter two characters also distinguish it from the quadrate referred to the smaller lepidosauromorph.

The slender posterior pillar expands dorsally and ventrally into condyles for the squamosal and articular respectively, although the latter is larger. The dorsal condyle is small and triangular, with the articular surface (damaged in ZPAL RV/1029) restricted to the posterodorsal surface. This suggests that the upper part of the quadrate might have been inclined backward at its articulation with the squamosal. The ventral condyle carries a narrow U-shaped surface (open anteromedially) with a small dorsolateral extension that forms the inferior margin of a distinct notch (see below, *e.g.*, ZPAL RV/1029). Anterolaterally and anteromedially, the posterior pillar gives attachment to the conch and the pterygoid wing respectively, the angle between them being acute. The large conch is shallow and lacks a raised tympanic crest. Between it and the ventral condyle is a notch that resembles the quadratojugal foramen of other taxa but without an obvious quadratojugal facet.

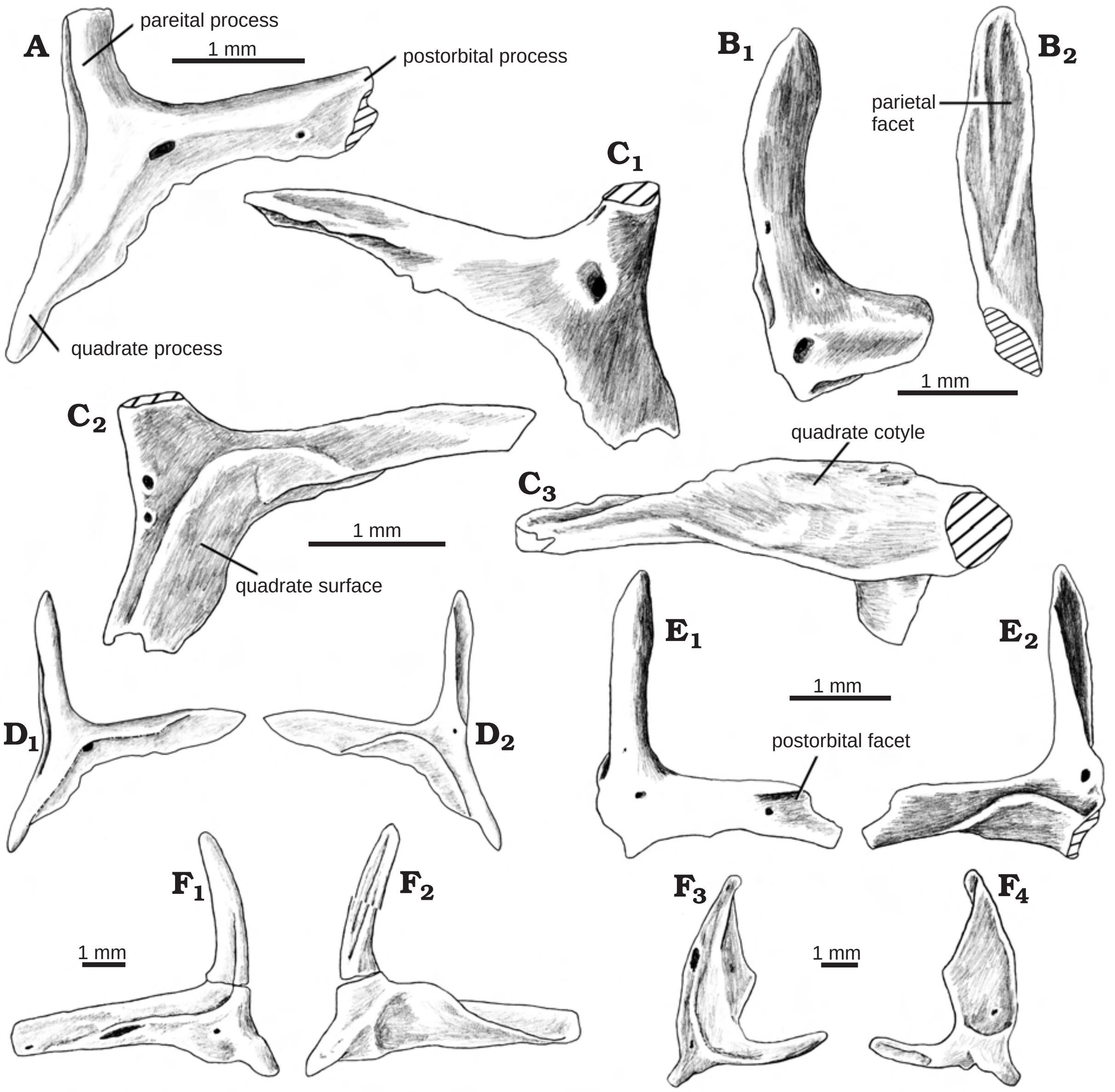

Fig. 14. **A**–**E**. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Rright squamosal ZPAL RV/1015, in dorsolateral view. **B**. Right squamosal dorsal parietal process ZPAL RV/1013, in dorsolateral (B_1) and posteromedial (B_2) views. **C**. Left squamosal ZPAL RV/1011, in dorsolateral (C_1), ventromedial (C_2), and ventral (C_3) views. **D**. Reconstruction of a right bone, in dorsolateral (D_1) and ventromedial (D_2) views; out of scale. **E**. Almost complete right bone ZPAL RV/147, in dorsolateral (E_1) and ventromedial (E_2) views. **F**. *Kuehneosaurus*, Late Triassic, Emborough Quarry, England. Left squamosal BMNH R.12877, in dorsolateral (F_1), ventromedial (F_2), dorsal (F_3), and ventral (F_4) views.

It is possible that a reduced quadratojugal was incorporated into the expanded ventral part of the quadrate (as in the basal rhynchocephalian *Gephyrosaurus*, Evans 1980), but this would require confirmation from a juvenile specimen. Medially, the pterygoid wing is thin and always broken, except at the base. Its lower margin arises from the ventral condyle at a sharp angle before levelling out into the pterygoid facet. At this point, the wing bears a shallow rugosity.

Comparison with Late Triassic kuehneosaurs: The quadrate of *Icarosaurus* is not exposed on the holotype. That of *Kuehneosaurus* (*e.g.*, BMNH R12894–12896, Fig. 15B, C) is very similar to the quadrate of *Pamelina* in the slender posterior pillar, narrow dorsal articular region, large lateral conch, and rugose pterygoid wing. They differ, however, in several respects. The dorsal condyle, though small, is mediolaterally broader in *Kuehneosaurus*, and the ventral condyle has a stronger anteroposterior curvature. There is no notch in the ventral part of the conch as in *Pamelina*, but one small specimen (BMNH R12895, Fig.

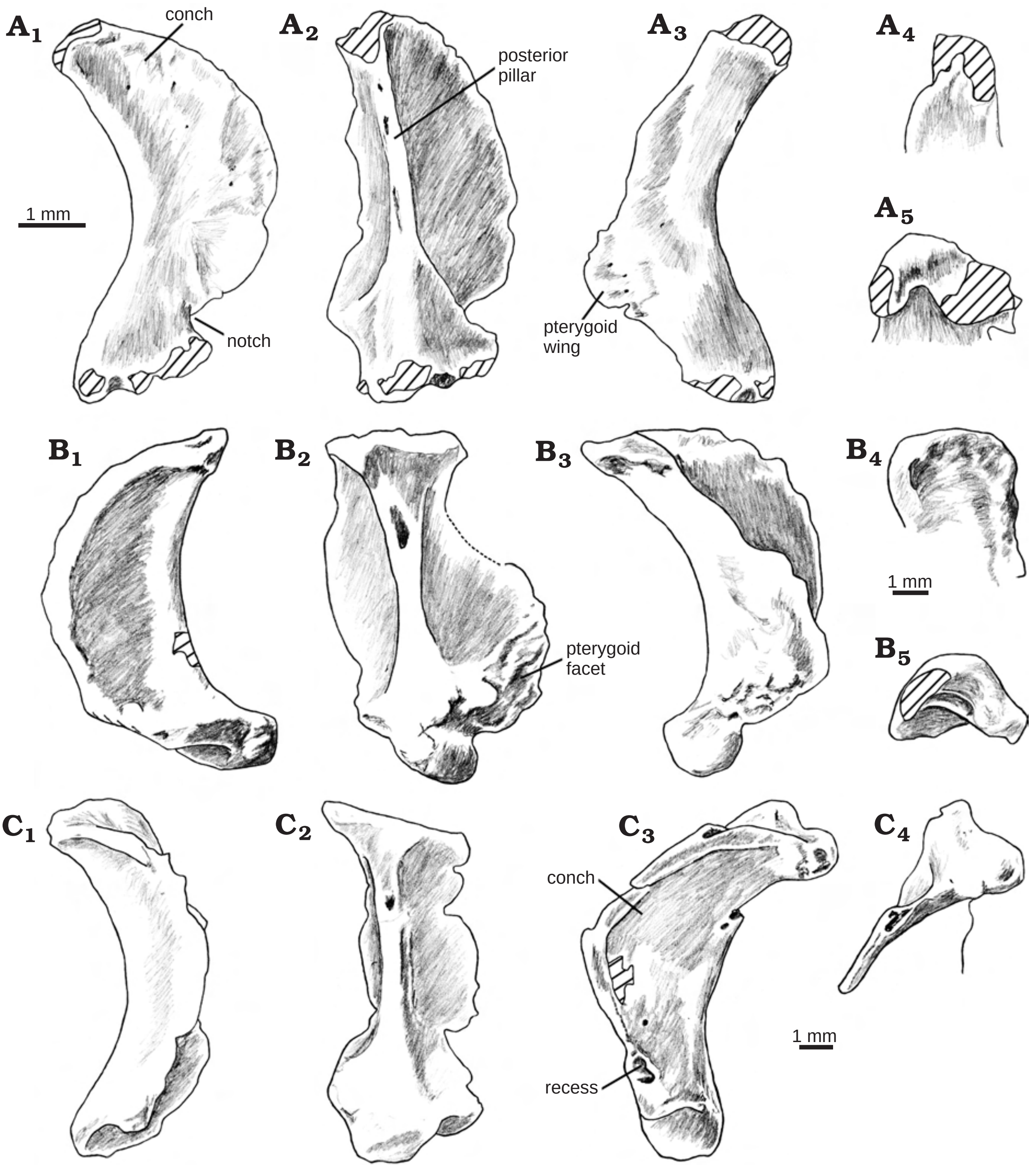

Fig. 15. **A**. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Right quadrate ZPAL RV/1029, in lateral (A_1), posterior (A_2), medial (A_3), posterodorsal (A_4), and ventral (A_5) views. **B**, **C**. *Kuehneosaurus*, Late Triassic, Emborough Quarry, England. **B**. Left quadrate BMNH R.12894, in lateral (B_1), posterior (B_2), medial (B_3), posterodorsal (B_4), and ventral (B_5) views. **C**. Left quadrate BMNH R.12895, in medial (C_1), posterior (C_2), lateral (C_3), and dorsolateral (C_4) views.

15C_3) has a small deep recess on this edge that is very similar to that seen in juvenile specimens of *Gephyrosaurus* in which the rudimentary quadratojugal has been detached. It could be an attachment point for a quadratojugal or quadratomandibular ligament, but raises the possibility that *Kuehneosaurus* had incorporated a reduced quadratojugal into the ventral part of the conch.

The small dorsal head, facetted pterygoid wing, and slender squamosal provide a perplexing functional complex. The structure of the squamosal and the small dorsal quadrate condyle suggests the possibility of movement between these bones, but independent quadrate movement would have been limited by the quadrate-pterygoid overlap and (inferred from rugosities) strong ligamentous binding. It is possible that this

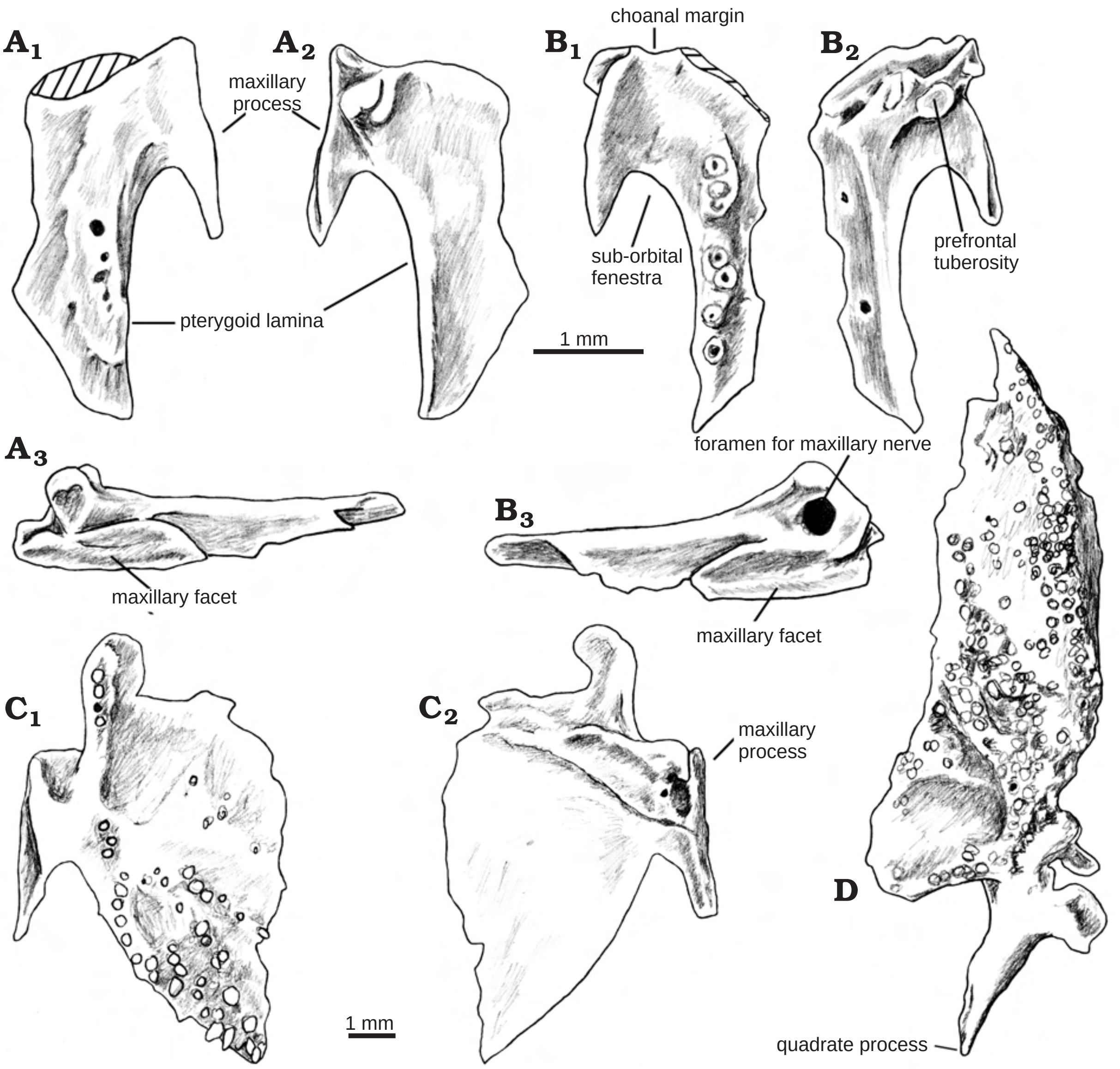

Fig. 16. **A**, **B**. Palatines tentatively attributed to *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Left bone ZPAL RV/1066, in ventral (A_1), dorsal (A_2), and lateral (A_3) views. **B**. Right bone ZPAL RV/1067, in ventral (B_1), dorsal (B_2), and lateral (B_3) views. **C**, **D**. *Kuehneosaurus*, Late Triassic, Emborough Quarry, England. **C**. Right palatine BMNH R.12890, in ventral (C_1) and dorsal (C_2) views. **D**. Right pterygoid BMNH R.12885, in ventral view.

arrangement allowed a mediolateral swing of the quadrates about the dorsal joint with the squamosal, with the movement tending to separate the pterygoids about the interpterygoid fenestra. The weak lower jaw symphysis would accord with this. Such a movement, while not homologous to squamate streptostyly, could have aided the swallowing of larger prey items. It is possible that the extensive palatal dentition, including the apparent redevelopment of holding teeth on the parasphenoid (in *Kuehneosaurus* and *Icarosaurus*) and their presence on the pterygoid wing (*Kuehneosaurus*), might be related to this, in providing a gripping surface on the roof of the mouth and pharynx.

Palatine. — Palatine elements are surprisingly rare for the smaller Czatkowice reptiles. Fig. 16A, B shows two palatines (ZPAL RV/1066, 1067) that are very tentatively attributed to *Pamelina* on the basis of their size (smaller than the "protorosaur", larger than the second lepidosauromorph) and delicate construction (similar to the frontals and parietals). Only the stronger mid-section of the bone is preserved in each case, with the maxillary process separating a posterior embayment (the margin of the suborbital fenestra) from the curved anterior margin (marking the rear of the choana). The maxillary process is dorsoventrally flattened, giving a narrow maxillary contact surface that is V-shaped in section and tapers posteriorly. Its dorsal surface bears an irregular rugosity for the prefrontal (either directly or through strong connective tissue, see also Prefrontal). Where complete, a thin bridge of bone links the anterolateral edge of the prefrontal rugosity to a small anteromedial shelf, thus enclosing a short canal for the maxillary nerve and blood vessels passing from the orbit to the maxilla. The pterygoid lamina extends backward almost parallel to the maxillary facet, leaving only a narrow gap for the suborbital fenestra. Dorsally the lamina is featureless; ventrally its lateral edge bears a tooth row. This is bordered medially and posteriorly by the pterygoid facet. Without further specimens, the presence or absence of additional tooth rows remains unknown.

Comparison with Late Triassic kuehneosaurs: Small diapsid palatines have a common form, differing mainly in their relations to other bones and the pattern of tooth rows. The palatine of *Kuehneosaurus* (*e.g.*, BMNH R12890, Fig. 16C) is generally similar to that attributed to *Pamelina*, as preserved, in bearing a row of teeth along the medial margin of the choana, in having a weak choanal gutter, and in weak development of the prefrontal boss. The more complete specimens of *Kuehneosaurus* show a diffuse scatter of small teeth over the palatal surface. The palatines of *Icarosaurus* are not known.

Pterygoid. — The pterygoid of *Kuehneosaurus* (*e.g.*, BMNH R12885, Fig. 16D) is a long, broad plate-like bone with a heavy cover of small sharp denticles that are not arranged in distinct rows. Unlike most derived diapsids, *Kuehneosaurus* also had a single or double tooth row on the pterygoid flange. The basipterygoid fossa is widely open but lacks a concavity, suggesting at best limited movement. The pterygoid process is short and sharply inturned (mirroring the shape of the dorsal skull margin). Facets on the quadrate show there was a broad overlap, but the pterygoid is very thin and broken at this point. The pterygoid flange is essentially horizontal and not massive. In *Icarosaurus* the ventral surface of the skull has been partially prepared, but does not provide any useful details of pterygoid morphology.

This bone has not been identified for *Pamelina*, despite its distinctive form and the presence of many well-preserved, and much smaller, pterygoids attributed to the small lepidosauromorph. However, the pterygoid plate of *Kuehneosaurus* is extremely thin and rarely preserved (that illustrated in Fig. 16D was specially prepared). It is likely that a similar bone in the Czatkowice 1 material would have fragmented during acid preparation, and there are a large number of extensively toothed pterygoid fragments from Czatkowice that could belong to *Pamelina*.

Sphenoid. — The most common sphenoid elements in the Czatkowice collection are attributed to *Osmolskina* and the "protorosaur"; only rare representatives of other types have been found. One morphotype is represented by several specimens (*e.g.*, ZPAL RV/1048–1050), but none is complete. They are attributed to *Pamelina* on the basis of size (too large to fit the pterygoids of the small lepidosauromorph) and morphology (the sphenoids of the procolophonids have a distinct form with anteriorly directed basipterygoid processes). In ventral view (Figs 10D, 17A$_1$, B$_2$), the bones appear pentaradiate, with a broad-based anterior parasphenoid rostrum, relatively slender basipterygoid processes that are directed laterally with only a slight anterior curvature, and a flared posterior parasphenoid plate. There are no denticles. The borders of the parasphenoid are clearly visible anteriorly as raised crests, but become less distinct at the base of the rostrum in large individuals. There was no enclosed vidian canal and the internal carotid foramina are clearly visible perforating the bone at the level of the basipterygoid processes. Dorsally (Fig. 17A$_2$, B$_2$), the foramina open into the posterolateral margins of an elongated, but shallow, hypophysial fossa. The dorsum sellae is weakly developed as a short horizontal plate with shallow lateral concavities for the retractor bulbi eye muscles, separated in the midline by a slight ridge. There are no abducens foramina or grooves for these nerves, and they presumably passed through soft tissue dorsal to the bone. Bilaterally, each basipterygoid process is subdivided by a strong crest into a flattened anterior region and a deeply posterior concavity that extends along the posterolateral margin of the bone.

Comparison with Late Triassic kuehneosaurs: The sphenoid of *Pamelina* is broadly similar to that of *Kuehneosaurus* (*e.g.*, BMNH R12647, Fig. 17C) in terms of overall shape, the orientation of the basipterygoid processes, the dorsal division of the basipterygoid processes into two parts with the strong posterolateral concavities, and the weak development of the dorsum sellae, although this region is even less developed in *Kuehneosaurus* than *Pamelina*. The posterolateral wings of the parasphenoid are more flared in *Kuehneosaurus* and the anterior part of the hypophysial fossa is truncated by a pair of anteromedial crests that meet in the midline at the base of the parasphenoid rostrum. On the ventral surface, *Kuehneosaurus* fur-

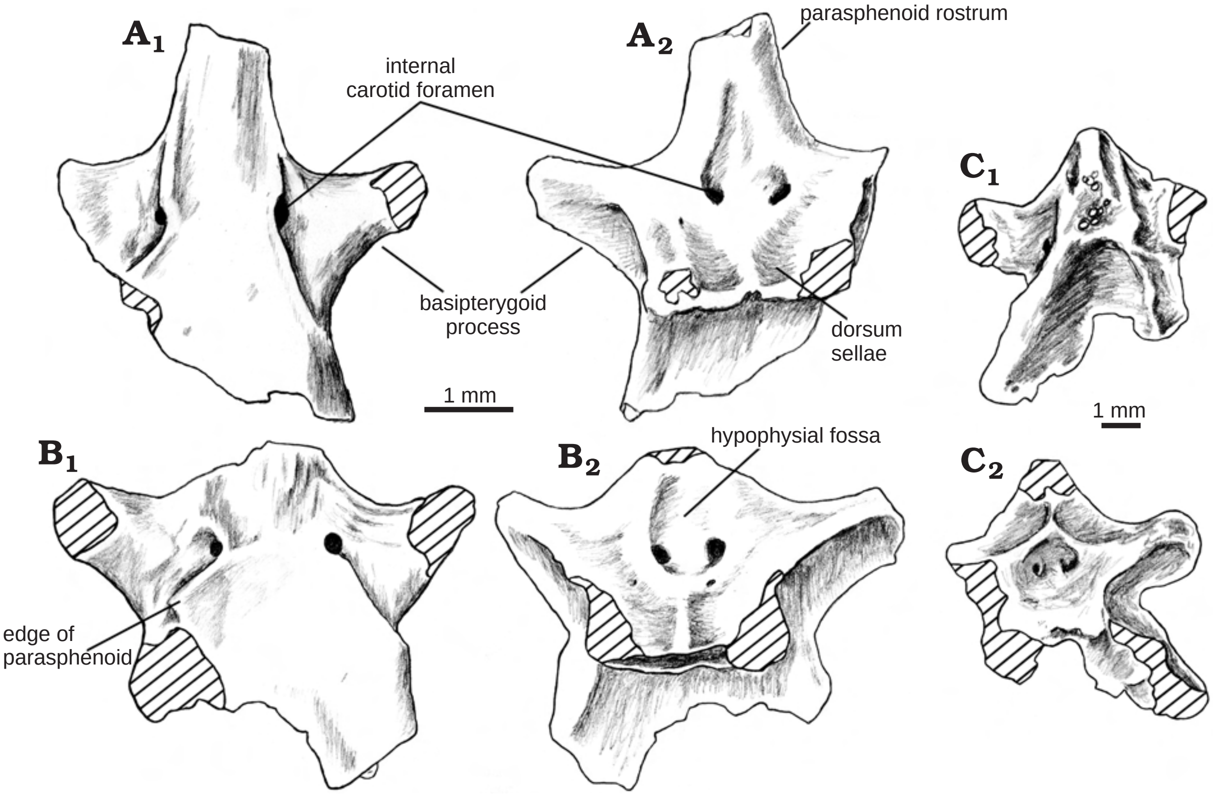

Fig. 17. **A**, **B**. *Pamelina polonica* gen. et sp. n. **A**. ZPAL RV/1048, in ventral (A_1) and dorsal (A_2) views. **B**. ZPAL RV/1049, in ventral (B_1) and ventral (B_2) views. **C**. *Kuehneosaurus*, Late Triassic, Emborough Quarry, England. Sphenoid BMNH R12647, in ventral (C_1) and dorsal (C_2) views.

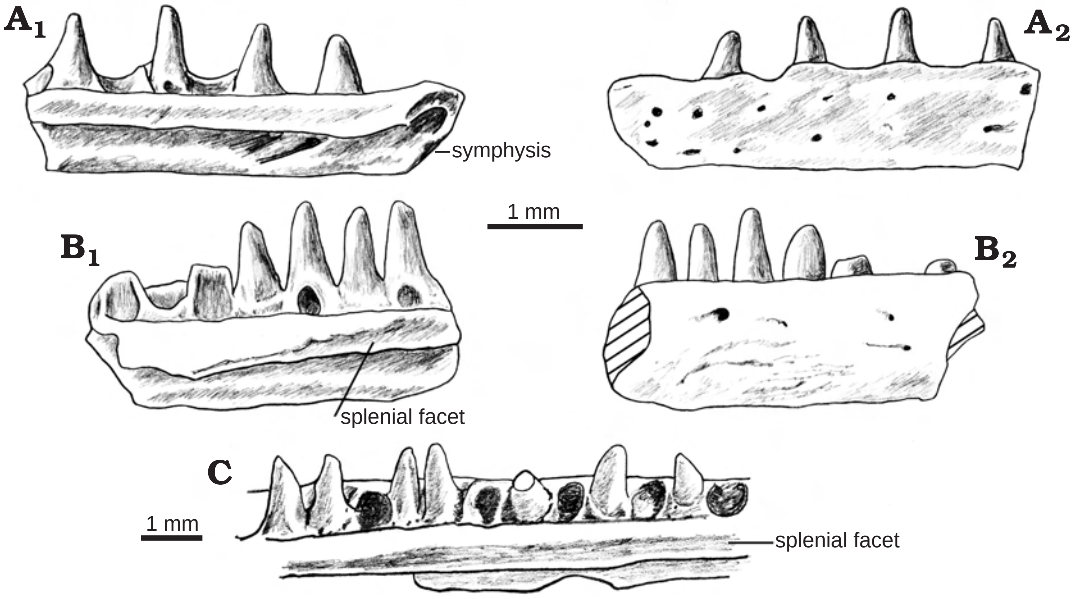

Fig. 18. **A**, **B**. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Symphysial region of a left dentary ZPAL RV/ 1047, in medial (A_1) and lateral (A_2) views. **B**. Mid-section of a right dentary ZPAL RV/1046, in medial (B_1) and lateral (B_2) views. **C**. *Kuehneosaurus*, Late Triassic, Emborough Quarry, England. Section of a larger right dentary BMNH R.12904, in dorsomedial view.

ther differs in that the posteromedial part of the bone bears a deep concavity, bordered anteriorly by a ridge. The other striking difference is the presence of a small cluster of denticles at the base of the parasphenoid rostrum in both *Kuehneosaurus* and *Icarosaurus* (Colbert 1970) but not *Pamelina*. If the attribution of these bones is correct, it suggests that this apparently primitive feature of the Late Triassic genera is a reacquisition, perhaps related to prey handling in the mouth just prior to swallowing (see above).

Dentary. — The dentary is a long shallow bone with parallel dorsal and ventral margins (no curvature of the ventral margin) and a shallow subdental ridge (Figs 2F, G, 18A_1, B_1). An estimated 25–30 dentary teeth were present. The symphysis is terminal and is divided between the upper and lower margins of the Meckelian fossa (ZPAL RV/1047). A facet on the subdental ridge shows that the splenial did not reach the symphysis, leaving the Meckelian fossa open for a short distance. The entry foramen for the inferior alveolar canal lies towards the back of the jaw. ZPAL RV/1046 (Fig. 18B_1) is a partial left dentary of *Pamelina* showing a clear pattern of alternate tooth replacement.

Comparison with Late Triassic kuehneosaurs: The dentary of *Pamelina* closely resembles that of *Kuehneosaurus* (*e.g.*, BMNH R12904, Fig. 18C) in terms of the long narrow shape, the position of the splenial facet, the shallow subthecodont tooth implantation, and the simple conical teeth. As currently known, the dentary of *Icarosaurus* also conforms to this description.

Dentition. — The teeth of *Pamelina* are simple isodont cones with weak apical striae in well preserved specimens. They are weakly implanted by their circular bases into a shallow groove on the alveolar margin. This type of implantation best fits the definition of subthecodont. It closely resembles the implantation of *Kuehneosaurus*. The teeth bear replacement pits indicating active replacement from the lingual side.

POSTCRANIAL SKELETON

Many small postcranial elements have been recovered from Czatkowice. Of these, only vertebrae, some fragmentary ribs, and a set of ilia can be attributed with any confidence to *Pamelina*, but there are a large number of very thin-walled long bone fragments that may well pertain to the genus.

Vertebrae. — The axial skeleton is represented by a series of vertebrae referred to *Pamelina* on the basis of number and size. These vertebrae share a common overall structure but show differences that permit cervical, anterior and posterior dorsal, sacral and caudal vertebrae to be recognised. Fig. 19A shows a posterior dorsal vertebra showing the key features of this vertebral type. All have a lightly amphicoelous, but non-notochordal (amphiplatyan), centrum that is lightly built and contains cavities. The neural spines are relatively short and the neurocentral sutures are closed in the adult. The zygapophyses are narrow and rather elongated, with a distinctive morphology. The articular surface is significantly smaller than the total planar surface, resulting in the development of an anterior shelf in front of the neural arch. Posteriorly a ventral shelf connects the postzygapophyses, enclosing a triangular cavity, presumably for strong ligaments and intervertebral muscle slips. The only other Czatkowice reptile that approaches *Pamelina* in some aspects of vertebral morphology is the “protorosaur”. The major differences are the greater robusticity of the “protorosaur” bones, the greater diameter and generally more ventral position of the transverse processes, and the greater angle between the anterior and posterior zygapophyses. In addition, the cervical vertebrae differ fundamentally in length (much shorter in *Pamelina*), while in the trunk region, the “protorosaur” vertebrae shorten markedly and those of *Pamelina* become somewhat longer. Moreover, the “protorosaur” trunk vertebrae have anteroposteriorly short spines with expanded spine tables and the postzygapophyses are long with a deep V-shaped cleft between them. Dorsal vertebrae of *Pamelina* have longer narrower neural spines extending almost to the rear of the vertebra, with a smaller postzygapophyseal recess.

Presacral vertebrae. — The vertebrae from different parts of the column can be discriminated from one another on the basis of centrum length, centrum width, centrum cross-sectional shape (*e.g.*, keeled or not), the number and position of rib facets, and the orientation and diameter of the transverse processes (Figs 20, 22). All vertebrae bear transverse processes, but being thin-walled and hollow, these are usually damaged. In a few specimens (*e.g.*, ZPAL R/V1198 and 1199), however, the short transverse process ends in a distinct and regular oval rim. These processes are interpreted as essentially complete (with a length roughly half that of the transverse width of the neural arch), but with the articular surface unossified. The relatively few dorsal rib heads recovered (Figs 19B, C, 20B, C) have a similar structure.

The atlas and axis have not been identified with confidence, but the remaining cervical vertebrae are characterised by relatively short centra that are pentagonal in cross-section, with a slightly rounded mid-ventral

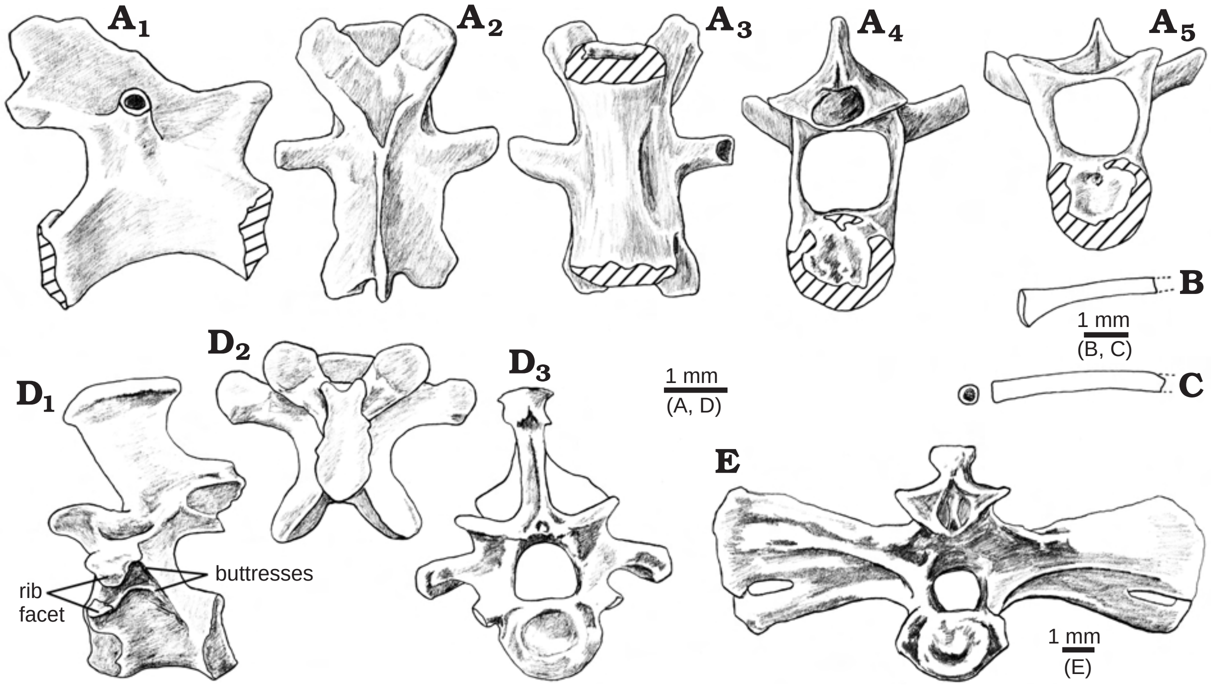

Fig. 19. A–C. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Posterior dorsal vertebra ZPAL RV/1199, in right lateral (A_1), dorsal (A_2), ventral, (A_3), posterior (A_4), and anterior (A_5) views. **B**, **C**. Dorsal rib fragments attributed to *Pamelina*. **B**. ZPAL RV/1214, in side view. **C**. ZPAL RV/1211, in terminal and side views. **D**, **E**. *Kuehneosaurus*, Late Triassic, Emborough Quarry, England. **D**. Cervicodorsal vertebra BMNH R/12983, in left lateral (D_1), dorsal (D_2), and anterior (D_3) views. **E**. Anterior dorsal vertebra BMNH R.12991, in posterior view, showing the depth of the transverse process (with diapophysis and parapophysis merging) and posterior pocket between zygapophyses.

keel. In lateral view, the ventral margin of the centrum is distinctly concave. The transverse process is small in cross-section and is directed dorsolaterally. There is also a parapophysis that gradually ascends from the anterior edge of the centrum towards the transverse process. ZPAL RV/1194–1197 characterise this vertebral region (Figs 20A, 22A). In ZPAL RV/1196 and 1197 the parapophysis is still at the anterior edge of the centrum, but a ridge may connect it to the transverse process (ZPAL RV/1197, Fig. 21A). In ZPAL RV/1194, a more posterior vertebra, the parapophysis has moved away from the edge and the transverse process is buttressed by anterior and posterior ridges (Fig. 22B_1). In the more fragmentary ZPAL RV/1195 (not figured), the parapophyses are in different positions on the two sides, low on the left and close to the transverse process on the right. Cervical vertebrae are not very numerous in the Czatkowice collection and *Pamelina* may have had a rather short neck.

ZPAL RV/612 (Fig. 21B) and ZPAL RV/1203 (Fig. 22C) are dorsal vertebrae with a centrum that is rounded in cross-section. The transverse process has a larger diameter and is more laterally directed, and the neural spine is longer. By comparison with other reptiles, this vertebral type is likely to be transitional between the cervicals and more typical dorsals (*i.e.*, an anterior dorsal) since the strongest ribs and processes are generally those that relate to the pectoral girdle (muscle attachments), and both centrum length and cross-section (wider than deep) are intermediate between those of the cervical and dorsal series. ZPAL RV/1204 (Figs 20E, 22D) is a vertebra of similar type to ZPAL RV/1203 with a stout transverse process to which is fused the proximal end of a rib that is directed straight laterally (Figs 21E, 22D_2–D_5). This fusion of the rib to the vertebra is unusual and, if not pathological, suggests rib fixation at the level of the neck-trunk boundary (see below).

ZPAL RV/1198 and 1199 (Figs 19A, 20D) are more typical dorsal vertebrae, here interpreted as being from the middle to posterior dorsal series. Vertebrae of this type are by far the most numerous. They differ from the cervicals in having longer centra (ca. 1.5 × the length of the cervicals) that are rounded in cross-section, no parapophyses, and transverse process set high on the neural arch. In lateral view, the centrum is again ventrally concave and the zygapophyses are slightly more elongated than on preceding vertebrae. In ZPAL RV/1198 the left transverse process is almost complete. It angles upward and is slightly expanded at the tip. ZPAL RV/1201 and 1202 are shorter but the transverse processes remain small in diameter.

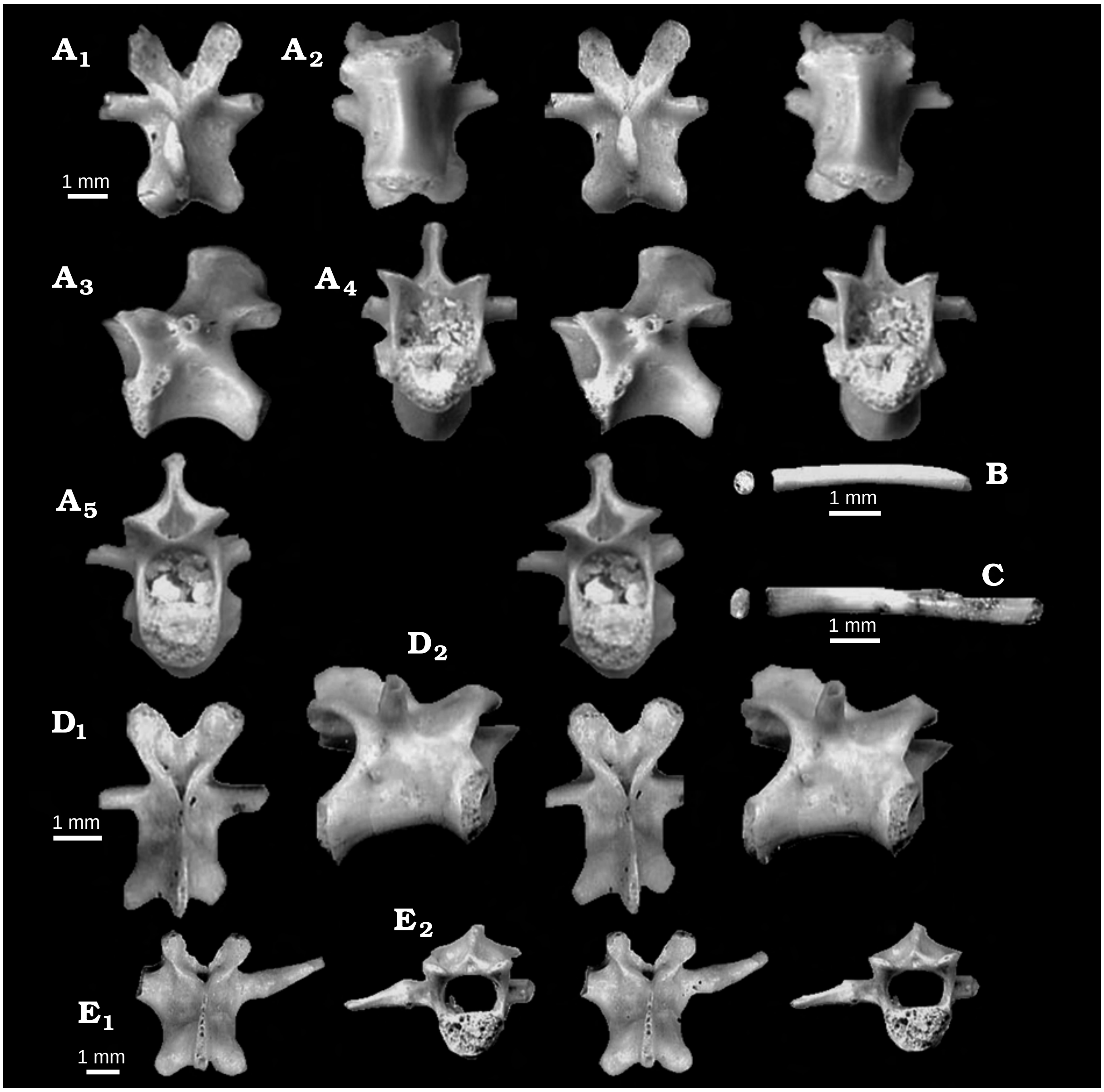

Fig. 20. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Vertebrae and ribs. **A**. Cervical vertebra ZPAL RV/1194, in dorsal (A_1), ventral (A_2), left lateral (A_3), anterior (A_4), and posterior (A_5) views. **B**. Attributed dorsal rib ZPAL RV/1211, in terminal and side views. **C**. Attributed dorsal rib ZPAL RV/1215, in terminal and side views. **D**. Posterior dorsal vertebra ZPAL RV/1199, in dorsal (D_1) and right lateral (D_2) views. **E**. Anterior dorsal vertebra with fused rib ZPAL RV/1204, in dorsal (E_1) and anterior (E_2) views. SEM micrographs; all but B, C stereo-pairs.

Only one damaged sacral vertebra has been identified (ZPAL RV/1205, Fig. 22E). It is probably, but not certainly, a second sacral as the ribs are positioned towards the front of the centrum. This vertebra has a much heavier build than typical dorsal vertebrae, with a wide shallow centrum and neural arch. On the right side, the line of fusion between the sacral rib and the vertebral body is just visible on the specimen (not shown in figure).

Vertebrae have been identified from both proximal and distal parts of the tail. ZPAL RV/1206 is a rather short (even allowing for breakage) postsacral vertebra with transverse processes that are arched posteriorly. ZPAL RV/627 and RV/1207–1209 are more typical anterior caudals that show some elongation of the neural arch and long transverse processes that may be recurved (ZPAL RV/1207, 1208, Fig. 22F_2, F_3) or straight (ZPAL RV/627, Fig. 21C). Ventrally, these vertebrae lack a groove for the caudal blood vessels. ZPAL RV/1210 (not shown) is a more distal caudal in which the transverse processes have been reduced to a short lateral ridge. Further posteriorly, this ridge disappears and the vertebrae elongate further with the development of a ventral groove for the caudal blood vessels. No caudal vertebra shows any trace of an autotomy septum.

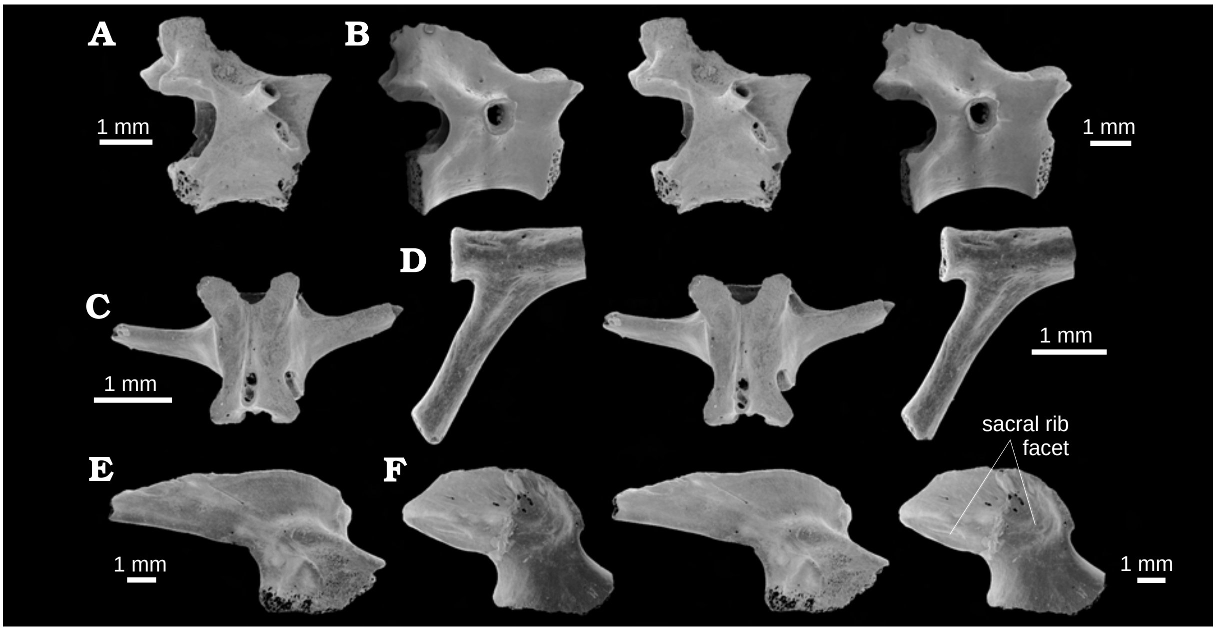

Fig. 21. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Postcranial bones. **A**. Cervical vertebra with double rib facet ZPAL RV/617, in right lateral view. **B**. Anterior dorsal vertebra ZPAL RV/612, in right lateral view. **C**. Anterior caudal vertebra ZPAL RV/627, in dorsal view. **D**. Possible posterior cervical rib ZPAL RV/936. **E**. Right ilium ZPAL RV/981, in lateral view. **F**. Left ilium ZPAL R/V555, in medial view. SEM stero-pairs.

Comparison with Late Triassic kuehneosaurs: The vertebrae of *Pamelina* resemble those of *Kuehneosaurus* and *Icarosaurus* in having narrow, laterally compressed neural arches, some elongation of the transverse process, and some support of the processes by extra ridges, although the ridges in *Pamelina* are more weakly developed than the distinct buttresses of the Late Triassic taxa, especially *Kuehneosaurus* (Fig. 19D). *Pamelina* also resembles the Late Triassic taxa in having short cervicals and long posterior dorsals (*e.g.*, Colbert 1970, p. 118, table 1), but this elongation of the posterior dorsals is seen in the Late Permian glider *Coelurosauravus* (Evans 1982; Evans and Haubold 1987), the Late Triassic archosauromorph *Mecistotrachelos* (Fraser 2007), and the living *Draco*. It has been interpreted as a functional adaptation, either to keep the elongated wing elements clear of the hind limb as the wing folds or to give extra flexibility in the posterior spine (Colbert 1970, p. 108), but it should be noted that similar elongation occurs in some modern climbing lizards like *Calotes* (personal observation). In *Kuehneosaurus* and *Icarosaurus*, the cervical neural spines are much taller than those of *Pamelina* with distinct spine tables (Fig. 19D). In *Kuehneosaurus* (but possibly not in *Icarosaurus*, Colbert 1970, p. 107), cervicals four to seven bear three rib attachment points on each side of the vertebra, with the upper transverse process becoming increasingly prominent. The central pseudoparapophysis has been lost in presacral eight, but the parapophysis itself then elongates until it is almost the same length as the transverse process. Between presacrals twelve and thirteen the parapophysis fuses with the transverse process to form a single deep lateral process, and the transverse processes themselves become elongate (Fig. 19E). *Pamelina* does not show this highly derived morphology. Rather a single parapophysis gradually moves up towards the transverse process and fuses with it in the anterior dorsals. *Icarosaurus* may have been similar (Colbert 1970). Three-headed ribs occur around the neck-trunk boundary in a number of extinct reptile taxa (Thulborn 1979), including the “protorosaur” from Czatkowice (Borsuk-Białynicka and Evans 2009b), and are thought to provide a point of stability at the base of the neck (Thulborn 1979). It is possible that the apparently immobile rib on ZPAL RV/1204 of *Pamelina* played a similar, but non-homologous, role. In *Draco* the deepest and most robust ribs and transverse processes are also in this region.

Ribs. — The ribs of *Pamelina* have proved difficult to recover. Being both slender and very thin-walled they do not withstand acid preparation of the matrix. Amongst those fragmentary specimens that might be attributed to *Pamelina*, there are two types. The first, represented by specimens like ZPAL RV/936 (Fig. 21D), 997, 1212, and 1213, has two distinct heads, with a short tuberculum and a longer capitulum. ZPAL RV/1213 is shorter and more curved than ZPAL RV/1212 which runs outward. These could be cervical ribs, reflecting

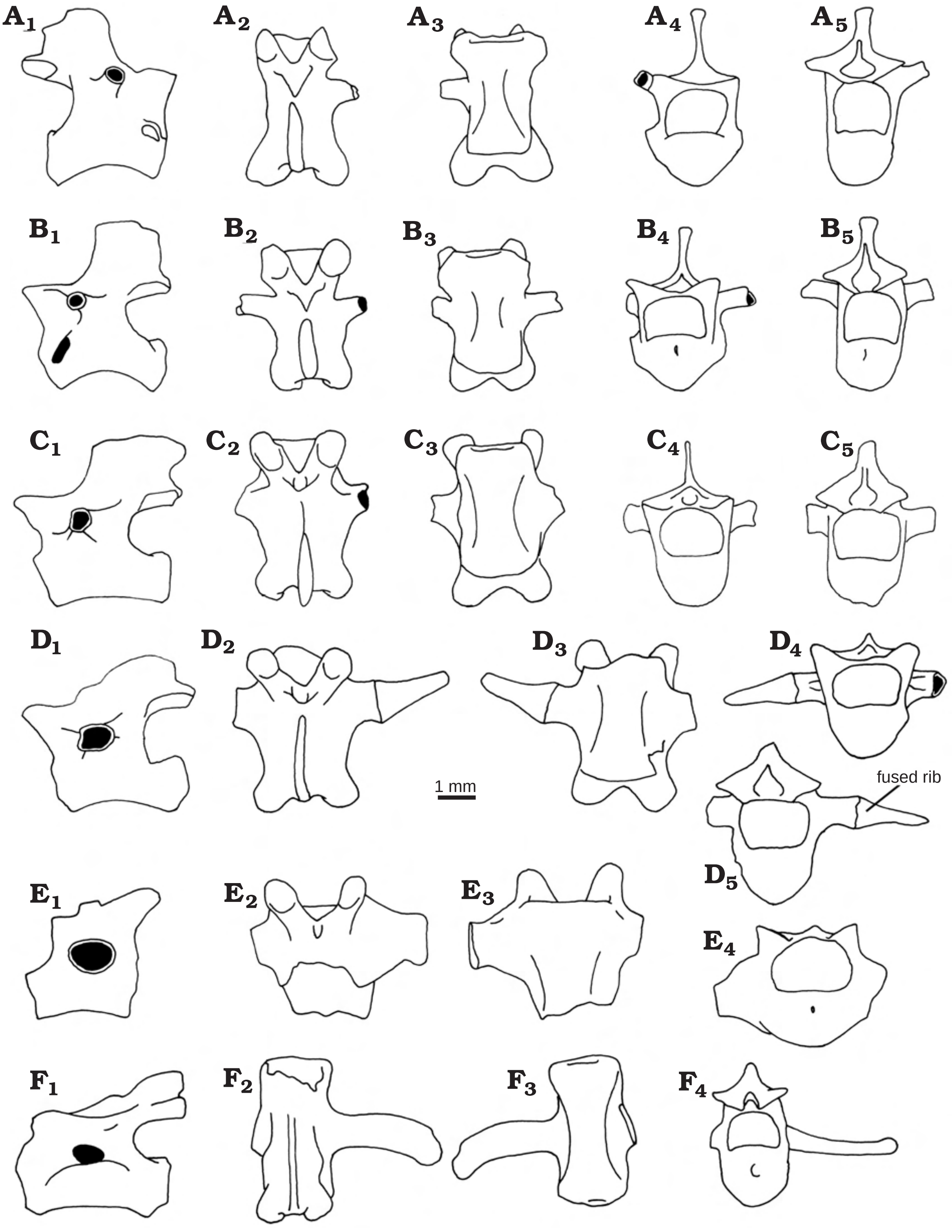

Fig. 22. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Anterior cervical vertebra ZPAL RV/1197, in right lateral (A_1), dorsal (A_2), ventral (A_3), anterior (A_4), and posterior (A_5) views. **B**. Posterior cervical vertebra ZPAL RV/1194, in left lateral (B_1), dorsal (B_2), ventral (B_3), anterior (B_4), and posterior (B_5) views. **C**. Anterior dorsal vertebra ZPAL RV/1203, in left lateral (C_1), dorsal (C_2), ventral (C_3), anterior (C_4), and posterior (C_5) views. **D**. Anterior dorsal vertebra with broken rib attached on right side ZPAL RV/1204, in left lateral (D_1), dorsal (D_2), ventral (D_3), anterior (A_4), and posterior (D_5) views. **E**. Partial sacral vertebra ZPAL RV/1205, in right lateral (E_1), dorsal (E_2), ventral (E_3), and anterior (E4) views. **F**. Anterior caudal vertebra ZPAL RV/1208, in left lateral (F_1), dorsal (F_2), ventral (F_3), posterior (F_4) views.

the strong separation of the parapophysis and diapophysis, although this is tentative. The single headed dorsal ribs are much more fragile and are identified on the basis of their similarity in proximal structure, diameter, and wall thickness to the transverse processes and to the rib attached to ZPAL RV/1204 (*e.g.*, ZPAL RV/1214, Fig. 19B). ZPAL RV/1211 and 1215 are among the best of these, although they are only proximal fragments (Figs 19B, C, 20B, C). The head is circular and almost hollow (like the transverse processes described above) but in this case is partially filled with loose cancellous bone that formed part of the articular surface. This part of the rib is completely straight rather than curved as it would be in a typical reptile. Many other straight rib fragments of similar type and diameter have been recovered.

Comparison with Late Triassic kuehneosaurs: The rib fragments attributed to *Pamelina* are tantalising, especially those of the dorsal series, as they suggest the presence of laterally extended ribs of unknown length. They differ from the ribs of both *Kuehneosaurus* and *Icarosaurus* in being more gracile (those of *Kuehneosaurus*, in particular, are very deep in cross-section) and there are none of the three-headed ribs that strengthen the anterior edge of wing in at least the British kuehneosaurs.

Long bones. — No limb elements have been attributed with confidence to *Pamelina* but there are many thin-walled long bone fragments that are similar in build to the bones of *Kuehneosaurus* and *Draco* and may therefore pertain to *Pamelina*.

Pelvis. — Four iliac types have been recognised amongst the small non-archosaurian reptile bones from Czatkowice. One is clearly attributable to a procolophonian (short upright blade) and another to the small lepidosauromorph (consistent small size, prepubic process, angled blade). The other two are rather similar in shape (anterior expansion of blade accommodating first sacral rib facet, supraacetabular buttress) but they differ in details of blade shape, in the presence or absence of an anterior tuberosity (a feature that can vary with size but seems to be consistent here across a size range), and in the depth of the medial rib facets. Both

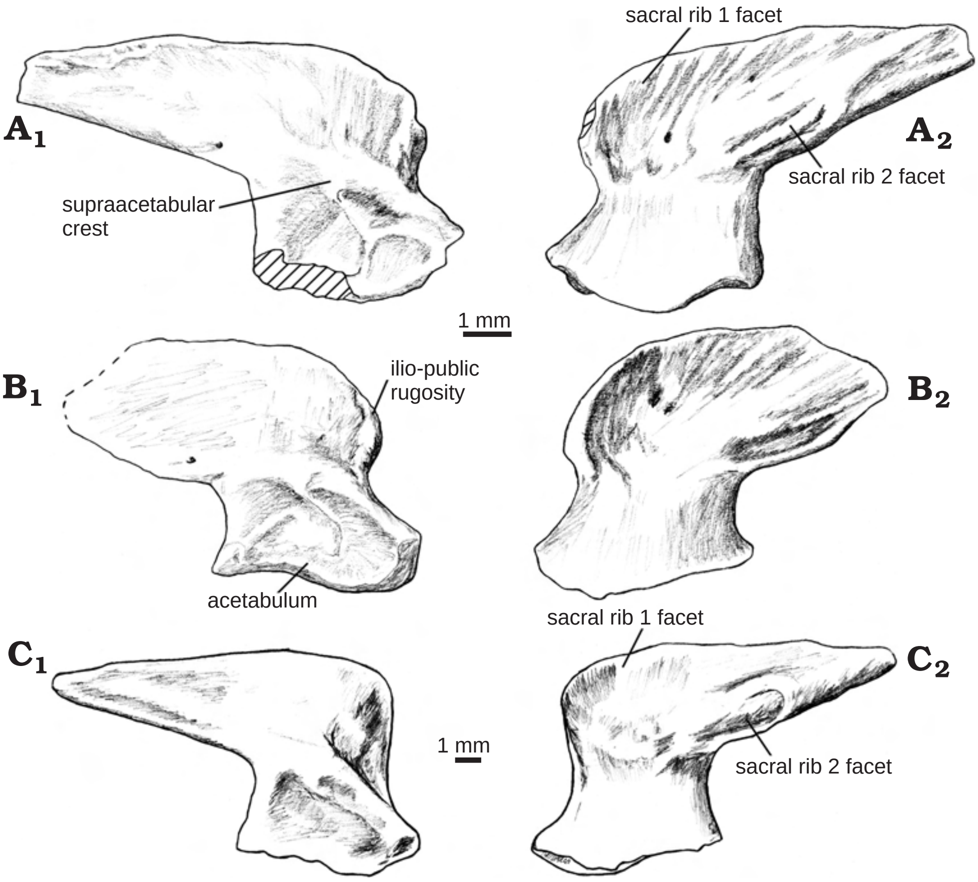

Fig. 23. **A**, **B**. *Pamelina polonica* gen.et sp. n, Early Triassic of Czatkowice 1, Poland. **A**. Right ilium ZPAL RV/981, in lateral (A_1) and medial (A_2) views. **B**. Left ilium ZPAL RV/555, in lateral (B_1) and medial (B_2) views. **C**. *Kuehneosaurus*, Late Triassic, Emborough Quarry, England. Right ilium BMNH. R12925, in lateral (C_1) and medial (C_2) views.

are represented by a range of sizes, but the upper range of one type exceeds the size range of *Pamelina* and is thus more reasonably attributed to the "protorosaur". The smaller morphotype is therefore tentatively attributed to *Pamelina* (*e.g.*, ZPAL RV/555 and 981, Figs 21E, F, 23A, B).

ZPAL RV/981(Figs 21E, 23A) is a right bone from a large individual. The blade has a rounded anterior margin that consistently bears a rugosity for the attachment of the ilio-pubic ligament (Snyder 1949, 1952, 1954). Further posteriorly, the blade tapers to a point, although the dorsal margin is almost straight throughout. Without the puboischiadic plate, it is difficult to be certain of the orientation of the blade. The medial side bears a deep anterior concavity for the first sacral rib, with a smaller, elongated rugosity for the second rib along the posteroventral margin of the blade. The lateral acetabulum is deepened by a strong supraalveolar crest that has the form of a curved tuberosity, sharply demarcated from the main acetabular cavity. The articular surface, however, is more limited in its extent, occupying the anteroventral corner of the acetabulum and, in larger individuals, extending onto the lower part of the supraacetabular crest. There is no prepubic process.

No other pelvic elements can be attributed to *Pamelina* with any degree of confidence, although there are both pubes and ischia of appropriate size. None shows any trace of a thyroid fenestra, but equally, this thin central part of the puboischiadic plate is usually broken away.

Comparison with Late Triassic kuehneosaurs: The iliac blade of *Kuehneosaurus* (Fig. 23C) is closely similar in shape to that attributed to *Pamelina* (rounded anterior margin with expansion, posteriorly tapering blade, strongly curved supraalveolar ridge/tuberosity, paired medial sacral rib facets with the anterior facet at the anterior edge of the bone and the smaller, more horizontally placed second facet placed on the posteroventral edge). *Icarosaurus* (Colbert 1966, 1970) has a shorter, more triangular iliac blade. Ventrally, the pelvis of *Icarosaurus* is characterised by a peculiar small thyroid fenestra that is fully enclosed between the pubis and ischium (unlike that of lepidosaurs that extends into the symphysis). However, this feature may vary in the British kuehneosaurs. In one associated specimen (BMNH uncatalogued), for example, there appears to have been no thyroid fenestra.

DISCUSSION

Phylogenetic analysis. — The reconstructed skull morphology of *Pamelina* shows that it was a diapsid. Given its age, this presents three main possibilities: a stem diapsid; an early archosauromorph; or a lepidosauromorph (or a clade more closely related to lepidosauromorphs than archosauromorphs). As shown in the preceding section, *Pamelina* shows striking similarities to the kuehneosaurs, but in order to test this, *Pamelina* was coded into the diapsid data matrix of Müller (2004). Müller obtained a cladogram in which kuehneosaurs emerged as the sister taxon of the drepanosaurs — a group of odd, arboreal and aquatic specialists known from the Upper Triassic of Italy (Calzavara *et al.* 1980; Pinna 1986; Renesto 1994), Britain (Renesto and Fraser 2003) and North America (Berman and Reisz 1992; Colbert and Olsen 2001). This small clade fell, not with lepidosauromorphs, but outside the Neodiapsida of Benton (1985). Senter (2004) reported a similar placement for drepanosaurs alone whereas Modesto and Sues (2004) have drepanosaurs at the base of Archosauromorpha. I reran Müller's analysis using PAUP 3.0 (Swofford 1993) (random addition sequence, TBR branch swapping, multistate characters interpreted as polymorphism, rooted on Seymouriidae and Synapsida) with some (ca. 5%) of Müller's codings for kuehneosaurs and lepidosaurs corrected, some missing data for *Kuehneosaurus* added, and with the inclusion of *Pamelina* and the small Czatkowice lepidosauromorph (see Evans and Borsuk-Białynicka 2009). Due to the size of the data matrix, only a heuristic search was possible. This yielded seven equally parsimonious, but weakly supported, trees (tree length [L] = 998; consistency index [CI] = 0.428; rescaled consistency index [RC] = 0.234). The strict consensus tree (not shown) showed traditional clades (archosauromorphs, thalattosaurs, sauropterygians, lepidosaurs, kuehneosaurs — including *Pamelina*), but with very poor resolution. Hill (2005) had similar problems. The 50% Majority Rule Tree (Fig. 24) is more fully resolved, but the tree support values are low. Nonetheless, *Pamelina* grouped unequivocally with the Late Triassic kuehneosaurs, again as the sister group of drepanosaurs, and within a traditional lepidosauromorph clade. These results match those of Müller (2004) in grouping drepanosaurs and kuehneosaurs, although they share few synapomorphies. Müller (2004) cited two, the enclosed thyroid fenestra in the pelvis and the increased angulation of the zygapophyses in the posterior dorsal

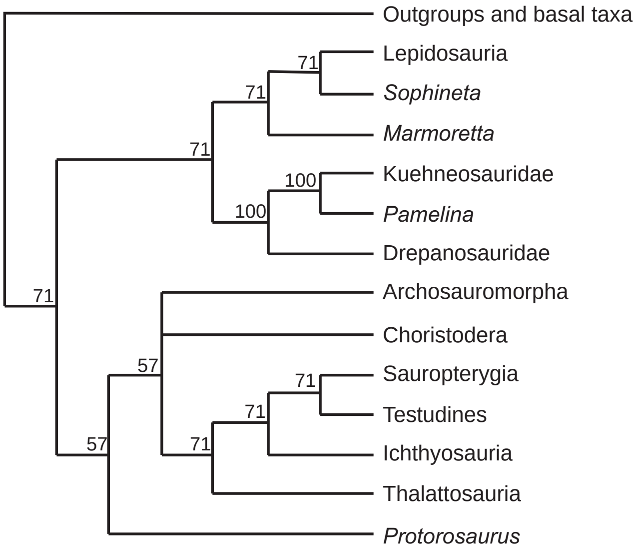

Fig. 24. 50% Majority Rule consensus of seven equally parsimonious trees obtained from a heuristic search using the diapsid data set from Müller (2004) with some character codings added or updated (note that although all the taxa from the original matrix were included in the analyses, they have been grouped within their respective clades in the figure).

series. The second of these is also found in *Draco* and is likely to be functional (and thus potentially convergent). The first is unusual but, as noted above, may be variable in the British kuehneosaurs and remains unknown in *Pamelina*. The skull of drepanosaurs is still only partially known, but has recently been described for *Megalancosaurus* by Renesto and Dalla Vechia (2005). Although *Megalancosaurus* and kuehneosaurs (now including the Early Triassic *Pamelina*) share a jugal with little development of the posterior process, this is a primitive neodiapsid character and there are many differences between their skulls: the large nares are separated by a long dorsomedial process of the premaxilla in *Megalancosaurus* (confluent in kuehneosaurs); the premaxilla lacks a posterolateral process (present in kuehneosaurs); the lacrimal is long, slender and lies within the orbital rim (large and makes little or no entry into the orbital rim in kuehneosaurs); there is a distinct anterior rostrum formed by a large premaxilla (short preorbital region in kuehneosaurs); and the quadrate lacks a lateral conch (prominent in kuehneosaurs).

Implications. — Reptilian gliders have been recorded from five different periods over the last 250 million years: the Late Permian (*Coelurosauravus*, Madagascar, Germany, UK; Evans 1982; Evans and Haubold 1987; Frey *et al.* 1987); the Middle–Late Triassic (*Sharovipteryx* and possibly *Longisquama*, Kyrgyzstan; Sharov 1970, 1971; Gans *et al.* 1987; Unwin *et al.* 2000); the Late Triassic (*Kuehneosaurus*, *Kuehneosuchus*, UK, Robinson 1962, 1967a, b; *Icarosaurus*, USA, Colbert 1966, 1970; *Mecistotrachelos*, USA, Fraser 2007); the Early Cretaceous (*Xianglong*, China, Li *et al.* 2007); and the present day (the living agamid lizard *Draco*, South-East Asia). The detailed morphology of the wing differs in each case and the gliding adaptations almost certainly arose independently. In the coelurosauravids, the gliding surface is made up of a series of elongate rib-like elements that may be dermal in origin (Frey *et al.* 1987). In *Sharovipteryx*, the wing is simply a skin flap (Sharov 1971; Gans *et al.* 1987). *Longisquama* is more enigmatic in possessing a series of long distally expanded scales that may have projected into a dorsal crest (Sharov 1970) or extended laterally into a parachuting surface (Haubold and Buffetaut 1987). However, *Mecistotrachelos* (a long necked Carnian ?archosauromorph, Fraser 2007), *Xianglong* (an Early Cretaceous lizard, Li *et al.* 2007), *Draco*, and the kuehneosaurs have each developed a gliding surface consisting of extended ribs borne on variably elongated transverse processes.

Gliding provides an energy-efficient and safe way for a small animal to move around its habitat, as well as a very effective escape strategy, and there are a limited number of ways of constructing a gliding surface. With the exception of the enlarged hands and feet of some gliding frogs, most living gliders and parachuters use an extension of the skin between the fore- and hind limbs (as did *Sharovipteryx*, Gans *et al.* 1987). If ribs, or rib-like structures, can be elongated into this skin flap, then the gliding surface has extra strength and flexibility, as trunk musculature can be used to actively change the shape and orientation of the "wing" (Russell and Dijkstra 2001; Russell *et al.* 2001).

Losos *et al.* (1989) have shown that even a small increase in rib length, coupled with a flattening of the body during descent, is enough to allow a usually terrestrial lizard (*e.g.*, the agamid *Leiolepis*) to control a fall, even though both the morphology and the behaviour probably evolved to permit better thermoregulation and threat display. These same selection factors are likely to have been behind the initiation of rib elongation in the ancestors of the various long-ribbed gliders, but for a climbing animal there would have been the added advantage of increasingly controlled descent. Until now, however, each of these specialised reptilian gliders has appeared in the record without any obvious ancestral stage. The recognition of an Early Triassic kuehneosaur, some 40 million years before the first records of the group in Britain and North America, is therefore of interest, even if the limited information on the postcranial skeleton constrains discussion of its gliding abilities. The dorsal vertebrae of *Pamelina* resemble those of *Kuehneosaurus* in being bilaterally somewhat compressed, amphiplatyan, and rather elongated — especially in the posterior dorsal region. This elongation of the posterior dorsals may be associated with increased flexibility of the posterior dorsal spine (Colbert 1970), used by *Draco* in steering during flight. Although the transverse processes in *Pamelina* are much shorter and more gracile than those of the Late Triassic kuehneosaurs, they are longer than those of *Coelurosauravus* (personal observations) and there is some evidence that the dorsal ribs extended out laterally. The closest similarity is to the living *Draco* (personal observations, *e.g.*, TMM M-8673) which has transverse processes of similar length, limited buttressing, and very slender ribs. Like the kuehneosaurs and *Draco*, *Pamelina* also shows evidence of skeletal weight reduction. Taken together, these observations suggest that *Pamelina* is likely to have had at least parachuting abilities. In fact, its small size may mean that *Pamelina* had an advantage over the much larger *Kuehneosaurus*, as recent work (McGuire and Dudley 2005) has shown that the largest and heaviest species of *Draco* are less efficient gliders than their smaller congenitors. This is consistent with recent work on the gliding abilities of kuehneosaurs (Stein *et al.* 2008) which concluded that while the long ribbed *Kuehneosuchus* was capable of gliding, the heavier, shorter ribbed *Kuehneosaurus* was probably not.

CONCLUSIONS

Pamelina is the earliest representative of the specialised kuehneosaurs, predating known British and American taxa by nearly 40 million years. Although the skull is closely similar to those of the Late Triassic genera (Fig. 25), *Pamelina* is postcranially less specialised. Long expanded transverse processes, deep anterior gliding ribs, and strongly buttressed dorsal vertebrae characterise a Late Triassic kuehneosaur clade of which *Pamelina*

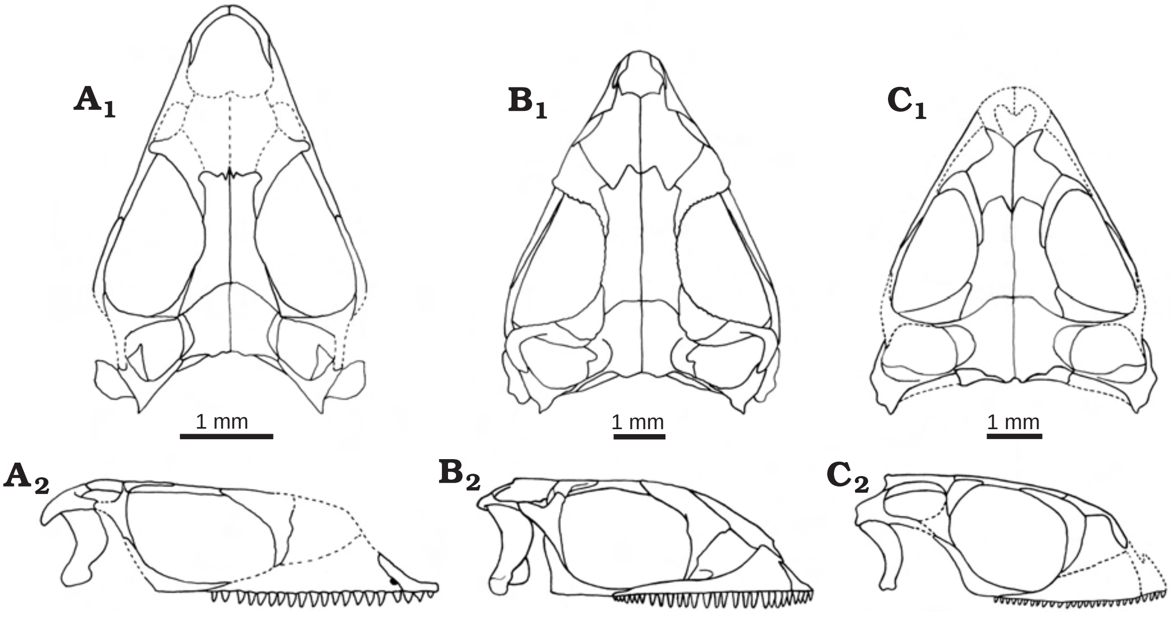

Fig. 25. Comparison of the skulls of *Pamelina* (**A**), *Kuehneosaurus* (**B**), and *Icarosaurus* (**C**), in dorsal (A_1, B_1, C_1) and lateral (A_2, B_2, C_2) views.

is almost certainly the primitive sister taxon. As such, *Pamelina* provides some insights into the evolution and early history of this enigmatic group, although more information is needed on the postcranial skeleton before it is possible to discuss functional morphology in any detail. Nonetheless, there is now evidence for a series of small long-“ribbed” reptilian parachuters/gliders extending from the Late Permian coelurosauravids and the Early–Late Triassic kuehneosaurs and *Mecistotrachelos*, through to the Early Cretaceous *Xianglong*, and then the living gliding agamid *Draco*. The hiatus between *Xianglong* and *Draco* is almost certainly an artefact of collection and preservation. Although many of the early reptilian gliders seem to have lived in rather dry upland areas, modern ones (frogs, geckos, agamids, colugos, flying squirrels) are most abundant in the tropical rain forests of Asia, and this is not an ideal environment for the preservation of delicate skeletons.

Although *Pamelina* shows only a partial development of the unique postcranial morphology of the Late Triassic kuehneosaurs, its skull already shares most of the derived characters of the groups (*e.g.*, confluent nares, loss of the parietal foramen, reduced squamosal, relatively large quadrate, loss of the supratemporal). This supports the view (*e.g.*, Evans 1980, 1984, 2003) that kuehneosaurs represent an ancient lineage with roots in the Late Permian. Their skulls were superficially similar to those of squamates, but the groups were not closely related. *Pamelina* also demonstrates that major features of the distinctive kuehneosaur cranial morphology evolved before the development of the specialised postcranium.

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APPENDIX 1

Data matrix for *Pamelina* and Kuehneosauridae as added, or updated, in the Müller (2004) analysis. See reference for full character list and taxon matrix.

Pamelina	01000 10011 02011 022?1 10??? 1111? 10001 01011 0??00 111?1 ????? ????? ????? ????? ????? ????? ?0011 00010 200?? 1??00 ??02? 10??? ????3 00??? ?0?00 101?0 00??? ????0 ????? ????? ?0001 11??? ??1?0 ???1? ???0? ?0000 10?1
Kuehneosauridae	01000 10011 02011 02201 10101 11110 10001 0?011 0110? 11?01 11101 00000 00121 00112 011?1 ???10 00011 0?010 200?? 00000 10020 11?00 00003 00010 ?0000 10100 00??0 1??10 ??0?? 00?10 ?0000 1100? 00100 01?10 00?00 20000 1011

APPENDIX 2

Müller (2004) characters emended

Rhynchocephalia

2: 0 to 0&1. Premaxilla without (0) or with (1) postnarial process. Within rhynchocephalians, clevosaurs and some other isolated taxa have a strong postnarial process that restricts entry of the maxilla into the margin of the narial opening. The score should therefore be 0&1.

16: 1 to 0&1. Jugal extending no further than mid-cheek (0) or nearly to posterior end of skull. This is a variable character. First there is no differentiation as to whether the dorsal or ventral part of the jugal is involved — or both. The ventral ramus of the jugal does not extend posteriorly in *Pleurosaurus*, and there is no ventral ramus in *Priosphenodon*. The jugal is more extensive dorsally in these taxa, but this is not the same character.

57: 1 to 0&1 Supraglenoid buttress present (0) or absent (1) on scapulocoracoid. There is a buttress at least in *Gephyrosaurus* so it should be 0&1.

100: 1 to 0&1.Teeth present (0) or absent on palatine ramus of pterygoid. Primitive rhynchocephalians (*Gephyrosaurus*, *Diphydontosaurus*, *Planocephalosaurus*, etc.) have teeth on the palatine ramus of the pterygoid. The coding should therefore be 0&1.

105: 0 to 0&1. Second sacral rib not bifurcate (0) or bifurcate (1). It is slightly flanged rather than bifurcate in *Gephyrosaurus*, and it is not bifurcate in *Sphenodon*.

131: 1 to 0&1. Postorbital terminates prior to reaching posterior limit of parietal (0) or extends at least to posterior limit of parietal. This is presumably a mistake since even in *Sphenodon* it terminates anterior to the end of the parietal.

137: ? to 0&1. Floor of braincase with gap between basioccipital and basisphenoid (0) or elements fused to floor of brain cavity. Both conditions exist in rhynchocephalians, the primitive state in *Gephyrosaurus*, the derived one in *Sphenodon.*

144: ? to 1. Atlantal ribs are ossified (0) or not (1). They are not ossified.

161: 0&1 to 0. Medial wall of inner ear is unossified (0) or ossified (1). It is not ossified in any known rhynchocephalian.

182: 1 to 1&0. Lacrimal enters orbital margin (0) or remains excluded by prefrontal-maxillary contact. In *Gephyrosaurus* a very small lacrimal enters the orbital rim (0).

10/184 — 5.4%

Squamata

93: 1 to 0&1. Contact between ectopterygoid and jugal, restricted, equal or less than contact of pterygoid and ectopterygoid (0) or expanded caudally (1). Both states occur in squamates.

96: 1 to 0&1. Basipterygoid processes oriented anterolaterally (0) or laterally (1). The angle of the processes differs and in some (*e.g.*, *Uromastyx*) they are certainly anterolateral.

113: 1 to 0&1. Dorsal margin of ilium without (0) or with an anterior process (1). This feature varies in squamates according to locomotor style, *e.g.*, *Heloderma*, many anguids and some scincids lack the process.

115: 0 to 0&1. Supratemporal stout and short (0), or long and slender projecting far anteriorly (1). In varanoid lizards, a long supratemporal extends anteriorly along the margin of the parietal.

131: 1 to 0. Postorbital terminates prior to reaching posterior limit of parietal (0) or extends at least to posterior limit of parietal. As with rhynchocephalians, this is presumably a mistake, or ambiguously defined. The postorbital only rarely reaches back that far posteriorly.

137: 0 to 1. Floor of braincase with gap between basioccipital and basisphenoid (0) or elements fused to floor of brain cavity. This is perhaps ambiguously defined, because the basioccipital and basisphenoid meet in squamates to floor the brain cavity.

146: 1 to 0&1: Humeral distal articulations, distinct trochlea and capitellum (0) or low double condyle (1). At least some lizards seem to have a pronounced trochlea and capitellum.

161: 1 to 0&1. Medial wall of middle ear is unossified (0) or ossified (1). Squamates do generally have the derived condition, but an opening medial wall is found in some chameleons (*e.g.*, *Chamaeleo*) where the lateral opening of the recessus scala tympani is reduced.

166: 1 to 0&1. Lateral shelf on the surangular is absent (0) or present (1). This is variable in squamates.

9/184 — 5%

A SMALL LEPIDOSAUROMORPH REPTILE FROM THE EARLY TRIASSIC OF POLAND

SUSAN E. EVANS and MAGDALENA BORSUK-BIAŁYNICKA

Evans, S.E. and Borsuk-Białynicka, M. 2009. A small lepidosauromorph reptile from the Early Triassic of Poland. *Palaeontologia Polonica* **65**, 179–202.

The Early Triassic karst deposits of Czatkowice quarry near Kraków, southern Poland, has yielded a diversity of fish, amphibians and small reptiles. Two of these reptiles are lepidosauromorphs, a group otherwise very poorly represented in the Triassic record. The smaller of them, *Sophineta cracoviensis* gen. et sp. n., is described here. In *Sophineta* the unspecialised vertebral column is associated with the fairly derived skull structure, including the tall facial process of the maxilla, reduced lacrimal, and pleurodonty, that all resemble those of early crown-group lepidosaurs rather then stem-taxa. Cladistic analysis places this new genus as the sister group of Lepidosauria, displacing the relictual Middle Jurassic genus *Marmoretta* and bringing the origins of Lepidosauria closer to a realistic time frame.

Key words: Reptilia, Lepidosauria, Triassic, phylogeny, Czatkowice, Poland.

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INTRODUCTION

Amongst living reptiles, lepidosaurs (snakes, lizards, amphisbaenians, and tuatara) form the largest and most successful group with more than 7 000 widely distributed species. The two main lepidosaurian clades are Rhynchocephalia (the living *Sphenodon* and its extinct relatives) and Squamata (lizards, snakes and amphisbaenians). Currently, the earliest recorded rhynchocephalians are of early Late Triassic age (Carnian, Scotland and Germany, Fraser and Benton 1989), but these taxa are already quite derived, and it is clear that rhynchocephalian evolution began well before this time (Evans 2003). Similarly, although the earliest true lizards are from the Late Triassic (Datta and Ray 2006) and Early Jurassic (Evans *et al.* 2002), of India, and the Mid Jurassic of Britain (*e.g.*, Evans 1993, 1994a, 1998), their diversity at this time provides clear evidence of an earlier origin. On current evidence, therefore, we would predict that Rhynchocephalia and Squamata had diversified from more basal lepidosauromorphs by at least the Mid Triassic. Frustratingly, virtually nothing is known of this Early–Mid Triassic period of lepidosauromorph history, barring two very incomplete specimens from the Permo-Triassic of South Africa — *Paliguana* (a partial skull, Broom 1903; Carroll 1975) and *Saurosternon* (a postcranial skeleton, Carroll 1975, 1977, but see Müller 2004 for a different phylogenetic hypothesis). Furthermore, only four other taxa are currently placed on the lepidosaurian stem (*i.e.*, within Lepidosauromorpha but outside crown-group Lepidosauria). These are the Middle Jurassic *Marmoretta* (Evans, 1991) and the Late Triassic gliding kuehneosaurs (*Kuehneosaurus*, *Kuehneosuchus*, *Icarosaurus*; Robinson 1962, 1967a, b; Colbert 1966, 1970). All four are survivors of an earlier period in lepidosauromorph history. Of the many other taxa previously referred to the group from the Permian and Triassic (*e.g.*, *Coelurosauravus* Carroll, 1978; *Fulengia* Carroll *et* Galton, 1977; *Colubrifer* Carroll, 1982; *Lacertulus* Carroll *et* Thompson, 1982; *Blomosaurus* Tatarinov, 1978; *Santaisaurus* Sun, Li, Ye, Dong, *et* Hou, 1992; *Kudnu* Bartholomai, 1979), none are recognised as lepidosauromorphs and most can be attributed to other reptilian groups (*e.g.*, archosaurs, Evans and Milner 1989; procolophonians, Evans 2001). The Mid Jurassic *Tamaulipasaurus* (Clark and Hernandez 1994) is a problematic and highly specialized taxon, the affinities of which remain uncertain.

The Early Triassic microvertebrate assemblage of Czatkowice 1 is therefore unusual in containing two lepidosauromorphs. One, an early kuehneosaurid, is described elsewhere in this volume (Evans 2009); the other is smaller and more delicate. It is described here.

Institutional abbreviation. — ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

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MATERIAL AND METHODS

The original Czatkowice 1 material is karstic bone breccia from which bone is extracted by solution in weak acetic acid and the resulting residues sorted carefully. As outlined elsewhere, dentitions were first recognised and then matched (maxilla to dentary and to premaxilla) using high power Scanning Electron Microscopy (SEM) images of tooth morphology. Attribution of other elements is more tentative, but relies primarily on matching facets, sculpture pattern, and adult size, and to a lesser degree on relative commonality of the elements. For the small lepidosauromorph described in this paper, we are confident of our attribution of jaw elements to one another, and of the attribution of one set of small, delicately built vertebrae. Other elements of the skull and postcranial skeleton also figure in the description. Their attribution depends on a combination of size (consistent small size with little or no range), sculpture pattern, and fit.

Over the whole text, the term "relictual" is used to describe late survivors of basal phylogenetic lineages that co-occur with representatives of more derived lineages. The term "early" refers to the stratigraphic occurence of the discussed taxa. "Primitive" is used to refer to characters, and to taxa situated at or near the base of the lineage in question.

SYSTEMATIC PALEONTOLOGY

Clade Neodiapsida Benton, 1985

Clade Lepidosauromorpha Gauthier, 1984

Family uncertain

Genus ***Sophineta*** gen. n.

Type and only species: *Sophineta cracoviensis*.

Derivation of the name: To honour Professor Zofia Kielan-Jaworowska of the Instytut Paleobiologii PAN. Greek *sophia* (wisdom) is the classical root of the name Zofia.

Diagnosis. — As for type and only species.

Sophineta cracoviensis sp. n.

Derivation of the name: From *Cracovia*, the Latin name for Kraków, the closest major Polish city to the Czatkowice 1 locality, and also to recognise researchers at the University of Kraków (Drs Paszkowski and Wieczorek) for their pioneering work at the locality.

Holotype: ZPAL RV/175, a nearly complete right maxilla.

Type locality and horizon: Czatkowice 1 dated as Early Triassic (earliest Late Olenekian) based on local geology (the upper limit is the Röt transgression at the end of the Early Triassic) and faunal analysis (Shishkin and Sulej 2009).

Diagnosis. — A small lepidosauromorph that differs from Late Triassic kuehneosaurs, *Marmoretta* and the Czatkowice 1 kuehneosaur (Evans 2009) in having short notochordal vertebrae without transverse processes; differs from all kuehneosaurs in tooth implantation (pleurodont rather than subthecodont), the presence of paired rather than confluent nares, the presence of weakly developed zygosphenoidal articulations on the vertebrae, the possession of notochordal rather than amphiplatyan vertebrae, and tooth morphology (compressed keeled tooth tips rather than simple cones); differs from the Permo-Triassic *Paliguana* in having a deeper facial process on the maxilla and a much smaller lacrimal (as deduced from facets on the maxilla); differs from *Marmoretta* in that the latter has a specialised maxillary/premaxillary overlap whereby a long process from the maxilla fits into a slot in the lateral surface of the dorso-ventrally compressed premaxilla; resembles lepidosaurs in having weak zygosphenes, short vertebrae and single-headed ribs throughout the column, but differs in having a shallower pleurodont tooth implantation and the apparent absence of both a thyroid fenestra and functional caudal autotomy.

Referred specimens. — ZPAL RV/226–230, 445, 1086 (frontals); ZPAL RV/231, 232, 443 (parietals); ZPAL RV/1056 (prefrontal); ZPAL RV/233–235, 966, 967, 1060 (postfrontals); ZPAL RV/236–238, 1058, 1062 (postorbitals); ZPAL RV/10, 239–244, 965, 1054, 1059 (jugals); ZPAL RV/245–249, 1055, 1057, 1069 (squamosals); ZPAL RV/968–973 (pterygoids); ZPAL RV/13, and 974 (quadrates); ZPAL RV/3, 7, 174–178, 455, 472, 493, 823, 824 (maxillae); ZPAL RV/1061 (premaxilla); ZPAL RV/174, 189, 392, 493, 512, 1101 (dentaries); ZPAL RV/23, 627, 628, 1079, 1080, 1098, 1108, 1110, 1121 (vertebrae); ZPAL RV/948–950, 952, 959, 1053, 1063 (ilia).

Note. — Based on the dimensions of the holotype maxilla and comparative skull proportions in *Marmoretta* (Evans 1991), the total skull length is estimated as about 10 mm in *Sophineta*, with a body length (without tail) of about 30 mm. The skull to body (without tail) ratio in the early Jurassic basal rhynchocephalian *Gephyrosaurus* is 1/3 (Evans 1981).

SKULL BONES

As reconstructed (Fig. 1), the skull of *Sophineta* is that of a modified diapsid with a relatively short preorbital region. The orbits, narial openings and upper temporal fenestrae are large, and the lower temporal fenestrae are open ventrally. The quadrate was firmly held by its attachments to the pterygoid and squamosal but its arched posterior margin suggests the presence of a tympanic membrane. Although a pterygoid has been attributed to *Sophineta*, there is currently insufficient information to permit a palatal reconstruction.

Premaxilla. — The attributed premaxilla (Fig. 2B) has a long, dorsal nasal process that is anteroposteriorly deeper at the base than it is wide. It differs from that of the Czatkowice 1 protorosaur-grade diapsid (Borsuk-Białynicka and Evans 2009b) in having a nasal process with a broad, planar medial surface that met the opposite premaxilla in a firm joint. Posterolaterally, a slender process separates from the alveolar margin of the bone and clearly ran along the medial side of the maxilla. It bears a facet dorsally between itself and the alveolar margin. Presumably the tip of the maxilla overlapped the premaxilla at this point. There were four small teeth.

Maxilla. — The maxilla of *Sophineta* is best represented by the holotype ZPAL RV/175 (Fig. 2A), a nearly complete right bone, ca. 5 mm in total length. This shows a deep facial process that precludes the possibility of a large lacrimal contributing to the antorbital skull wall. The premaxillary process is short and vertical in orientation, with clearly distinct medial and lateral surfaces. There are 22–26 tooth positions.

The lateral surface of the maxilla (Figs $2A_4$, 3A) is smooth with a basal row of nutrient foramina and, above these, isolated subsidiary openings. There is no sculpture. Seen in medial view (Figs $2A_3$, 3B) the anterior, narial margin of the bone is gently curved and carries a shallow groove. Behind it, the maxilla formed the sidewall of the nasal chamber and bears a concavity to house parts of the nasal glands. Above this concavity the facial process is relatively tall with a rounded shape. The medial surface of the process bears three clear facets: anterior, central and posterior (Figs $2A_3$, 3A). The first of these extends over the anterior half of the facial process and must have received the nasal. Behind it there is a facet of similar size covering the posterior half of the facial process. Posteroventral to it, as a narrow band along the descending posterior margin, is a third facet. The only two bones that lie in this position in other reptiles are the prefrontal and the lacrimal. Where the lacrimal is large (*e.g.*, *Kuehneosaurus*), the prefrontal may have only a small posterior contact with the maxilla behind the lacrimal. In this case, the major facet on this margin of the maxilla would be that for the lacrimal. In the case of *Sophineta* this cannot be the arrangement because if the central facet were for the lacrimal it would form a small element wedged between the nasal and an extensive ventral process of the prefrontal (meeting the long facet on the posterior margin). It is more likely that the central facet is for a narrow prefrontal process with a shallow lacrimal extending medially along the posterior margin of the maxilla. Either way, the lacrimal did not make a significant contribution to the antorbital skull wall.

The maxilla shows a steady decrease in height posteriorly and the posterior three-quarters of the bone form an elongate shallow triangle with a straight ventral margin and a long sloping dorsal rim that formed the posterior, orbital, process. Medially (Figs $2A_3$, 3B), a strong shelf develops above the tooth row, and this is perforated by a large ovoid foramen that carried the maxillary nerve and accompanying blood vessels onto the superior alveolar canal of the maxilla. Between the second and fifth tooth positions posterior to this opening, the medial side of the alveolar shelf bears a

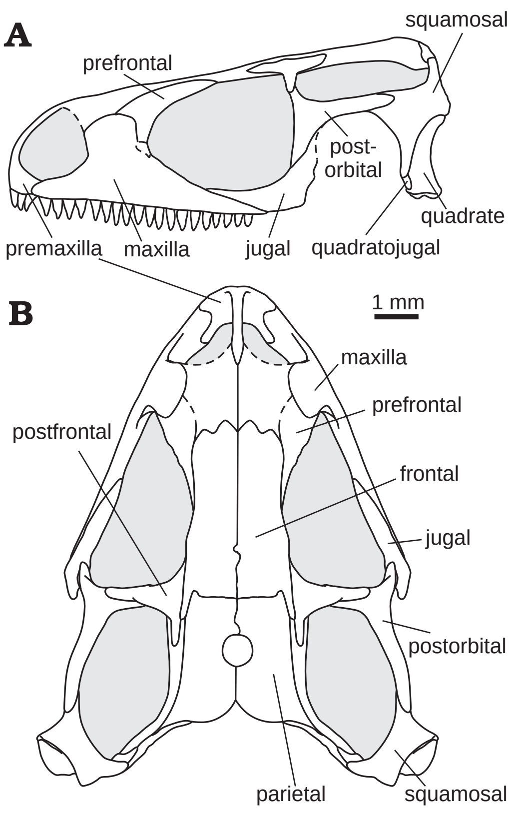

Fig. 1. *Sophineta cracoviensis* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Skull reconstruction in lateral (A) and dorsal (B) views.

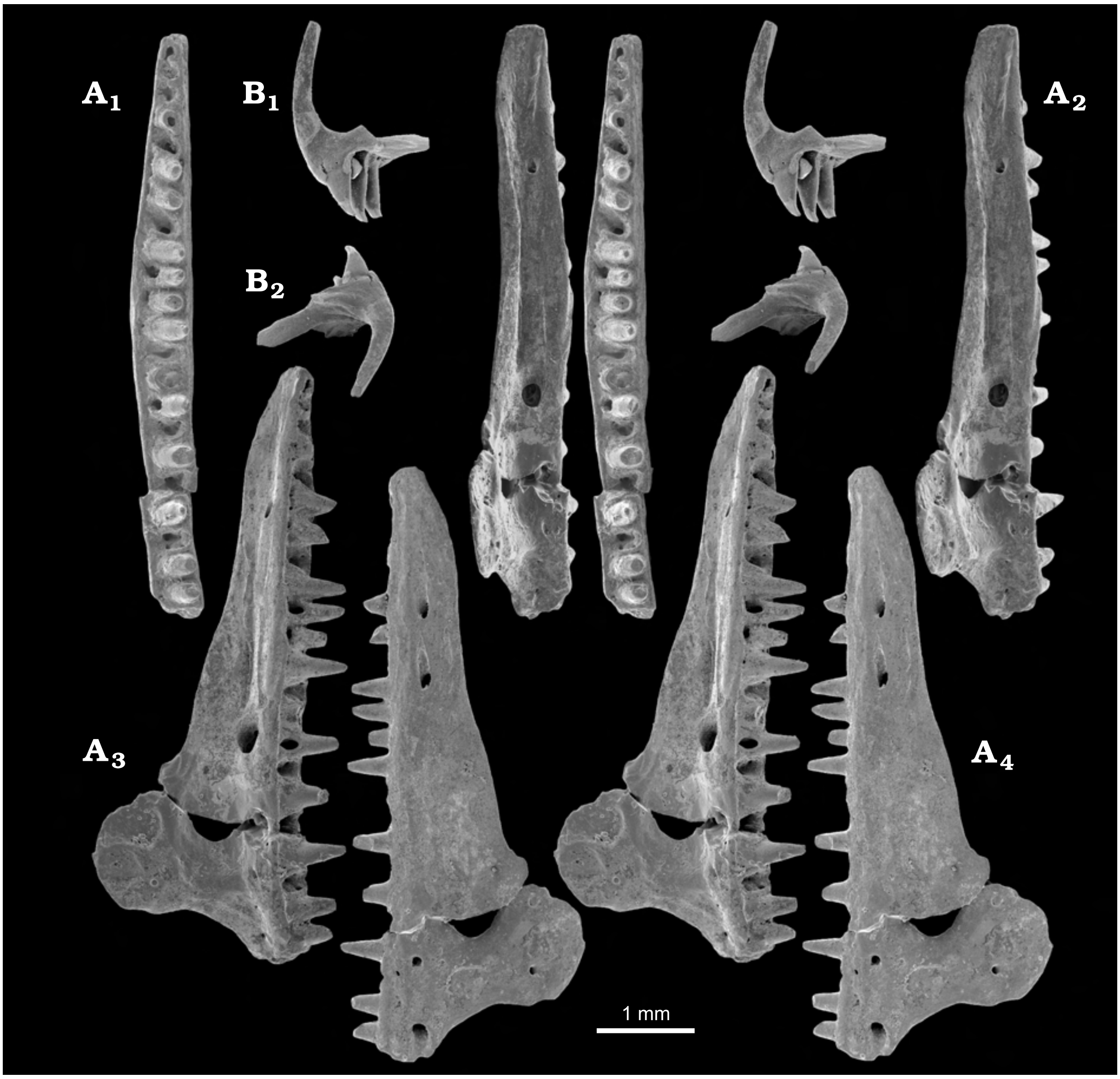

Fig. 2. *Sophineta cracowiensis* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Right maxilla ZPAL RV/175, the holotype, in occlusal (A_1), dorsomedial (A_2), medial (A_3), and lateral (A_4) views. **B**. Right premaxilla ZPAL RV/1061, in medial (B_1) and dorsal (B_2) views. SEM stereo-pairs.

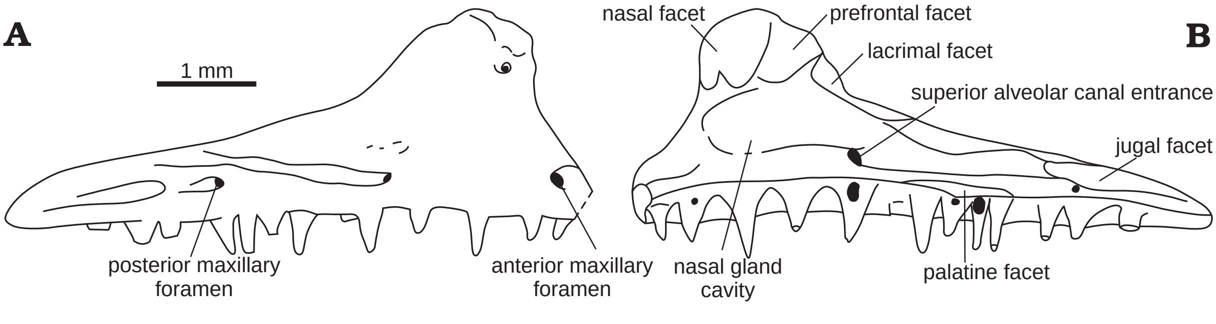

Fig. 3. *Sophineta cracoviensis* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Right maxilla in lateral (A) and medial (B) views. Mainly on the basis of ZPAL RV/175.

shallow facet for the maxillary process of the palatine (Fig. 3B). Further posteriorly, the supraalveolar shelf develops a gutter-like facet for the anterior process of the jugal. The remainder of the facet extends inside the dorsal lamina of the maxilla and its anterior limit is clearly circumscribed. The jugal did not reach the anterior orbital margin and formed only the posterior and posteroventral margin of the orbit.

Frontal. — Several paired frontals and parietals are known from the Czatkowice 1 assemblage and attributing them to the jaw species relies on a combination of matched sculpture, facets, size, and distribution. The frontal attributed to *Sophineta* is well-represented by both right (Fig. 4A) and left bones (Fig. 4G). The frontal is slender and lightly sculptured dorsally with a pattern of low rounded ridges and tubercles. The bone is dense and solid. Ventrally (Figs 4A, $5A_1$) the frontal is divided into medial and lateral parts by a strong crista cranii (subolfactory process). The medial half is narrowest between the orbits and widens anteriorly and posteriorly. It is concave, with the concavity deepening anteriorly in the region of the olfactory chamber. Laterally (Fig. $4A_2$) the orbital margin slopes dorso-laterally and bears strong deep facets for the prefrontal and postfrontal. The medial suture forms a simple joint anteriorly, with a small right-over-left overlap and a weakly interdigitating edge posteriorly (Figs $4A_1$, $5A_1$). There is an anterior shelf facet for the nasal, flanked laterally by a slender facet for the prefrontal that is almost confluent with the nasal facet. The nasal facet has the shape of an inverted “W” (Fig. $5A_1$) with each frontal sending a triangular process into the back of the nasal bone. Posterolaterally, the prefrontal facet extends onto the lateral surface (Fig. $4A_1$). Posteriorly the frontal is drawn into medial and lateral processes separated by a strong incision (Fig. 4G). The lateral process bears a strong ventral facet (Fig. $4A_1$) and covers the anterolateral surface of the parietal. It is notched along its outer margin by the postfrontal. The medial process varies in shape and appears to have abutted rather than overlapped the corresponding part of the parietal. Thus the frontoparietal margin was “M” shaped (Fig. 4G).

Variation: The frontals referred to *Sophineta* vary in their level of sculpture (some are unsculptured), in the degree of lateral separation of the prefrontal and postfrontal facets (the separation is greatest in small specimens, *e.g.*, Fig. 4G), and least in more mature specimens, *e.g.*, Fig. 4A), and in the precise shape of the posterior margin (with a triangular or squared median process), but there is a gradation between morphologies and it seems likely that these differences are due to age and sex rather than being taxonomically significant.

Parietal. — ZPAL RV/443 (Fig. 4C) is a well-preserved right parietal with a dorsal sculpture pattern matching that of the frontal (Fig 4C, D_2). The bone has a relatively long anterior plate and a long tapering postparietal process that extends laterally, and slightly ventrally, at roughly 45° to the main axis of the bone. The median area of the bone is usually damaged but is clearly seen to enclose a large parietal foramen. Behind this, the parietals seem to be separated in many specimens as the medial edges are angled Fig. $4D_2$). Whether this is a developmental feature or indicates the presence of postparietals is not clear. Anteriorly, the parietal bears incised lateral facets (Figs $4D_1$, 5F) for the frontal and postfrontal, but centrally the bone is serrate. The lateral margins are vertical with small adductor surfaces but no development of ventral crests. The postparietal process has a distal slot facet for the squamosal.

Variation: Parietals of *Sophineta* display a size-related variation in their level of sculpture (more in larger specimens), in the shape of the posteromedial edge, and in the extent of the facet for the squamosal/supratemporal. The shape of the posteromedial edge seems to depend on the extent of a thin bony flange running medially from the base of the postparietal process. In some specimens (*e.g.*, ZPAL RV/232), this appears to be a separate ossification and it is possible that it represents a remnant of a postparietal centre. Laterally, the slot facet for the squamosal varies in position from well along the postparietal process (large specimens, Fig. 4C) to close to the base of the process (small specimens, *e.g.*, Fig. $4D_2$). However, there is again a gradation in structure and this seems to depend on the degree of ossification over what begins as an open groove on the dorsal face of the process. The groove gradually closes in a proximodistal direction during growth, pushing the proximal limit of the facet closer to the end of the process, but whether this simply reflects ossification into the periosteum or the gradual ossification of a supratemporal centre is not clear.

Prefrontal. — Prefrontals are attributed only tentatively to *Sophineta* on the basis of size, rarity, and consistency of form in relation to the maxilla. This bone, represented by ZPAL RV/1056, has a shallow orbital margin and a thin facial lamina with two facets. The posterior facet (probably for a small lacrimal) is more shallow that the anterior one (for the facial process of the maxilla).

Postfrontal. — The postfrontal (Figs 4F, 5C, D) is attributed on a combination of fit and sculpture pattern (*e.g.*, ZPAL RV/233–235 and 1060). It is a roughly triangular bone, broadest dorsally and tapering ventrally.

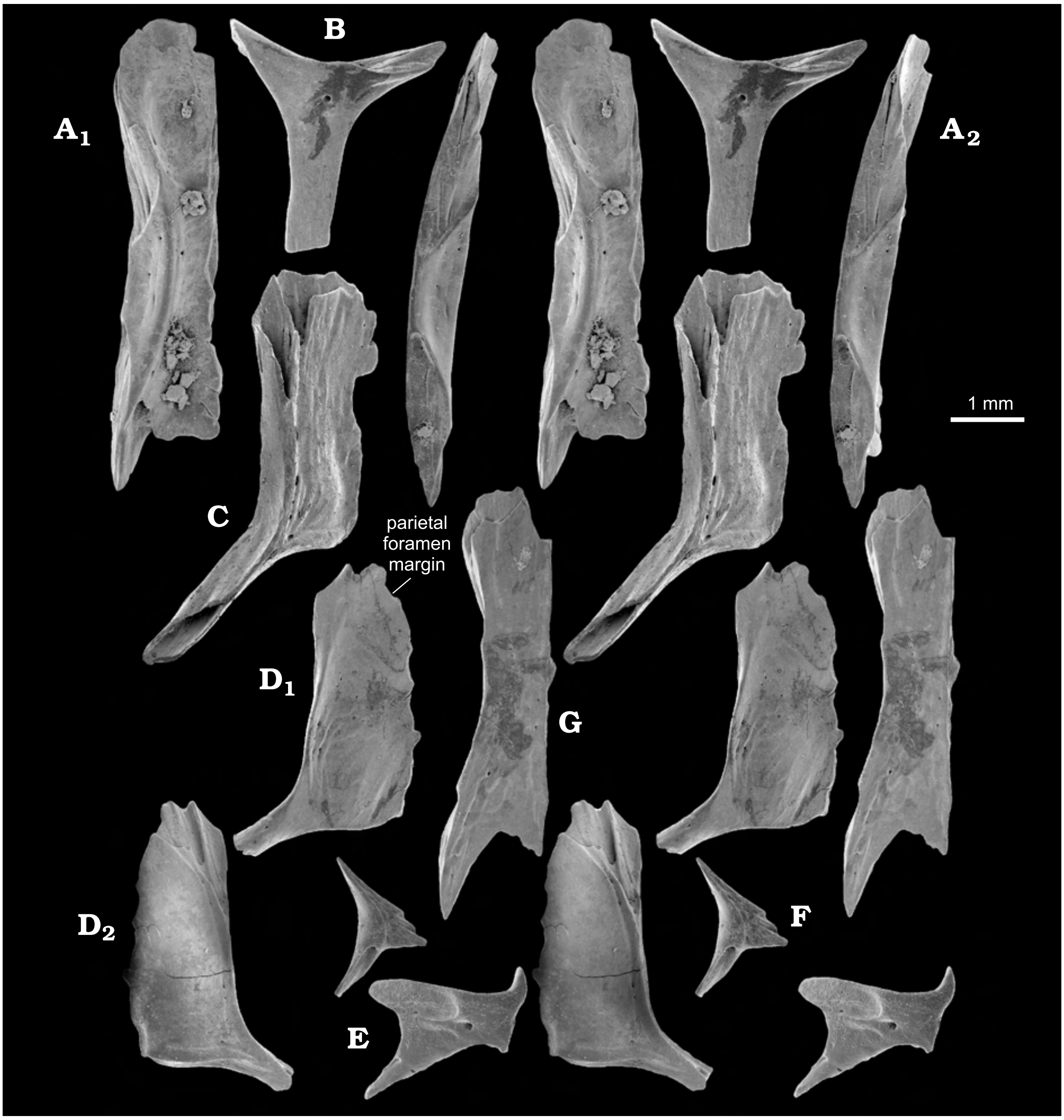

Fig. 4. *Sophineta cracoviensis* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Right frontal ZPAL RV/227, in ventral (A_1) and lateral (A_2) views. **B**. Right postorbital ZPAL RV/237, in lateral view. **C**. Left parietal ZPAL RV/443, in dorsal view. **D**. Right parietal ZPAL RV/231, in ventral (D_1) and dorsal (D_2) views. **E**. Left squamosal ZPAL RV/245, in dorsal view. **F**. Left postfrontal ZPAL RV/233, in dorsal view. **G**. Right frontal ZPAL RV/226, in dorsal view. SEM stereo-pairs.

The dorsal part is divided into two short tapering processes that fit into corresponding recesses on the frontal and parietal respectively. The ventrolateral process is longer and more slender. It carries a posteroventral slot facet for the postorbital (Fig. 5C). The parietal and postorbital facets are separated for short distance and the postfrontal thus entered, though only slightly, the margin of the upper temporal fenestra.

Postorbital. —This triradiate bone is attributed on the basis of fit and bone type (Figs 4B, 5G). It is quite common and is represented by more than 20 specimens (*e.g.*, ZPAL RV/236, 237, 1058, and 1062). The bone is characterised by short dorsal (postfrontal) and ventral (jugal) processes and a long slender posterior (squamosal) process, although this is broken in many specimens. The postfrontal process bears a flat anterior facet that receives the postfrontal, the pointed tip slotting into a small recess in the back of that bone. The ventral process forms another simple overlap with the anterior margin of the jugal. The squamosal process is

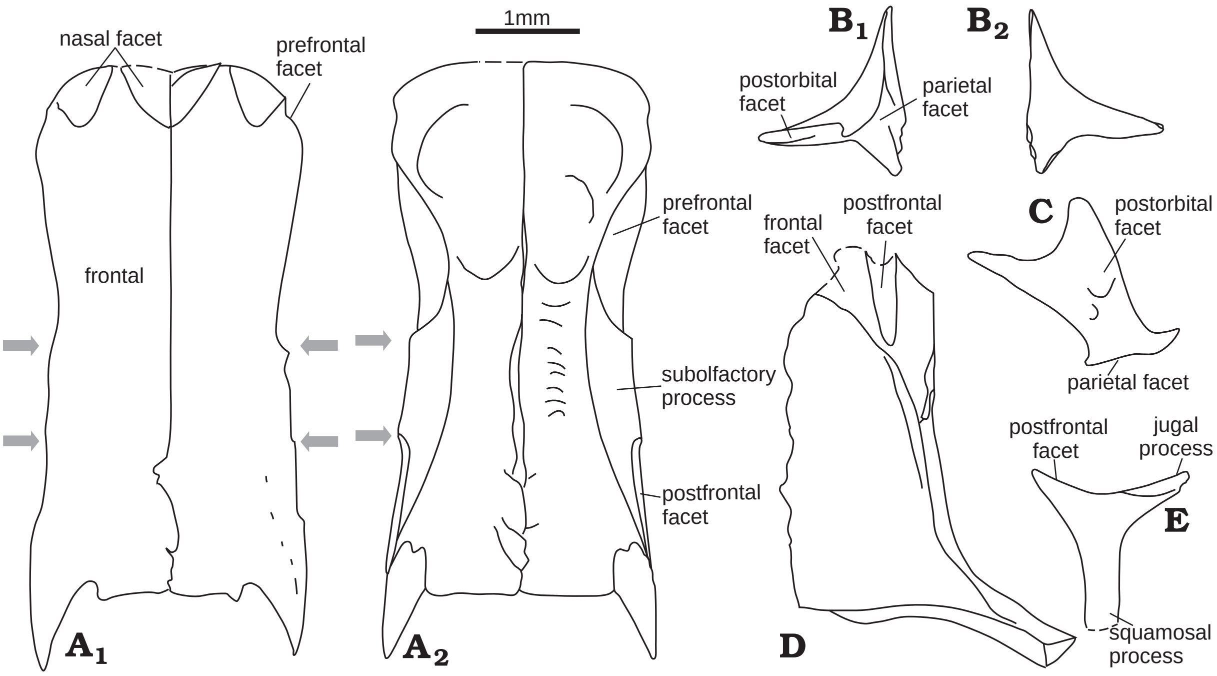

Fig. 5. *Sophineta cracoviensis* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Reconstruction of skull bones. **A**. Frontals, in dorsal (A_1) and ventral (A_2) views. **B**. Right postfrontal ZPAL RV/233, in ventral (B_1) and dorsal (B_2) views. **C**. Left squamosal ZPAL RV/245, in dorsal view. **D**. Right parietal ZPAL RV/231, in dorsal view. **E**. Right postorbital ZPAL RV/237, in lateral view.

long and mediolaterally flattened, with a long, tongue-like squamosal facet at its tip. The jugal and squamosal facets are well separated from one another. This and the long postorbital are consistent with the general elongation of the medial margins of the upper temporal fenestra due to the long postparietal process.

Jugal. — Jugals are rare elements at Czatkowice 1. Amongst the small elements, there are two types of jugal. In a previous paper (Borsuk-Białynicka *et al.* 1999), one of these (ZPAL RV/10) was tentatively attributed to the smaller of the two Czatkowice 1 lepidosauromorphs, and the recovery of further specimens lends support to this (some of the larger jugals of this type bear the characteristic sculpture pattern found on other attributed bones). These are the commonest type of jugal and come in a range of sizes (Fig. 6). The smallest specimens are essentially biradiate with an anterior maxillary process, a posterodorsal postorbital process, a central, flanged body, and a very small posteroventral spur (Fig. 6B). The latter feature becomes less pronounced in the largest specimen ZPAL RV/1059 (Fig. 6C) as the main body of the bone thickens. In the latter specimen, considered mature, the sculpture has become exaggerated along the posterior edge giving a scalloped edge to the bone that is completely natural. The postorbital process carries a facet along its anterior margin for the postorbital bone (Fig. 6C_2). This facet slots into the corresponding "wrap-around" facet on the postorbital, and is divided into two surfaces — a small anterolateral surface and a wider anteromedial surface. There is no trace of a squamosal facet apically and the jugal and squamosal probably did not meet. The maxillary process bears a convex ventromedial facet for the orbital process of the maxilla. At the medial junction of the anterior and dorsal processes, there is a large rugose facet for the ectopterygoid (Fig. 6C_2).

Variation: the main variation is in the size of the posterior spur and the depth of the ectopterygoid facet (shallow in small specimens). Given the likelihood of some time-averaging for the Czatkowice 1 assemblage, the possibility that some of these differences might be taxonomically significant cannot be excluded. However, the differences between the specimens in size, thickness, outline and surface sculpture falls within the range of ontogenetic variation in extant lizards (see *e.g*, Stephenson 1960; Presch 1969; Rieppel and Crumly 1997; Barahona and Barbadillo 1998). It has no effect on either the phylogenetic analysis or the reconstruction.

Squamosal. — Several tiny quadriradiate squamosals (*e.g.*, ZPAL RV/245–249) are tentatively attributed to *Sophineta* (the Czatkowice 1 kuehneosaur has a reduced squamosal). They are similar to the bones of basal diapsids, but also to those basal rhynchocephalians (*e.g.*, *Gephyrosaurus*) in having a short

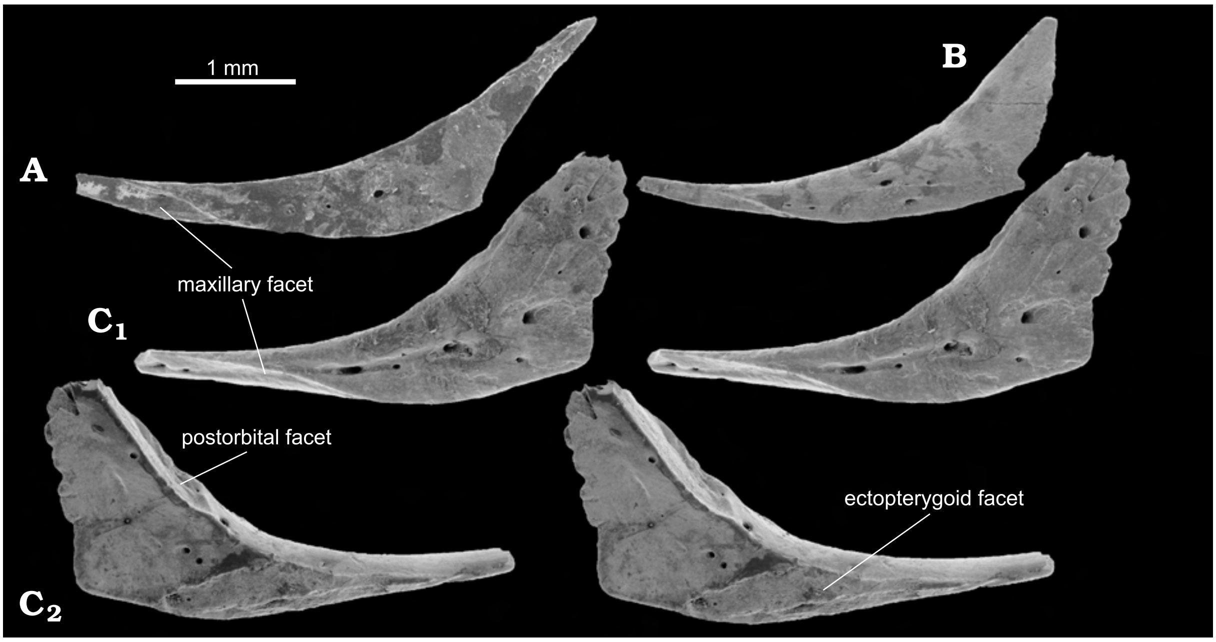

Fig. 6. *Sophineta cracoviensis* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Juvenile left jugal ZPAL RV/10, in lateral view. **B**. Mature right jugal ZPAL RV/243, in lateral view. **C**. Mature left jugal ZPAL RV/1059, in lateral (C_1) and medial (C_2) views. SEM micrographs; C stereo-pairs.

posteroventral process contributing to the dorsal rim of the tympanic membrane, a dorsomedial process that bears a short posterior groove facet that probably abutted a supratemporal, itself forming the link between squamosal and parietal (because it does not fit into the parietal slot facet); an anteroventral process meeting the anterior quadrate rim; and an anterior process to the postorbital (Figs 4E, 5E). The latter is elongate with a long anterodorsal facet suggesting the squamosal formed the major part of the ventrolateral and dorsal margins of the upper and lower temporal fenestrae respectively. Where preserved (*e.g.*, ZPAL RV/245), the tip of the anteroventral process carries a narrow facet that must be for a small quadratojugal. Although it is possible that these small bones represent juvenile elements of either the archosauriform, *Osmolskina*, or the protorosaurian-grade reptile, their relatively robust build and finished bone surfaces suggest they are not immature.

Quadrate. — Of the non-archosauriform quadrates of the Czatkowice 1 material, one type is common and clearly belongs to the protorosaur-grade reptile (Borsuk-Białynicka and Evans 2009b). Two other morphotypes, distinguished from the latter by their smaller size and finer structure, are associated here with the lepidosauromorph material. The first of these, represented by several specimens, is described elsewhere (Evans 2009) and recognized as the kuehneosaurid type. Specimens of the second morphotype are very rare, but are readily distinguished from the others and are tentatively attributed to *Sophineta*. Represented by specimens ZPAL RV/13 (Fig. 7A), and possibly ZPAL RV/974 (Fig. 7B_1, B_2), the *Sophineta* quadrate has a shorter, wider posterior pillar; less angulation of the medial wing and lateral conch (so that the anterior surface is flat rather than deeply grooved in contrast to the kuehneosaurid reptile from the same material); a wider dorsal head; and a deeper ventral condyle. The lateral quadratojugal notch is more open and rounded than that of the kuehneosaurid quadrate, and either bears a distinct quadratojugal facet on its ventral margin, or has a quadratojugal partially fused in place (ZPAL RV/13, Fig. 7A_2), as sometimes occurs in the basal rhynchocephalian, *Gephyrosaurus* (Evans 1980). In addition, the dorsal head bears a narrow anterolateral facet for the descending process of the squamosal. The morphology of the quadrate is thus compatible with that of the attributed squamosal, which also has a narrow ventral facet for a quadratojugal. In all its details, the bone is strikingly similar to that of *Gephyrosaurus*.

Pterygoid. — A series of small pterygoids are tentatively attributed to *Sophineta* on the basis of a consistent small size. Most specimens preserve the mid-section of the bone comprising the posterior part of the palatal plate, the basipterygoid joint, and the anterior part of the quadrate ramus. Together, specimens ZPAL

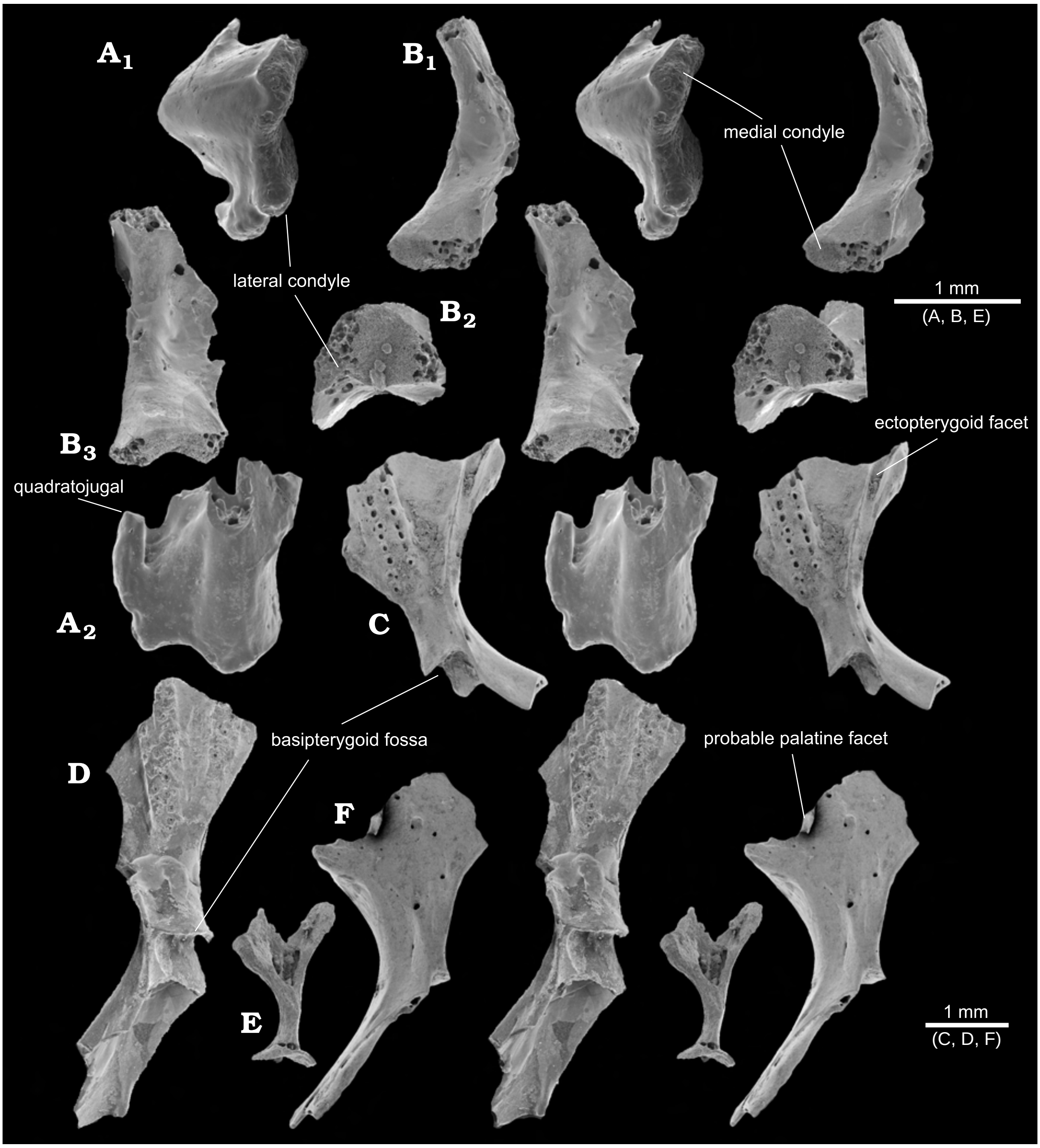

Fig. 7. *Sophineta cracoviensis* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Distal end of a left quadrate and quadratojugal ZPAL RV/13, in distal (A_1) and posterior (A_2) views. **B**. Left quadrate ZPAL RV/974, in medial (B_1) and posterior (B_2) views; distal condyle of the same (B_3, posterior to the right, lateral toward the bottom). **C**. Left pterygoid ZPAL RV/968, in ventral view. **D**. Right pterygoid ZPAL RV/746, in ventral view. **E**. Left ectopterygoid ZPAL RV/1142, in dorsal view. **F**. Left pterygoid ZPAL RV/969, in dorsal view. SEM stereo-pairs.

RV/968, 746, and 969 provide most details (Fig. 7C, D, F, respectively). The central part of the bone comprises the recess for the basipterygoid process of the sphenoid. If the palatal plate is oriented horizontally, then the basipterygoid fossa appears to open as much ventrally as medially. It seems likely therefore that in life the pterygoid was rotated slightly about its long axis so that the medial and lateral margins of the palatal plate were actually dorsomedial and ventrolateral in position. Posterior to the basipterygoid fossa, the bone extends into a narrow quadrate process that bears an elongate medial concavity for the pterygoideus attachment. Just behind the basipterygoid fossa in ZPAL RV/968 (Fig. 7C) the dorsal margin of the bone expands slightly into a weak epipterygoid eminence but there is, at best, only a weak indication of a facet on this spec-

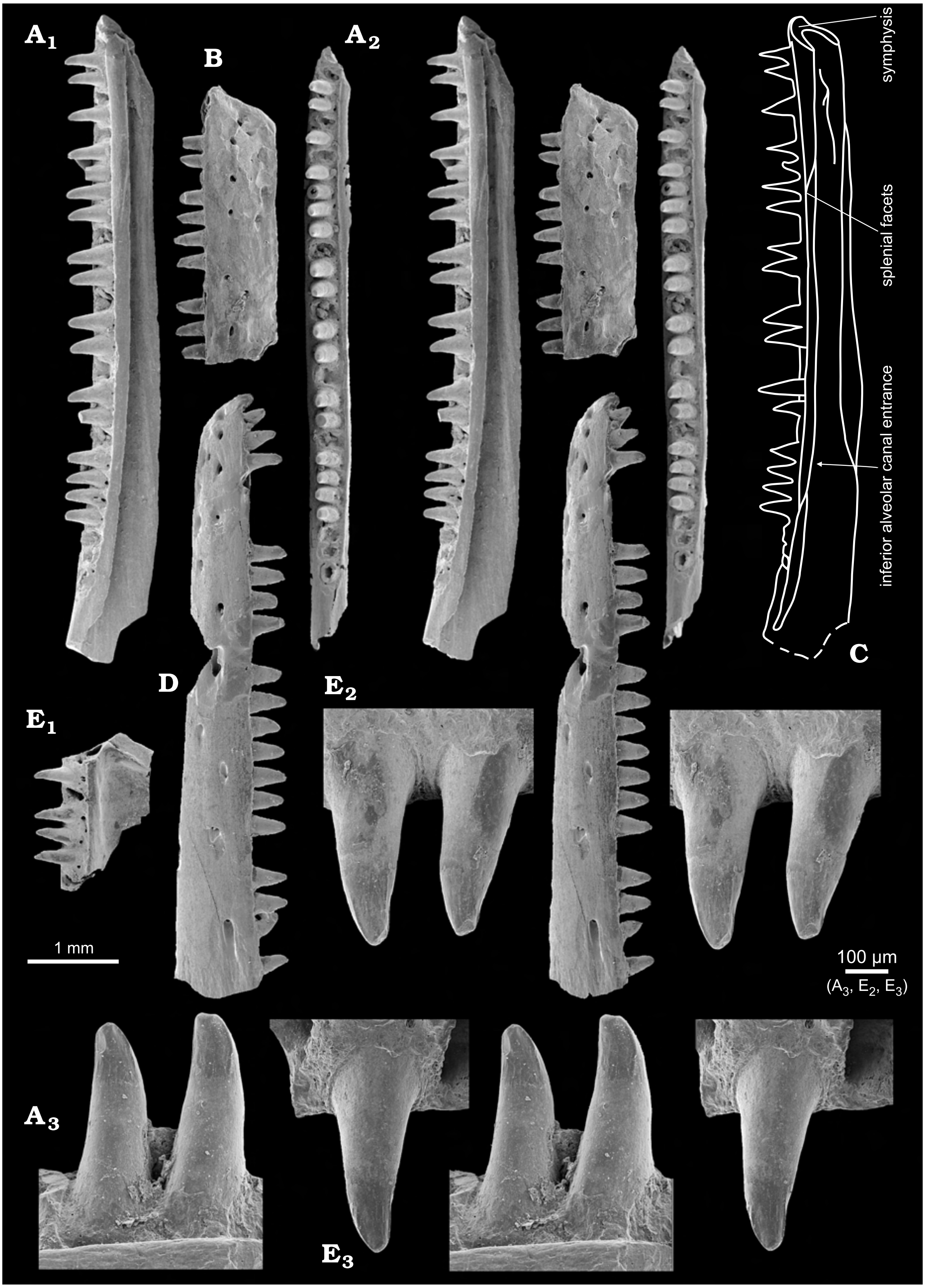

Fig. 8. *Sophineta cracoviensis* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Left dentary ZPAL RV/1101, in lingual (A_1) and occlusal A_2) views; two teeth of the same in lingual view (A_3). **B**. Anterior part of the right dentary ZPAL RV/174, in labial view. **C**. Left dentary reconstruction, in lingual view. **D**. Left dentary ZPAL RV/493, in labial view. **E**. Fragment of right maxilla ZPAL RV/176, in lingual (E_1) view; E_2, E_3 isolated teeth of the same. All but C SEM micrographs; all but C, E_1 stereo-pairs.

imen. Anterior to the basipterygoid fossa, the palatal plate fans out both medially and laterally. On the palatal surface traces of four tooth rows are preserved, the two lateral and two medial rows each running parallel to one another, but with the medial and lateral pairs separated from one another by a diverging gap. The medial rows begin on the inner edge of the pterygoid, but run directly anteriorly as the edge extends medially. They thus become increasingly separated from this edge. Laterally the bone expands into a pterygoid flange that ends in a deeper, flattened tuberosity. The flange bears dorsolateral and ventrolateral facets for the ectopterygoid. Further medially, the dorsal surface of the bone bears facets for the palatine — but the thinner, more anterior parts of these facetted surfaces are broken away.

Ectopterygoid. — ZPAL RV/1142 is a small left ectopterygoid (Fig. 7E) tentatively attributed to *Sophineta* on the basis of size, robusticity and fit. It closely resembles the ectopterygoid of *Gephyrosaurus* (Evans 1980) and other generalised lepidosaurs. The bone has a small, deep lateral head that met the jugal and an expanded, bifurcate medial head that slotted into the lateral margin of the pterygoid and bears anterior and posterior facets for that bone. Together the ectopterygoid and pterygoid formed a vertical flange that guided movements of the lower jaw. Between the medial and lateral heads is a slender neck that formed the posterior margin of the suborbital fenestra.

Braincase. — There are many small fragments of braincase bones, some of which must pertain to *Sophineta*. However, distinguishing these from juvenile bones of the other non-archosaurian diapsids is proving difficult and requires a more detailed survey of early lepidosauromorph braincase morphology than is possible here.

Dentary. — The dentaries (Fig. 8A–C) are relatively abundant in the material (*e.g.*, ZPAL RV/174, 189, 391, 512, and 1101) but are slender and usually break into several pieces. There were an estimated 25–30 tooth positions. The symphysis (Fig. 8A$_2$) is deep but only the upper half carries an articular surface; the lower half is a sharp blade. In medial view, the subdental ridge is moderately developed and of constant height with a clear facet for the splenial. The Meckelian fossa is fairly deep and is without a clear ventral rim, although this margin does carry a shallow facet through most of its length, either for the angular or the lower margin of the splenial. Behind the tooth row, the subdental ridge continues backward for some distance and bears a narrow horizontal facet for the coronoid. Close to the symphysial end, below tooth position 7, there is a consistent small foramen. The lateral surface is perforated by large nutrient foramina in a double row. The inferior alveolar canal enters the bone through a foramen towards the rear of the tooth row.

Dentition. — The teeth appear simple and conical but under scanning electron microscopy (Fig. 8A$_1$, A$_3$, E$_2$) are shown to have compressed and slightly keeled tips. This morphology assists in the attribution of elements from upper and lower jaws. The implantation is weakly pleurodont with the teeth attached to a labial jaw margin that is deeper than the lingual one. In many specimens there is a build up of ankylosing bone around the bases of these teeth (*e.g.*, Fig. 8A$_2$), perhaps to increase the robusticity. Teeth underwent continued replacement from the lingual surface, as shown by the pattern of replacement pits.

POSTCRANIAL SKELETON

Axial skeleton. — A subset of the Czatkowice 1 vertebrae are small and show a distinctive morphology (Figs 9, 10), very similar to that of the Jurassic *Gephyrosaurus* and of the living *Sphenodon*. All display a fully notochordal amphicoelous centrum but closed neurocentral sutures in all but the smallest specimens. All bear single headed rib facets (*e.g.*, Fig. 9C, E) without any development of transverse processes on trunk vertebrae, and all have strong zygapophyses with a weak medially angled component that matches the rudimentary zygosphene-zygantrum (Fig. 9D$_1$) system found in *Sphenodon* and *Gephyrosaurus*. The neural spines, though broken, have a broad base.

Cervical (ZPAL RV/1121) and dorsal (*e.g.*, ZPAL RV/1098, 1099,1108, and 1109) vertebrae have a keeled centrum, though more broadly so in the dorsals. There is no clearcut evidence of intercentra, but they are likely to have been present since they are retained in rhynchocephalians and in some basal squamates. In the sacral region, the ribs are usually fused to the centrum but, as in *Gephyrosaurus*, the suture lines are still visible in some specimens, and in juveniles they have separated (ZPAL RV/628, Fig. 10). ZPAL RV/627

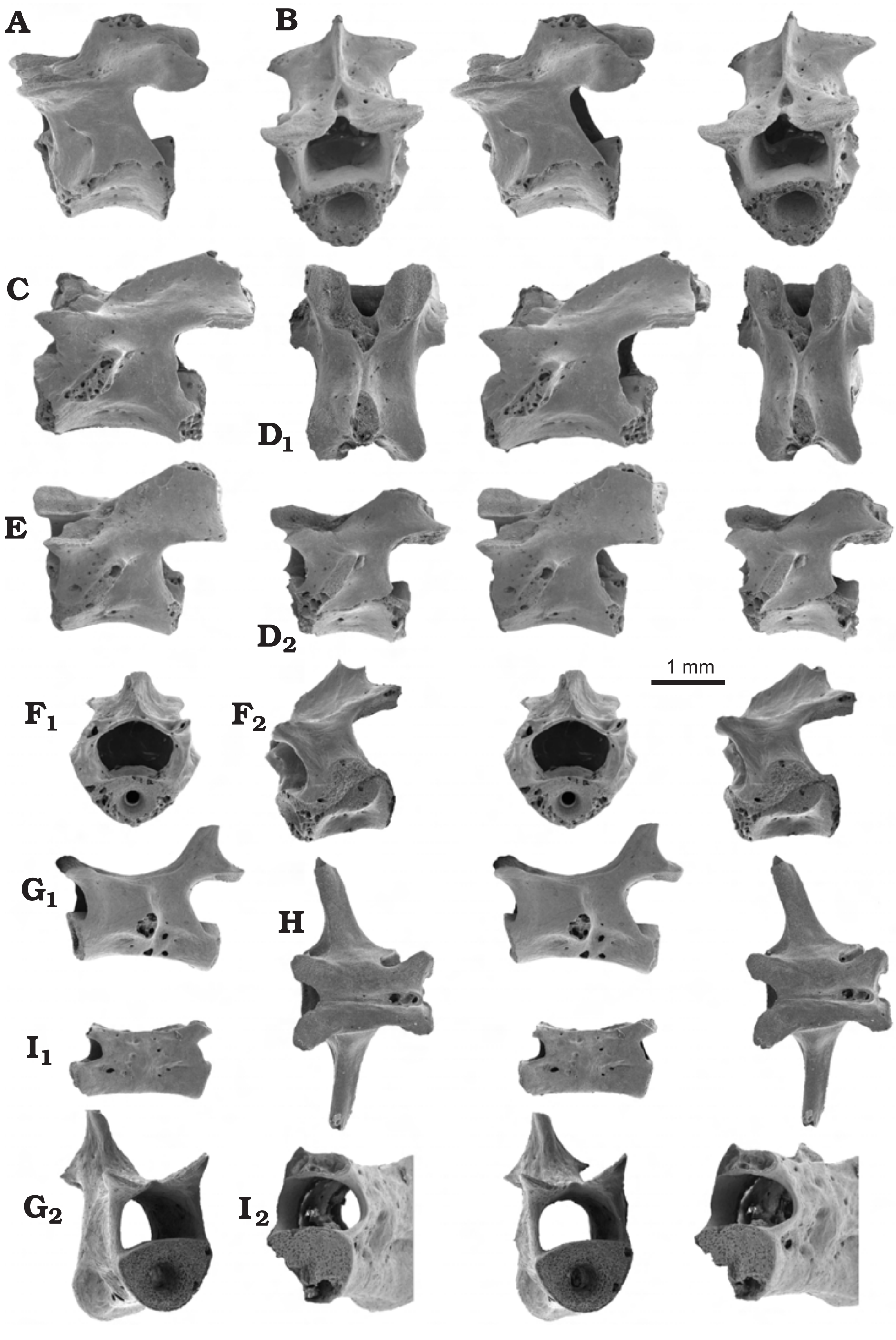

Fig. 9. *Sophineta cracoviensis* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Vertebrae. **A**. Cervical ZPAL 1121. **B**. Anterior dorsal ZPAL RV/1108. **C**. Dorsal ZPAL RV/1098. **D**. Juvenile dorsal ZPAL RV/1110. **E**. Dorsal ZPAL RV/1109. **F**. Sacral. **G**. Caudal ZPAL RV/1080. **H**. Anterior caudal ZPAL RV/627. **I**. Posterior caudal ZPAL RV/1079. Left side (A, C, D_2, E, F_2, G_1), cranial (B, F_1, G_2), dorsal (D_1, H), right side (I_1), and caudal (I_2) views. SEM stereo-pairs.

(Figs 9H, 11D) appears to be an anterior caudal (probably caudal 2), with long, transverse processes that have a slight anterior angulation. Further posteriorly, the transverse processes remain long but become narrower and lose the angulation. ZPAL RV/1079, 1080 (Fig. 9G, I) are more posterior caudals, showing reduction of the transverse process, and elongation and a slight grooving of the midventral surface of the centrum. Although these vertebrae lack fully developed autotomy septa, some (*e.g.*, ZPAL RV/1079) show a disruption

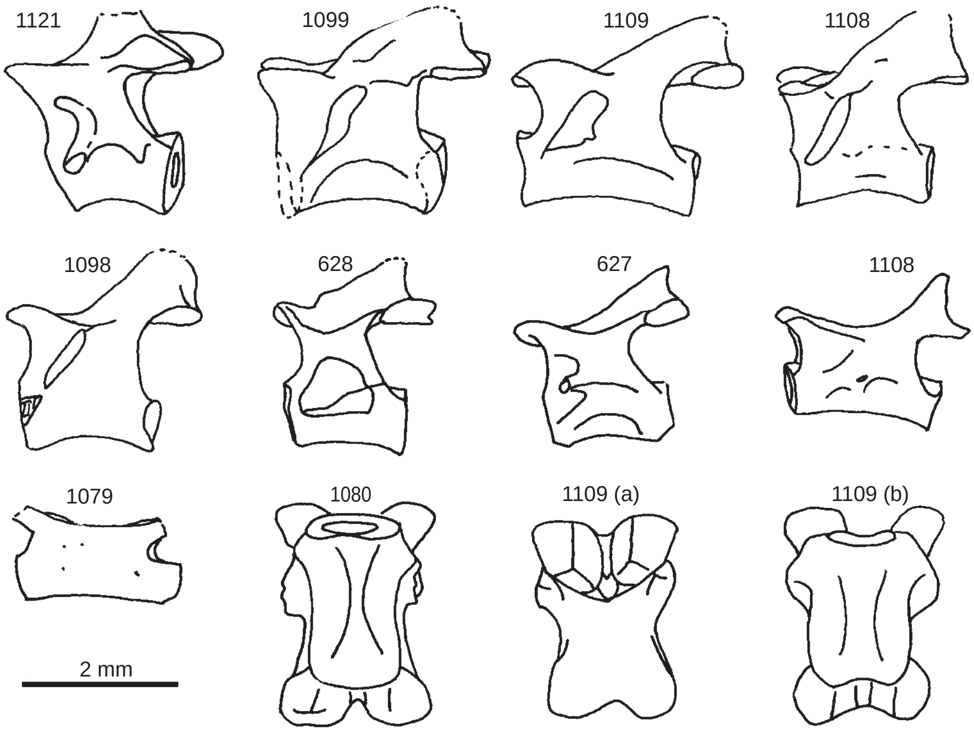

Fig. 10. *Sophineta cracoviensis* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Vertebrae from ZPAL RV/1121 to 1080 in a possible life sequence. Mostly those illustrated in Fig. 9. All but 1108, 1109 in left lateral view; 1108 and 1109 (b) in ventral view, 1109 (a) in dorsal view.

of the midventral groove similar to that in lepidosaurian vertebrae just anterior in position to the first with a fully developed fracture plane.

Forelimb. — The Czatkowice 1 remains include several humeri (mostly distal ends) but these differ in size and in the presence or absence of an entepicondylar foramen or groove. The smallest and most gracile of these elements probably, but not certainly, pertain to *Sophineta* and have a distinct elongate entepicondylar foramen (Fig. 11B). Whether or not the ectepicondylar foramen was completely enclosed is unclear since the distal end of the bone is usually poorly ossified or damaged.

Hind limb. — There are five distinct types of ilia in the Czatkowice 1 assemblage, including morphotypes that clearly fit into the archosauromorph or procolophonoid pattern. However, members of one set (*e.g.*, ZPAL RV/948–950, 952, 959, 1053, and 1063) (Fig. 11A, C, E, F) are uniformly small and broadly match the iliac type of relatively unspecialised basal rhynchocephalians such as *Gephyrosaurus* (Evans, 1981) and *Diphydontosaurus* (SEE personal observation). These ilia almost certainly belong to *Sophineta*. Each has an elongated blade set at roughly 45° to the horizontal but with a slight posteroventral curvature. The acetabulum is rather shallow and there is only a weak supraacetabular buttress. Anteroventrally, in good specimens, the margin is drawn out into a slender tapering prepubic process (Fig. 11E). On the medial aspect, the facets for the first and second sacral ribs are seen to lie fully on the iliac blade, with their long axes following the line of the blade.

As yet, no ventral pelvic elements have been attributed to *Sophineta*, but none of the numerous small ischia and pubes from the Czatkowice 1 material suggests any emargination of the puboischiadic suture. There is thus no evidence for the presence of a thyroid fenestra.

Variation: There is some ontogenetic/size variation in the shape of the iliac blade and the presence or absence of an anterior tubercle. In very small individuals, the blade is of fairly uniform width but in larger individuals the posteroventral border of the shaft expands a little, probably in concert with a strengthening of the sacroiliac joint (Fig. 11E_1). Similarly, some specimens have an almost straight anterodorsal margin (Fig. 11C), some are more arched (Fig. 11A). The largest specimens can bear a distinct tubercle (Fig. 11E) marking the position of the iliopubic ligament and its associated musculature.

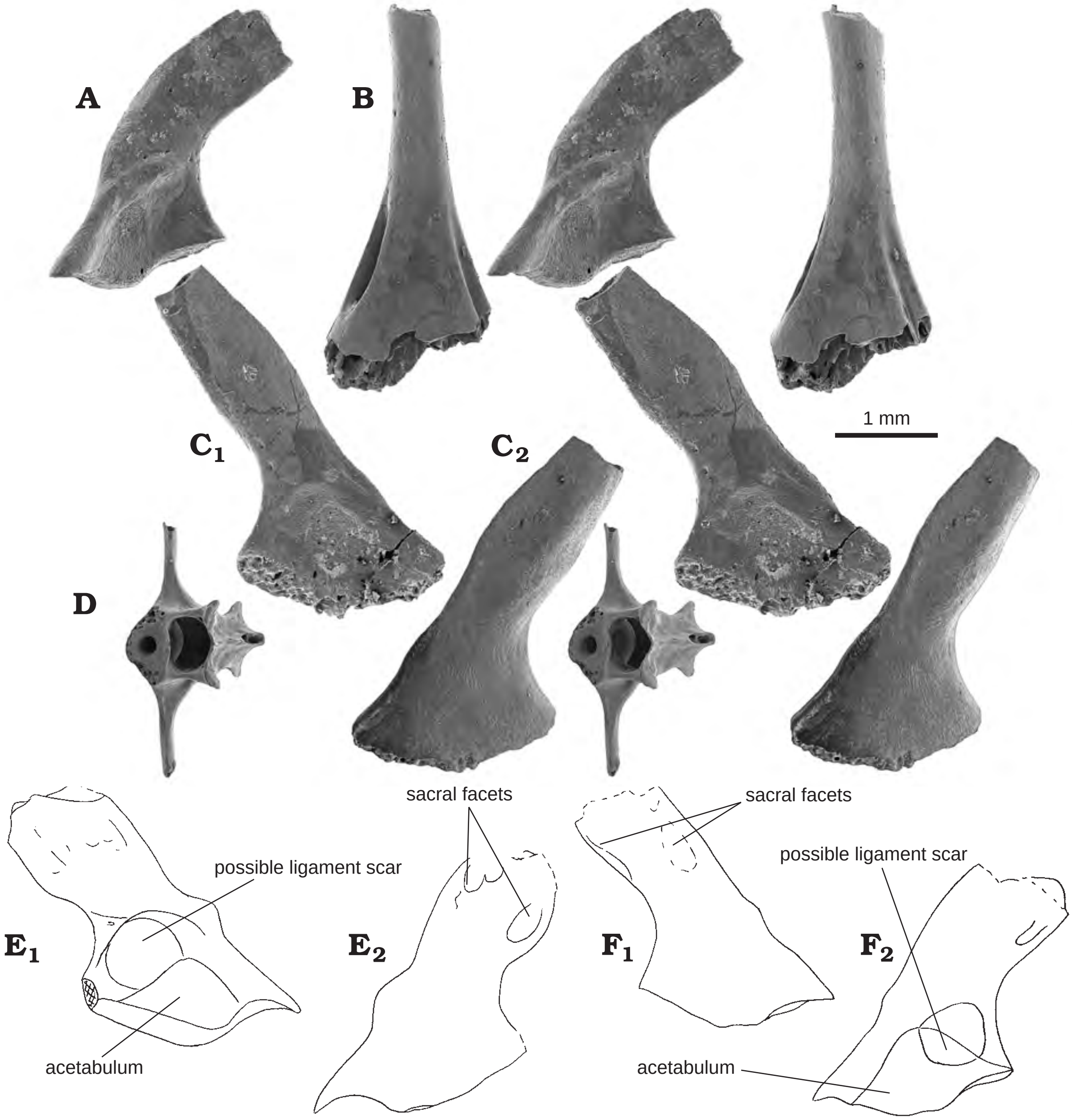

Fig. 11. *Sophineta cracoviensis* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Left ilium ZPAL RV/876, in lateral view. **B**. Right humerus ZPAL RV/1145, in distal dorsal view. **C**. Right ilium ZPAL RV/959, in lateral (C_1) and medial (C_2) views. **D**. Anterior caudal ZPAL RV/627, in anterior view. **E**. Right ilium ZPAL RV/1053, in lateral (E_1) and medial (E_2) views. **F**. Left ilium ZPAL RV/1063, in medial (F_1) and lateral (F_2) views. A–D SEM stereo-pairs.

DISCUSSION

PHYLOGENETIC ANALYSIS

A matrix of 77 characters (Waldman and Evans, 1994) and 11 taxa: *Petrolacosaurus*, *Coelurosauravus*, and *Youngina*, representing basal diapsids; *Prolacerta* representing archosauromorphs; *Saurosternon*, *Paliguana*, *Kuehneosaurus*, and *Marmoretta* considered basal lepidosauromorphs; *Gephyrosaurus* (a basal rhynchocephalian) and Squamata representing crown-group lepidosaurs; and *Sophineta* (Appendix 1) has been used for a phylogenetic analysis using PAUP version 3.1 (Swofford, 1993). A branch-and-bound search yielded 5 most parsimonious trees (MPT's) (Tree length [L] = 129; Consistency Index [CI] = 0.736; and

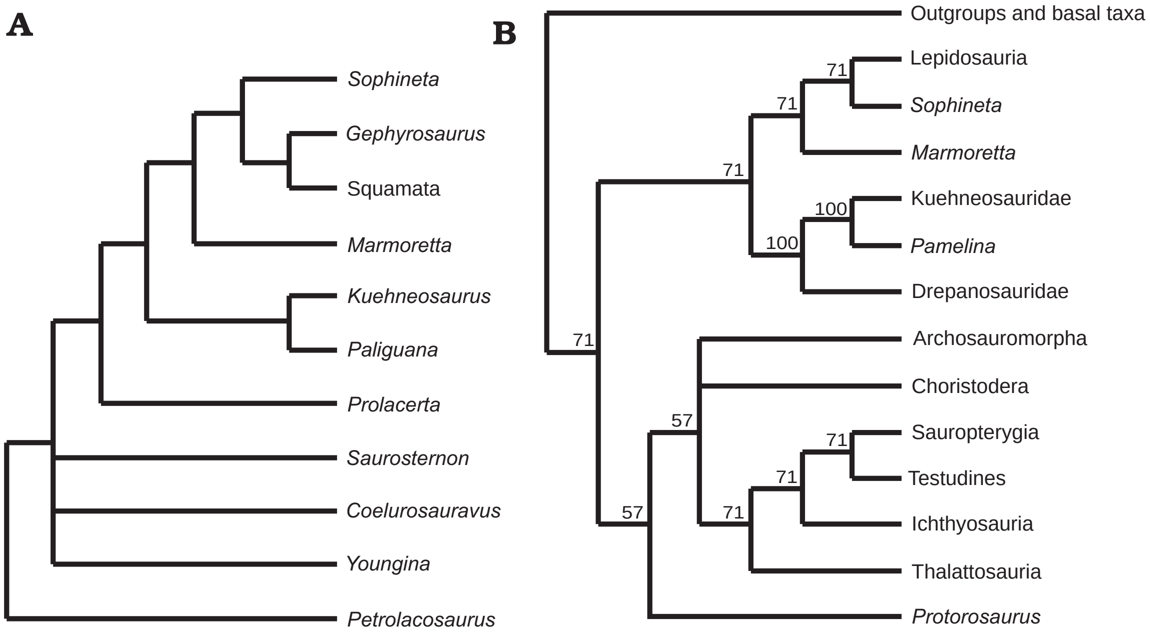

Fig. 12. **A**. The strict consensus tree of the diapsid interrelationships based on Waldman and Evans' (1994) matrix with *Sophineta* added. **B**. The 50% Majority Rule Tree based on Müller's (2004) matrix with *Sophineta* added.

Rescaled Consistency Index [RC] = 0.458). In all trees, *Sophineta* emerged as the sister group of Lepidosauria, one node above the Middle–Late Jurassic *Marmoretta*. Fig. 12A shows the strict consensus tree. Thus *Sophineta* is not a lepidosaur, but is close to the base of this important clade.

Recently, Müller (2004) published a detailed phylogenetic analysis of diapsids in which the kuehneosaurs, generally regarded as lepidosauromorphs, emerged as the sister taxon to the arboreal drepanosaurs at the base of neodiapsids. *Marmoretta*, *Sophineta*, and the Czatkowice 1 kuehneosaur (Evans 2009) have been added to the matrix (Appendix 2), including new data on kuehneosaurs and with some correction of the codings for rhynchocephalians and squamates (see Appendix 3). One of us (SEE) ran a Heuristic search (Random addition sequence, Tree-bisection-reconnection [TBR] branch swapping, replicates, rooted with outgroups, Seymouriidae, Synapsida, multistate characters treated as polymorphism: the matrix is too large to run a Branch and Bound search). This resulted in seven equally parsimonious trees with weak support values (L = 998, Consistency Index = 0.428, Rescaled Consistency Index = 0.234). The Strict Consensus of these trees is almost completely unresolved above the Araeoscelida, but the 50% Majority Rule Tree (Fig. 12B) places *Sophineta* as the sister group of Lepidosauria, with *Marmoretta*, and then kuehneosaurs as consecutive outgroups. The addition of Czatkowice 1 protorosaur (Borsuk-Białynicka and Evans 2009b) to the matrix resulted in three equally parsimonious trees (L = 1008; CI = 0.425; RC = 0.232), the Strict Consensus of which was better resolved and, for the lepidosauromorph at least, is identical to the cladogram shown in Fig. 12B. The differences are with respect to the relationships between archosauromorphs, testudines, choristoderes, ichthyosaurs, sauropterygians and thalattosaurs, and that is not at issue here.

IMPLICATIONS

The early history of lepidosaurs is very poorly known. On the stem of Archosauria, there are a series of relatively well known groups — rhynchosaurs, trilophosaurs, "protorosaurs", stem archosaurs (basal Archosauriformes), all of which help in understanding the structural and functional evolution of the group. For Lepidosauria, the only known stem taxa are the specialised Triassic kuehneosaurs (but see Müller 2004; and Evans 2009), the Middle Jurassic *Marmoretta*, and the very fragmentary Permo-Triassic *Paliguana* and *Saurosternon*. Currently, the most primitive known crown-group lepidosaur is the basal rhynchocephalian *Gephyrosaurus* (Evans 1980, 1981), but it has been difficult to know which of its skull characters are genuinely plesiomorphic, which autapomorphic (since the states in outgroups are obscure), and which already approaching the derived rhynchocephalian condition (*e.g.*, the posterior process on the jugal; the quadriradiate squamosal).

Sophineta thus provides an important point of comparison, both from its Early Triassic age and its position close to the base of Lepidosauria (Fig. 13). It appears to be unspecialised as far as its postcranium is known — unlike gliding kuehneosaurs or the possibly aquatic *Marmoretta*. *Sophineta* vertebrae are almost indistinguishable from those of the primitive rhynchocephalian *Gephyrosaurus* (low synapophyses, notochordal centrum, weak zygosphene/zygantral system), whereas those of *Marmoretta* are more like those of kuehneosaurs in having a solid, platycoelous centrum and in retaining transverse processes (albeit very short ones). In contrast, the skull characters of *Sophineta,* including the tall facial process of the maxilla, reduced lacrimal, and pleurodonty all resemble those of early crown-group lepidosaurs rather than those of stem-taxa. In *Sophineta* the unspecialized vertebral column is thus associated with the fairly derived skull structure, whereas kuehneosaurs combine a highly derived postcranial morphology with a skull that retains many plesiomorphic states (including a large lacrimal, low facial process of the maxilla, teeth on the pterygoid flange, teeth on the parasphenoid, and a weak subthecodont form of tooth implantation). The late surviving *Marmoretta* (Mid Jurassic, UK: Evans 1991; Late Jurassic, Portugal: SE personal observation), apparently positioned one step crownward of kuehneosaurs, represents a level of organisation not dissimilar to that of the Early Triassic *Sophineta* in terms of some skull characters (dental, maxillary, lacrimal and jugal traits), while showing autapomorphies in others (*e.g.*, the parietal crest and deep vertical parietal flanges, Evans 1991).

CHARACTER EVOLUTION IN LEPIDOSAUROMORPH REPTILES

As noted above, the description of *Sophineta* and its interpretation as a lepidosauromorph close to the origin of Lepidosauria provides an opportunity to reassess character evolution within the group. In the following section, key characters are examined and discussed in the light of the new data, and areas needing further work are highlighted.

Paired dorsal roofing bones. — All the small non-archosauriform reptiles from Czatkowice 1 have paired frontals and parietals, a trait regarded as plesiomorphic. This is the condition found in basal taxa like *Petrolacosaurus* (Reisz 1981), *Araeoscelis* (Reisz, Berman, *et* Scott, 1984), and *Youngina* (Gow 1975); in archosauromorphs (*e.g.*, *Prolacerta*, Gow 1975); and in lepidosauromorphs (*e.g.*, *Paliguana*, kuehneosaurs, Carroll 1975, 1977; Colbert 1966, 1970). It was probably also the condition in basal lepidosaurs as the frontals and parietals are paired in *Sphenodon* and the frontals are paired in many modern lizards, and the parietals are paired in the primitive Late Jurassic lizard *Bavarisaurus* (Evans 1994b). The fusion of the frontals and of the parietals in the basal rhynchocephalian *Gephyrosaurus* (Evans 1980) and in *Marmoretta* (Evans 1991) is therefore probably a derived condition.

Retention of parietal foramen. — An open parietal foramen placed in the mid-parietal suture, well back from the fronto-parietal suture, is the primitive diapsid condition (*e.g.*, Gow 1975; Reisz 1981). This is a plesiomorphic character state in *Sophineta*. Robinson (1962, 1967a) suggested a fronto-parietal position for the parietal foramen in *Kuehneosaurus* but the supposed foramen is simply a gap in the midline between the paired frontals and paired parietals (SEE personal observation). Thus kuehneosaurs are specialised in lacking a parietal foramen.

Size of the facial process of the maxilla and size of the lacrimal. — In primitive diapsids, the lacrimal is a large bone that spans much of the antorbital region from the orbit to the naris above a low maxilla. In the lepidosauromorph lineage there is a gradual reduction in the size of this bone and a concomitant increase in the size of the facial process of the maxilla. In the Triassic kuehneosaurs, the lacrimal remains large, above and behind a relatively low maxilla (Robinson 1962, 1967a; Colbert 1970); in the Mid Jurassic genus *Marmoretta*, the facial process of the maxilla is taller and the lacrimal apparently reduced (Evans 1991). In *Gephyrosaurus* (Evans 1980), as an example of a relatively basal lepidosaur, the facial process of the maxilla is tall and the lacrimal confined to the orbital rim. The lacrimal of *Sophineta* has not been recovered, but the facial process of the maxilla is relatively tall and there appears to have been only a small facet here, and on the prefrontal, for a lacrimal.

Maxilla enters orbital margin. — The primitive diapsid condition seems to be for the jugal to extend along the ventral edge of the orbital margin (*e.g.*, *Petrolacosaurus*), contacting the lacrimal or prefrontal anteriorly. In *Sophineta*, the facets on the posterior process of the maxilla make it clear that the maxilla made a major contribution to the ventral border of the orbit which is thus a derived condition.

Postfrontal enters margins of upper temporal fenestra. —This was a character listed by Gauthier *et al.* (1988) as diagnostic of lepidosauromorphs, the postfrontal being excluded both in basal diapsids and in archosauromorphs by the contact of the dorsal ramus of the postorbital with the parietal. The reassessment of the position of *Youngina* as a basal diapsid rather than a lepidosauromorph renders this character problematic. It reflects the enlargement of the upper temporal fenestra, and perhaps a reduction in the degree to which its anterior margin (or the posterior margin of the orbit) is braced. Facets on the postfrontal of *Sophineta* suggest the postfrontal made a small entry into the margin of the upper temporal fenestra.

Incomplete lower temporal arcade. — "Loss" of the lower temporal arcade was once considered to be a unique derived character of squamates and their immediate ancestors. With the recognition that a complete lower temporal arcade is absent in a number of small diapsids with no relationship to lepidosauromorphs (*e.g.*, *Prolacerta*, Parrington 1935; Gow 1975; *Tanystropheus* Wild 1973; *Coelurosauravus*, Evans 1982), it is generally accepted that the bar was either lost several times independently, or is a synapomorphy at the level of Neodiapsida (or earlier) with subsequent reacquisition in several lineages. The latter view is the more parsimonious.

Kuehneosaurus and *Marmoretta* both have a fairly large jugal with a strong body but no posterior process. This may mean that the longer posterior jugal process of *Gephyrosaurus* was actually a derived character, associated with a trend that eventually led to the re-establishment of the lower temporal bar in many later rhynchocephalian lineages (Whiteside 1986) and in at least one squamate (Lü *et al.* 2008). *Sophineta* has a gracile jugal with only a very slight posterior angle which would be thus plesiomorphic.

Reduction of the anteroventral process of the squamosal. — In diapsids, the squamosal is primitively quadriradiate, with a posterodorsal process to the parietal/ supratemporal, a posteroventral process overhanging the quadrate and contributing to the frame for the tympanic membrane, an anterior process to the postorbital, and an anteroventral process that runs along the anterior margin of the quadrate and may meet the quadratojugal if this is retained. Rhynchocephalians retain the plesiomorphic squamosal morphology; kuehneosaurs have modified it, reducing the squamosal to a narrow bar in a manner analogous to the squamosal reduction in squamates. The functional reasons for this are not yet clear. The quadrate of kuehneosaurs is not streptostylic in the squamate sense since it retains a strong pterygoid/quadrate suture (SEE personal observation). The condition in *Sophineta*, as interpreted here, is plesiomorphic.

Retention of the quadrate/pterygoid overlap. — Squamate streptostyly involves changes in the dorsal and ventral attachments of the quadrate to the bony skull by reduction of the squamosal, modification of the supratemporal and paroccipital so that they contribute to the support of the quadrate head, loss of the quadratojugal, and extreme reduction of the quadrate/pterygoid overlap. Kuehneosaurs have modified the dorsal articulation, by changing the shape of the squamosal (but they lose the supratemporal, and the paroccipital process is not involved, Robinson 1967a), but the pterygoid/quadrate overlap remains extensive. In *Sophineta*, a strong pterygoid/quadrate overlap seems also to have been retained.

Quadrate conch. — One of the features considered diagnostic for Lepidosauromorpha is the presence of an expanded lateral quadrate conch (*e.g.*, Gauthier *et al.* 1988). This conch is present in *Paliguana* (SEE personal observation), in kuehneosaurs, in lizards, and in *Gephyrosaurus* and many other rhynchocephalians (but secondarily lost in *Sphenodon*), although it is sometimes a composite of the quadrate and quadratojugal (*e.g.*, some rhynchocephalians). In *Paliguana* there is no trace of a separate quadratojugal, but the presence of a large foramen perforating the lateral part of the conch suggests the quadrate may, indeed, be composite. In the Late Triassic kuehneosaurs, there is no trace of a foramen, but it is possible that a quadratojugal was incorporated into the ventrolateral margin of the conch (see also the description of the Czatkowice 1 kuehneosaur, Evans 2009). The quadrate attributed to *Sophineta* has composite conch, with a quadratojugal foramen enclosed between the quadrate and a reduced quadratojugal. This was probably the primitive lepidosaurian condition.

Palatal dentition. — Early diapsid reptiles have an extensive palatal dentition with multiple rows of teeth on the vomers, palatines, pterygoids and parasphenoid. The Triassic kuehneosaurs also have an extensive palatal dentition, although it is not clearly organised into rows (SEE personal observation). In more crownward lepidosauromorphs, no teeth are present on the parasphenoid or the pterygoid flange, but basal rhynchocephalians like *Gephyrosaurus* retain an essentially primitive pattern, except for the enlargement of the lateral palatine row, a derived character of all rhynchocephalians. In squamates, the palatal dentition is much reduced, with only a scatter of pterygoid teeth (and more rarely palatine and vomerine teeth) in many taxa, or none at all. This loss of the palatal dentition must be related in some way to changes in feeding efficiency, since palatal teeth serve to increase the frictional resistance of the palate and thus aid grip. *Sophineta* has a pterygoid dentition similar to that of *Gephyrosaurus*, but the palatine is not known. Like *Gephyrosaurus*, but unlike *Kuehneosaurus*, it lacks teeth on the pterygoid flange.

Parasphenoid teeth. — In some primitive taxa, the parasphenoid — as a dermal element — bears small palatal teeth. This condition is present in both *Icarosaurus* and *Kuehneosaurus* (probably as a secondary condition, see Evans 2009) but not in either *Marmoretta* or *Gephyrosaurus*. The condition is still to be determined in *Sophineta* because no parasphenoid has been identified as yet (but equally, we have not recovered any toothed parasphenoids from the deposit).

The following braincase characters have not yet been reorganized in *Sophineta*, but we note them here as a basis for future work.

Parabasisphenoid, **development of the dorsum sella and the presence of abducens foramina**. — In modern lizards and rhynchocephalians, the hypophysial fossa is walled posteriorly by a strong ridge, the dorsum sellae, that contains paired concavities for the origin of ocular muscles and is perforated by foramina for branches of the abducens nerve. In kuehneosaurs the dorsum sellae is much lower and the abducens nerves presumably passed through soft tissue above it. The morphology of the parasphenoid in *Sophineta* is still unknown.

Parabasisphenoid — closure of vidian canal. — In extant lizards, the lateral edges of the parasphenoid are extended and co-ossified with the overlying basisphenoid to enclose bilateral vidian canals for the palatine ramus of the facial nerve and the internal carotid artery. In rhynchocephalians, basal lepidosauromorphs including kuehneosaurs, and also basal diapsids, the lateral margins of the parasphenoid remain as raised crests, leaving open grooves for the contents of the vidian canal.

Prootic — crista prootica and alary processes. — In extant lizards, the anterodorsal corner of the prootic is usually developed into a process or flange of varying length (the alar process of the prootic). This process is absent or at most rudimentary in rhynchocephalians but is developed to a small degree in the Late Triassic *Kuehneosaurus* (SEE personal observation). Similarly, in extant lizards, a distinct bony flange, the crista prootica, usually overhangs and protects the lateral foramen for the facial nerve, forming a canal for the anterior (palatine) and posterior (hyomandibular) branches of that nerve. In modern lizards, the crest also gives attachment to part of the protractor pterygoid musculature. A small crest exists in kuehneosaurs (SEE personal observation).

Opisthotic — ventral ramus. — Robinson (1962, 1967a) listed the ventral ramus of the opisthotic as a character linking “prolacertiforms” (then thought to be related to the ancestry of lizards) and kuehneosaurs. However, the ventral ramus is more widespread in its distribution (*e.g.*, in basal rhynchosaurs, Evans 1986 and basal archosauriforms *e.g.*, *Osmolskina* see Borsuk-Białynicka and Evans 2009a).

Basioccipital and exoccipital. — In primitive diapsids, the basioccipital and paired exoccipitals are separate ossifications enclosing all or most of the foramen magnum. In squamates, the exoccipital becomes co-ossified at an early stage with the opisthotic to form a composite oto-occipital. A similar co-ossification also occurs in *Sphenodon*, although later and to a less extensive degree (*i.e.*, the two bones join dorsally above the metotic fissure, but not ventrally). In *Gephyrosaurus*, however, and also in *Marmoretta* and *Kuehneosaurus*, the exoccipital may be co-ossified with the basioccipital, having a suture with the opisthotic dorsally, but not fusing with it (the same ossification style occurs in the protorosaurid grade reptile from Czatkowice 1; Borsuk-Białynicka and Evans 2009b). This radically different pattern of ossification may be related to enclosure and subdivision of the metotic fissure in squamates. However, dorsal fusion of the opisthotic and exoccipital (like that of *Sphenodon*) also occurs independently in the archosauriform *Osmolskina* (Borsuk-Białynicka and Evans 2009a), and there is evidently some variation in this character within diapsids that would merit further investigation.

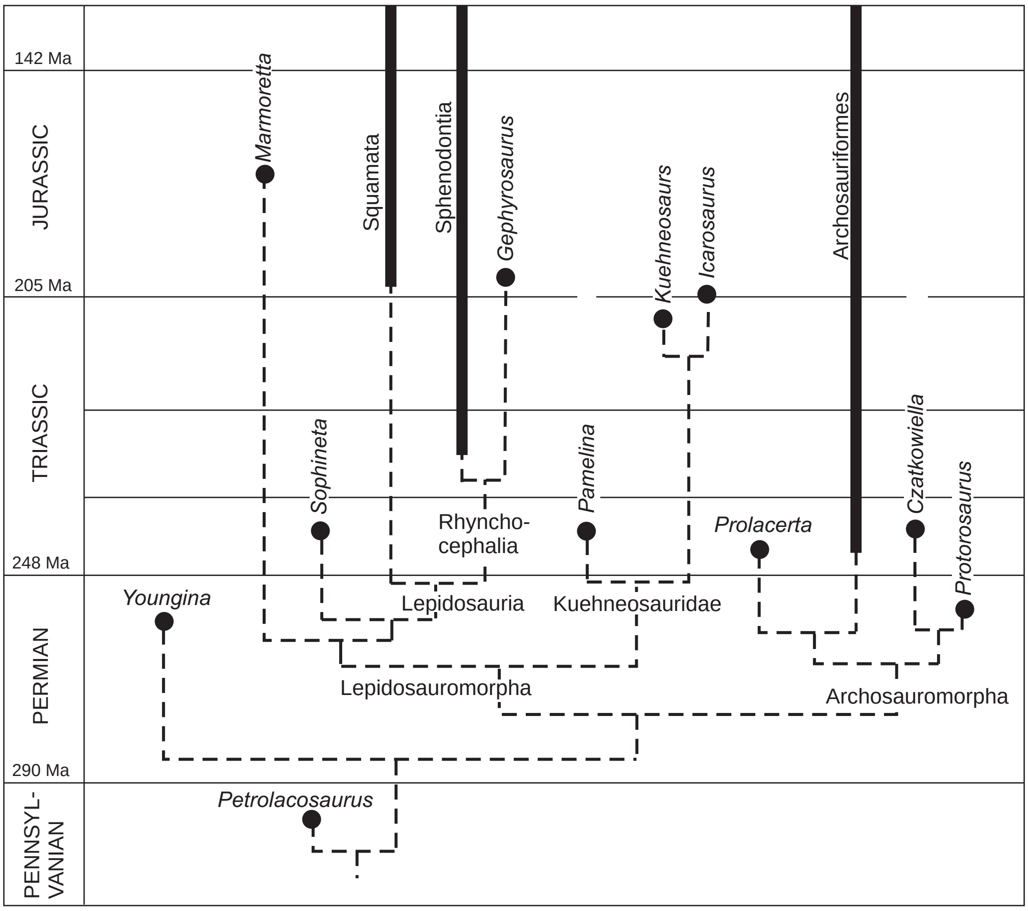

Fig. 13. Phylogenetic tree of basal diapsids in geological time based on the most parsimonious result of the present analysis.

Dentary symphysis. — The symphysial surface of the dentary is large and ovoid in *Gephyrosaurus* and *Marmoretta*, but is less extensive in both squamates and derived rhynchocephalians. However, the symphysis is also very weak in kuehneosaurs and in *Sophineta*, suggesting that this, rather than a massive symphysis, may be the plesiomorphic condition inherited by early lepidosaurs.

Vertebral morphology. — In rhynchocephalians, the vertebral centra are relatively short and retain an open notochordal canal. Since this condition is also found in *Youngina*, it was thought to be plesiomorphic for lepidosauromorphs as a whole. However, based on the condition in *Marmoretta* and kuehneosaurs, where the centra are weakly amphicoelous but solid, it is possible that the basal lepidosaurian condition represents a secondarily acquired (paedomorphic) trait. The vertebrae attributed to *Sophineta* resemble those of *Gephyrosaurus* in being notochordal and amphicoelous with a small zygosphene-zygantral system and a low, single synapophysis. *Marmoretta* and kuehneosaurs differ in having rather elongate vertebrae, lacking zygosphenes, and in having at least some development of transverse processes.

Lepidosaurs are also characterised by the presence of an autotomy septum in the caudal vertebrae, although this has been lost secondarily in some squamate taxa. None of the many small caudal vertebrae in the Czatkowice 1 bone assemblage shows a fully developed autotomy plane, but some of the caudals in *Sophineta* resemble *Gephyrosaurus* caudals in which the septum had not quite developed (*i.e.*, vertebrae lying just in front of the first with an autotomy septum). It may be, therefore, that the caudals of *Sophineta* show an incipient development of autotomy, although the developmental basis of this character is poorly understood.

Pelvis. — The ilium attributed to *Sophineta* has a relatively small acetabulum, and a simple angled blade like that of some basal lepidosaurs. It also shows the distinctive prepubic process found in some lepidosaurs (*e.g.*, *Gephyrosaurus*, *Sphenodon*). However, it seems unlikely that *Sophineta* pelvis had a thyroid fenestra since none of the small ischia or pubes in the collection show any trace of emargination. In lepidosaurs, this foramen emarginates the ventral midline, separating the pubis and ischium at the symphysis.

CONCLUSIONS

Skeletal morphology and phylogenetic analysis support the hypothesis that *Sophineta* is a lepidosauromorph close to the base of crown-group Lepidosauria. Although our knowledge of the genus remains incomplete, the structure of its skull and postcranial skeleton may help in establishing the polarity of lepidosaurian and lepidosauromorph characters in primitive lepidosaurs. *Sophineta* suggests that the quadriradiate condition of the squamosal and the presence of a small quadratojugal contribution to the quadrate conch were characters inherited by basal lepidosaurs, as was the long slender jaw with many small teeth, but the strong dentary symphysis in *Gephyrosaurus* may be a derived rather than plesiomorphic feature, as may the distinct posterior process on the jugal. In addition, some features of typical lepidosaurian postcranial structure (single headed-ribs, zygosphene-zygantrum, the prepubic process on the ilum) may characterise a more inclusive group, while others (caudal autotomy, thyroid fenestra) remain limited to the crown-group.

On the basis of the rhynchocephalian and squamate fossil records, the origins of crown-group Lepidosauria have been predicted to lie in the Late Permian or Early Triassic (*e.g.*, Evans 2003). However the paucity of basal lepidosauromorph remains left a significant gap in the fossil record for this important period. Until now, the only real clues to this key stage in lepidosauromorph evolution have come from relictual Jurassic taxa like *Gephyrosaurus* and *Marmoretta*. The Early Triassic *Sophineta* is important not only in filling a major temporal gap in the lepidosauromorph record, but also a morphological one, since it lies between the lepidosauromorph *Marmoretta* and the basal rhynchocephalian *Gephyrosaurus*, and provides a glimpse of the stem lepidosaurian condition.

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APPENDIX 1

Matrix of 77 characters used in the analysis as listed in Waldman and Evans (1994). Letters represent variable states as follows: A = 0&1&2; B = 0&1; C = 0&2

Petrolacosaurus	00000 00000 00000 00000 00100 00001 00000 000?0 ?0000 0000? ?0000 00000 1000? 00000 000?0 10
Youngina	01000 00000 00000 00000 00000 01101 00000 00000 00010 00000 ?0000 00010 00000 ????? ?0?00 00
Paliguana	00000 00000 ???01 ?10?? ????? 1?0?0 ?0?0? ??1?? ????? ????? ????? ????? ????? ????? ????? ??
Saurosternon	????? ????? ????? ????? ????? ????? ????? ????? ?0000 0000? 1010? 0???? ?000? ?0000 00?1? 00
Kuehneosaurus	00012? 100?0 11?11 11100 00100 10000 00100 01100 ?0000 12311 ?011? 11000 11001 00??? ?1?01 00
Marmoretta	1?02? ?0010 0??00 000?1 01??? 00010 01011 01?11 0000? 111?? ????? ?11?? 1?0?? ????? ????0 0?
Sophineta	1?001 10110 0000? 010?? ????? 110?0 0??0? ????2 0100? 001?? ????? ????? ???0? ????? ????0 0?
Gephyrosaurus	11001 11110 01?00 01001 1110? 11010 01111 01112 01100 00000 ?010? ?1101 11011 ?11?? 12?20 00
Squamata	111A1 10B?0 10111 01111 11112 11010 B12B0 11112 11101 201B1 21111 21101 12011 11111 12120 00
Prolacerta	000C1 11001 00000 00000 01001 10001 00000 011?0 ?0001 1100? ?0010 01000 00000 00100 11?01 11

APPENDIX 2

Character codings for *Sophineta* in the Müller (2004) analysis. See that reference for full character list and taxon matrix.

Sophineta	00000 11010 00011 02001 00??? 11?1? 1000? 01310 0??10 00??0 ????? ????? ????? ??0?? ????? ????? ?0000 0?001 20000 ????0 ??01? ?1??? ????? 000?? ?0?00 10111 10??? ????0 ????? ????? ?0000 11??? ???1? ???0? ?0010 ??210 00?1

APPENDIX 3

Characters changed in the codings of Müller (2004)

Rhynchocephalia

2: 0 to 0&1. Premaxilla without (0) or with (1) postnarial process. Within rhynchocephalians, clevosaurs and some other isolated taxa have a strong postnarial process that restricts entry of the maxilla into the margin of the narial opening. The score should therefore be 0&1

16: 1 to 0&1. Jugal extending no further than mid-cheek (0) or nearly to posterior end of skull. This is a variable character. First there is no differentiation as to whether the dorsal or ventral part of the jugal is involved — or both. The ventral ramus of the jugal does not extend posteriorly in *Pleurosaurus*, and there is no ventral ramus in *Priosphenodon*. The jugal is more extensive dorsally in these taxa, but this is not the same character.

57: 1 to 0&1 Supraglenoid buttress present (0) or absent (1) on scapulocoracoid. There is a buttress at least in *Gephyrosaurus* so it should be 0&1

100: 1 to 0&1.Teeth present (0) or absent (1) on palatine ramus of pterygoid. Primitive rhynchocephalians (*Gephyrosaurus*, *Diphydontosaurus*, *Planocephalosaurus* etc.) have teeth on the palatine ramus of the pterygoid. The coding should therefore be 0&1

105: 0 to 0&1. Second sacral rib not bifurcate (0) or bifurcate (1). It is slightly flanged rather than bifurcate in *Gephyrosaurus*, and it is not bifurcate in *Sphenodon*.

131: 1 to 0&1. Postorbital terminates prior to reaching posterior limit of parietal (0) or extends at least to posterior limit of parietal. This is presumably a mistake since even in *Sphenodon* it terminates anteriorly.

137: ? to 0&1. Floor of braincase with gap between basioccipital and basisphenoid (0) or elements fused to floor of brain cavity. Both conditions exist in rhynchocephalians, the primitive state in *Gephyrosaurus*, the derived one in *Sphenodon*.

144: ? to 1. Atlantal ribs are ossified (0) or not (1). They are not ossified.

161: 0&1 to 0. Medial wall of inner ear is unossified (0) or ossified (1). It is not ossified in any known rhynchocephalian.

182: 1 to 1&0. Lacrimal enters orbital margin (0) or remains excluded by prefrontal-maxillary contact. In *Gephyrosaurus* a very small lacrimal enters the orbital rim (0).

10/184 — 5.4%

Squamata

93: 1 to 0&1. Contact between ectopterygoid and jugal; restricted, equal or less than contact of pterygoid and ectopterygoid (0) or expanded caudally (1). Both states occur in squamates.

96: 1 to 0&1. Basipterygoid processes oriented anterolaterally (0) or laterally (1). The angle of the processes differs and in some (*e.g.*, *Uromastyx*) they are certainly anterolateral.

113: 1 to 0&1. Dorsal margin of ilium without (0) or with an anterior process (1). This feature varies in squamates according to locomotor style, *e.g.*, *Heloderma*, many anguids and some scincids lack the process.

115: 0 to 0&1. Supratemporal stout and short (0) or long and slender projecting far anteriorly (1). In varanoid lizards, a long supratemporal extends anteriorly along the margin of the parietal.

131: 1 to 0. Postorbital terminates prior to reaching posterior limit of parietal (0) or extends at least to posterior limit of parietal. As with rhynchocephalians, this is presumably a mistake, or poorly explained. The postorbital only rarely reaches back that far posteriorly.

137: 0 to 1. Floor of braincase with gap between basioccipital and basisphenoid (0) or elements fused to floor of brain cavity. This is perhaps poorly explained, because the basioccipital and basisphenoid meet in squamates to floor the brain cavity.

146: 1 to 0&1: Humeral distal articulations, distinct trochlea and capitellum (0) or low double condyle (1). At least some lizards seem to have a pronounced trochlea and capitellum.

161: 1 to 0&1. Medial wall of middle ear is unossified (0) or ossified (1). Squamates do generally have the derived condition, but an opening in the medial wall is found in some taxa where the lateral opening of the recessus scala tympani is reduced.

166: 1 to 0&1. Lateral shelf on the surangular is absent (0) or present (1). This is variable in squamates.

9/184 — 5%

A LONG-NECKED ARCHOSAUROMORPH FROM THE EARLY TRIASSIC OF POLAND

MAGDALENA BORSUK-BIAŁYNICKA and SUSAN E. EVANS

Borsuk-Białynicka, M. and Evans, S.E. 2009. A long-necked archosauromorph from the Early Triassic of Poland. *Palaeontologia Polonica* **65**, 203–234.

Czatkowiella harae gen. et sp. n. from the Early Triassic (earliest Late Olenekian) locality of Czatkowice 1, near Kraków, Poland, is characterised by a long slender neck, three headed ribs on some anterior dorsal vertebrae, and short broad neural spine tips in the dorsal vertebral series. Cladistic analysis suggests a relationship between *Czatkowiella* and the Late Permian long-necked reptile *Protorosaurus*, but fails to support a monophyletic Prolacertiformes. *Czatkowiella* and *Protorosaurus* do not group with either *Prolacerta* or the *Tanystropheus*/ *Macrocnemus* clade of other workers, and fall at the very base of Archosauromorpha. Thus the long-necked morphology of many archosauromorph taxa should be regarded as a primitive state within this group, reversed in some daughter lineages such as rhynchosaurs and trilophosaurs.

Key words: Archosauromorpha, Reptile, *Protorosaurus*, Early Triassic, Poland, microvertebrates.

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INTRODUCTION

A small diapsid reptile *Czatkowiella harae* gen. et sp. n. is here described from the Early Triassic fissure deposits of southern Poland (Czatkowice 1 near Kraków; Paszkowski and Wieczorek 1982). It is a basal archosauromorph with a general similarity to a group of taxa once referred to as prolacertiforms. When the Early Triassic diapsid *Prolacerta* was first reported from South Africa (Parrington 1935), it was classified as a "thecodont". Despite this, it was heralded as a lizard ancestor because of ventrally open lower temporal fenestra, although the long neck was unusual (Camp 1945). Its position remained controversial until Gow (1975) gave the first account of the postcranial skeleton. This information made it clear that *Prolacerta* was closer to archosaurs than to lizards. In his review, Gow linked *Prolacerta* to other genera, most notably the European Mid Triassic *Tanystropheus* and *Macrocnemus*. Over the next decades a broad series of other "prolacertiform" taxa were added: the Late Permian *Protorosaurus* (Britain and Germany; Seeley 1888) and *Eorasaurus* (Russia; Sennikov 1997); the Early Triassic *Boreopricea* and *Microcnemus* (Russia; Tatarinov 1978; Benton and Allen 1997; Huene 1940), *Prolacertoides* (China; Yang 1973) and *Vritramimosaurus* (Russia; Sennikov 2005); the Early to Mid Triassic *Jesairosaurus* (Morocco; Jalil 1997); the Mid Triassic *Rhombopholis* (Britain; Benton and Walker 1997), *Malutinisuchus* (Russia; Otschev 1986), *Pamelaria* (India; Sen 2003), and *Cosesaurus* (Spain; Sanz and Lopez-Martinez 1984); the Mid–Late Triassic *Malerisaurus* (India and North America; Chatterjee 1980, 1986); the Late Triassic *Langobardisaurus* (Italy; Renesto 1994); and the Early Jurassic *Tanytrachelos* (North America; Olson 1979). The Early Triassic *Kadimarkara* (Australia, Bartholomai 1979) is actually a misinterpreted, and poorly preserved, specimen of *Prolacerta*, extending the pan-Gondwanan range of this genus from South Africa (Gow 1975) and Antarctica (Colbert 1987) to Australia.

As traditionally diagnosed, "prolacertiforms" form a large, impressive pan-Pangaean assemblage, combining archosauromorph features (subthecodont teeth, presence of a posterolateral premaxillary process excluding or nearly excluding the maxilla from the narial margin, well developed transverse processes on dorsal vertebrae) with a characteristically long neck (elongation of individual vertebrae), dichocephalous cervical vertebrae in which the rib heads are small and lie close together on the anterior margin of the centrum, and a ventrally open lower temporal fenestra (*e.g.*, Benton 1985; Gauthier 1984; Evans 1987, 1988). However, there are problems. Many of the above named taxa (with the exception of *Macrocnemus*, *Tanystropheus*, *Prolacerta*, and *Protorosaurus*) are fragmentary and poorly known. In addition, recent cladistic analyses (*e.g.*, Dilkes 1998; Müller 2004) have rejected the monophyly of Prolacertiformes (see also Discussion). Although some subsets of taxa may be related to one another (*e.g.*, *Langobardisaurus*, *Macrocnemus*, *Tanystropheus*, *Tanytrachelos*), "prolacertiform" is essentially a gradal concept, with some taxa (notably *Prolacerta*) being closer to Archosauriformes than others (*e.g.*, tanystropheids) (*e.g.*, Dilkes 1998). Dilkes (1998) places the aberrant arboreal *Drepanosaurus* and *Megalancosaurus*, from the Late Triassic of Italy, in a clade with the main "prolacertiform" taxa (*Tanystropheus*, *Tanytrachelos*, *Macrocnemus*), but excludes *Prolacerta* itself.

Apart from *Czatkowiella*, the Czatkowice 1 assemblage includes a basal archosauriform *Osmolskina czatkowicensis* (Borsuk-Białynicka and Evans 2003, 2009) of *Euparkeria* size, procolophons (Borsuk-Białynicka and Lubka 2009), a kuehneosaurid (Evans 2009), a small lepidosauromorph reptile (Evans and Borsuk-Białynicka 2009b), a prefrog *Czatkobatrachus polonicus* of *Triadobatrachus* grade (Evans and Borsuk-Białynicka 1998, 2009a; Borsuk-Białynicka and Evans 2002), and some small temnospondyls (Szyszkin and Sulej 2009), and fish (Borsuk-Białynicka *et al.* 2003).

The objective of the present paper is to give an account of the morphology of those bones that may be confidently referred to *Czatkowiella harae*. The chemical preparation of the Czatkowice 1 breccia is finished. The material is housed in the Institute of Paleobiology, Polish Academy of Sciences.

Institutional abbreviations. — BPI, Bernard Price Institute for Palaeontological Research, University of Witwatersrand, Johannesburg, South Africa; PIN Institute of Paleontology, Russian Academy of Sciences, Moscow, Russia; ZPAL Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Acknowledgements. — We are indebted to Mariusz Paszkowski and Józef Wieczorek (Jagiellonian University, Kraków), who discovered the Czatkowice 1 breccia and offered it for study, and to the late Halszka Osmólska and Teresa Maryańska (Polish Academy of Sciences, Warsaw) who kindly transmitted the material to us. Thanks are also due to the referees for their helpful criticism, and particularly, to David Dilkes (University of Wisconsin) who did a major editorial work upon our manuscript. The following staff members of the Institute of Paleobiology, Polish Academy of Sciences in Warsaw helped us during our studies: Ewa Hara prepared the material, Cyprian Kulicki took SEM microphotographs, Marian Dziewiński photographs, Aleksandra Hołda-Michalska prepared most of the computer illustrations. We are grateful to colleagues from the Institute for their help in solving computer editorial problems, as well as Jane Pendjiky (UCL) for preparing computer Figs 14 and 15. We also thank Annalise Gottmann (Bonn) for advance information on *Protorosaurus*.

GEOLOGICAL SETTING

Discovered in 1978, the bone breccia of Czatkowice 1 was briefly studied by a team from the Institute of Geology of the Jagiellonian University in Kraków (Poland), and the geological setting was described (Paszkowski and Wieczorek 1982). More exact data concerning the geology is included in this volume (Paszkowski 2009). The material from the fissure exposure Czatkowice 1, described herein, has been dated as most probably Early Olenekian (Borsuk-Białynicka *et al.* 2003) in age, but has turned to come most probably from the earliest Late Olenekian (Shishkin and Sulej 2009). The deposition of the material of Czatkowice 1 probably occurred in a freshwater oasis within the arid circumequatorial belt of Northern Pangea.

MATERIAL AND METHODS

The description that follows is based on isolated and fragmentary bones extracted from a microvertebrate-bearing deposit containing the remains of at least four other small reptiles. Of these, *Czatkowiella* is overlapped by the archosauriform *Osmolskina* (Borsuk-Białynicka and Evans 2003) in the upper end of its size range, by *Pamelina* (Evans 2009) in the middle part of its range, and by *Sophineta* (Evans and Borsuk-Bialynicka 2009b) at the extreme lower end. This presents something of a challenge in terms of attributing elements, particularly with *Osmolskina* which is the more closely related taxon. For the smaller diapsids, we have used a combination of fit for individual elements and the general rule that if a bone of the same morphology occurs through a wide size range it is more likely to be *Czatkowiella*, since there is little variation in jaw size for the two small lepidosauromorphs. The structure of the dentition (using scanning electron microscopy) permits association of tooth-bearing elements, the maxilla then forming a template around which to fit other skull bones.

SYSTEMATIC PALEONTOLOGY

Subclass **Diapsida** Osborn, 1903

Clade Archosauromorpha Huene, 1946

Family uncertain

Genus ***Czatkowiella*** gen. n.

Type and only species: *Czatkowiella harae*.

Derivation of name: From the name of the type locality, Czatkowice 1 in southern Poland.

Diagnosis. — As for type and only species.

Czatkowiella harae sp. n.

Derivation of name: The species name reflects our gratitude to Ewa Hara, Institute of Palaeontology, Warsaw, who has been responsible for most of the preparation of Czatkowice 1 remains.

Type specimen: ZPAL R.V/100, a right maxilla with almost complete tooth row.

Type locality and horizon: Czatkowice quarry, Kraków, Poland. Fissure/cave infill dated as earliest Late Olenekian (Shishkin and Sulej 2009).

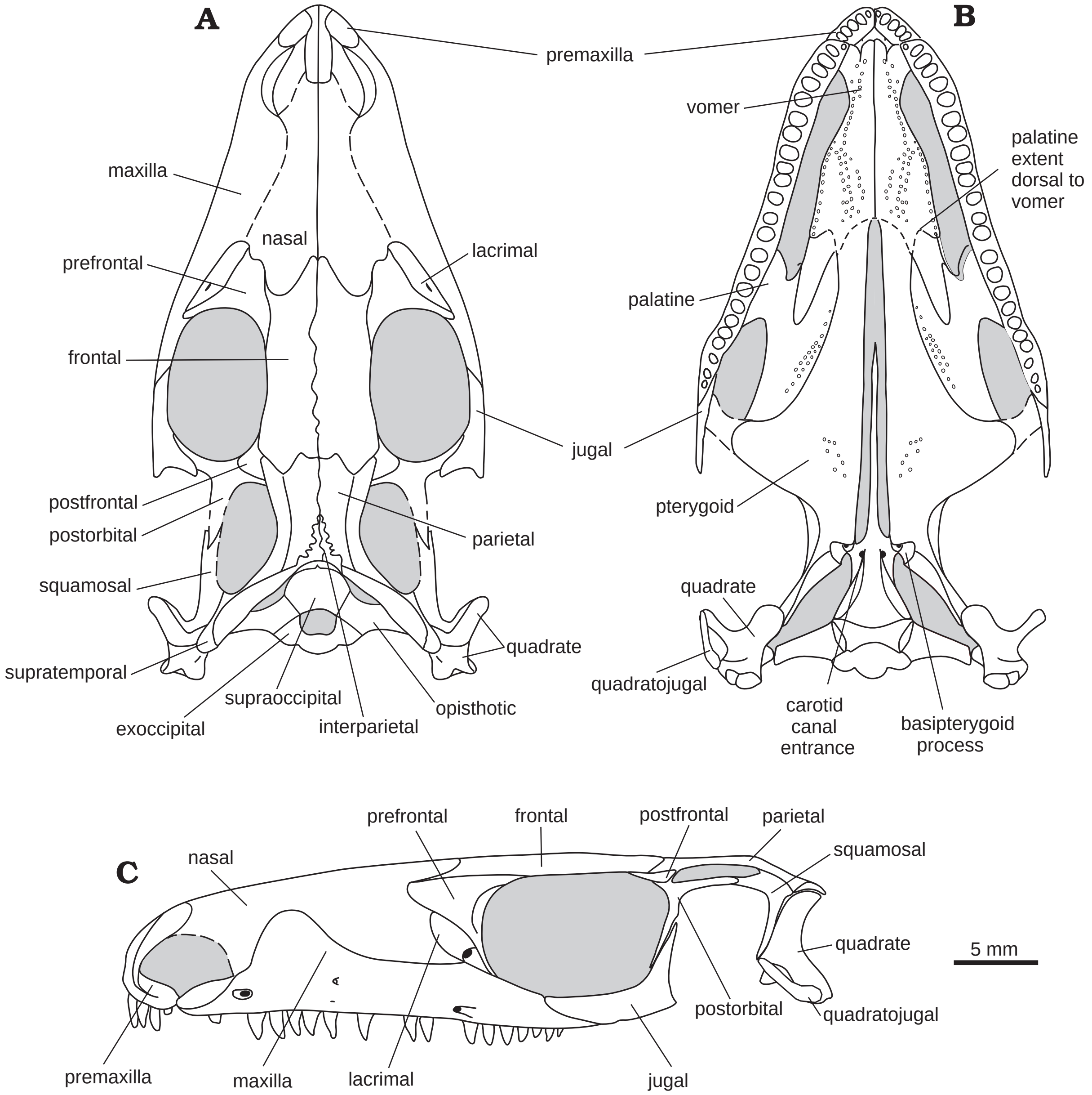


Fig. 1. *Czatkowiella harae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Reconstruction of the skull, in dorsal (A), ventral (B), and lateral (C) views.

Diagnosis. — *Czatkowiella* resembles early archosauromorphs (notably those traditionally grouped as "prolacertiforms"), and differs from lepidosauromorphs in having strongly elongated cervical vertebrae with long low neural spines and slender horizontally placed cervical ribs with an anterior process; it resembles the Late Triassic gliding kuehneosaurs and some archosauriforms, and differs from all described "prolacertiforms", in having three-headed ribs on some anterior trunk vertebrae, but differs from kuehneosaurs in that these ribs do not attach to the ends of elongated transverse processes; resembles *Rhombopholis* (Benton and Walker 1997) in having expanded spines on the dorsal vertebrae, but differs in the other vertebral characters noted above; resembles the Late Permian *Protorosaurus* in combining long cervical vertebrae and slender horizontal cervical ribs with a primitive premaxilla lacking a posterolateral process, but differs in having a biradiate postorbital bone, paired parietals without a median crest, and cervical vertebrae that are proportionally longer in relation to their height, in the possession of some three-headed ribs, in having short dorsal vertebrae with a greater development of a spine table, and in lacking the bifid caudal neural spines that characterise all specimens of the Late Permian genus (SEE personal observation). In its combination of characters, *Czatkowiella* is unique and justifies distinct generic status.

Dimensions. — As reconstructed in Fig. 1 on the basis of most frequent bones, the skull of *Czatkowiella harae* was about 40 mm in length (on average), and is thus much shorter than that of *Prolacerta broomi* B.P.I. 2675 (about 70 mm) as illustrated by Gow (1975, fig.12). However, the presence of very small (Fig. 3F) and very large (Figs 3E, 4F) maxillae demonstrates a range of variability that we consider to be intraspecific.

DERMAL SKULL ROOF BONES

Premaxilla. — There are many specimens of this bone, the best being ZPAL R/5 and 111 (Figs 2A, C, 4C, E), which are complete except for the end of the nasal process. The premaxilla has a dorsally convex oval body, bearing 3–5 tooth positions. The posterior margin of the premaxillary body is rounded, and the lateral surface bears no trace of a maxillary overlap facet. The connection between the premaxilla and maxilla was apparently weak and perhaps ligamentous (see below, maxilla). Thus almost the only bony attachment of the premaxilla to the skull is the weak joint with the nasal. The nasal process is a long, slim arcuate band of bone that rises first vertically and then runs back horizontally. This horizontal portion bears a slender ventral facet for the nasal. The nasal process is anteroposteriorly flattened with only a narrow medial edge for articulation with the contralateral bone (Figs $2A_2$, C, 4E). The alveolar portion of the bone lacks any development of a palatal process. Assuming the two nasal processes lie side by side anteriorly, the bodies of the two premaxillae must have lain at an angle to one another (Fig. 2C), leaving a triangular posterior space to receive the vomers. The dorsal surface of the premaxillary body contributed to the floor of the external nares.

Maxilla. — This is represented by numerous fragments of differing individual size and age. The best preserved specimen, ZPAL R.V/100 (Figs 2A, $3C_2$, C_3, $4A_1$), has an almost complete alveolar margin, including the anterior tip, but lacks the dorsal facial process. The posterior end is also missing but this may be reconstructed from a juvenile specimen (ZPAL R.V/471; Fig. 3F) that is complete posteriorly. This bone has 13 tooth positions posterior to the palatine foramen, instead of the seven present in the holotype. On this basis, the total tooth count is about 26–28. The teeth are weakly pleurodont (under the definition that the labial wall is higher than the lingual wall as seen in lingual aspect) and show a simple alternating pattern of tooth replacement, the replacement teeth eroding the base of the existing tooth from the medial side. The replacement slowed down or ceased in old individuals (Figs 3E, 4F).

The facial process may be partly reconstructed on the basis of specimen ZPAL V/101 (Fig. 3B), but its posterior border is damaged. The specimen shows the lateral surface to be convex, and the medial one correspondingly concave in section. A flat dorsomedial concavity on the facial process probably received the nasal (Figs $2A_2$, $3C_3$). The outline and extent of this facet are unclear. The maxilla contributed to at least the posteroventral margin of the large external naris with a long narrow premaxillary process. This process is in-turned medially, and triangular in transverse section. Its end probably abutted the premaxilla in a joint that was held by ligaments. The dorsolateral surface of the premaxillary process bears an oval, ridged area separated from the medial surface by a distinct crest. This ridged area may have served as an attachment point for ligaments holding the bones together. The medial surface of the premaxillary process bears a horizontal, longitudinal furrow (Fig. $2A_2$) that probably accommodated the vomer.

Along the anterior two-thirds of the bone, the alveolar margin is medially swollen to make the dental furrow deeply concave (Fig. $3C_3$). In the posterior one third, the margin becomes dorso-ventrally flattened into a supra-alveolar shelf that bears facets and neurovascular furrows and foramina. The largest of these foramina is the palatine foramen, situated on the dorsomedial surface of the maxilla roughly one third of the distance from the posterior tip of the specimen ZPAL RV/100. In modern lizards and *Sphenodon*, this foramen opens into the superior alveolar canal and gives passage to the maxillary artery and vein, and the maxillary branch of the trigeminal nerve (CV5ii). These structures presumably ran forward in a conspicuous furrow that extends along the posteromedial part of the supra-alveolar shelf, in the angle between it and the facial process. From there, they would have passed *via* the infraorbital foramen (palatine and maxilla combined, see below) to enter the palatine foramen and the superior alveolar canal. Small neurovascular branches then passed to the teeth, to the soft tissues of the mouth (perhaps *via* a small oblique groove running anteroventrad from the palatine foramen), and to the external surface of the upper jaw (*via* the small lateral maxillary foramina). The superior alveolar canal exits *via* a slightly larger foramen (Fig. $2A_1$) on the lateral side of the premaxillary process.

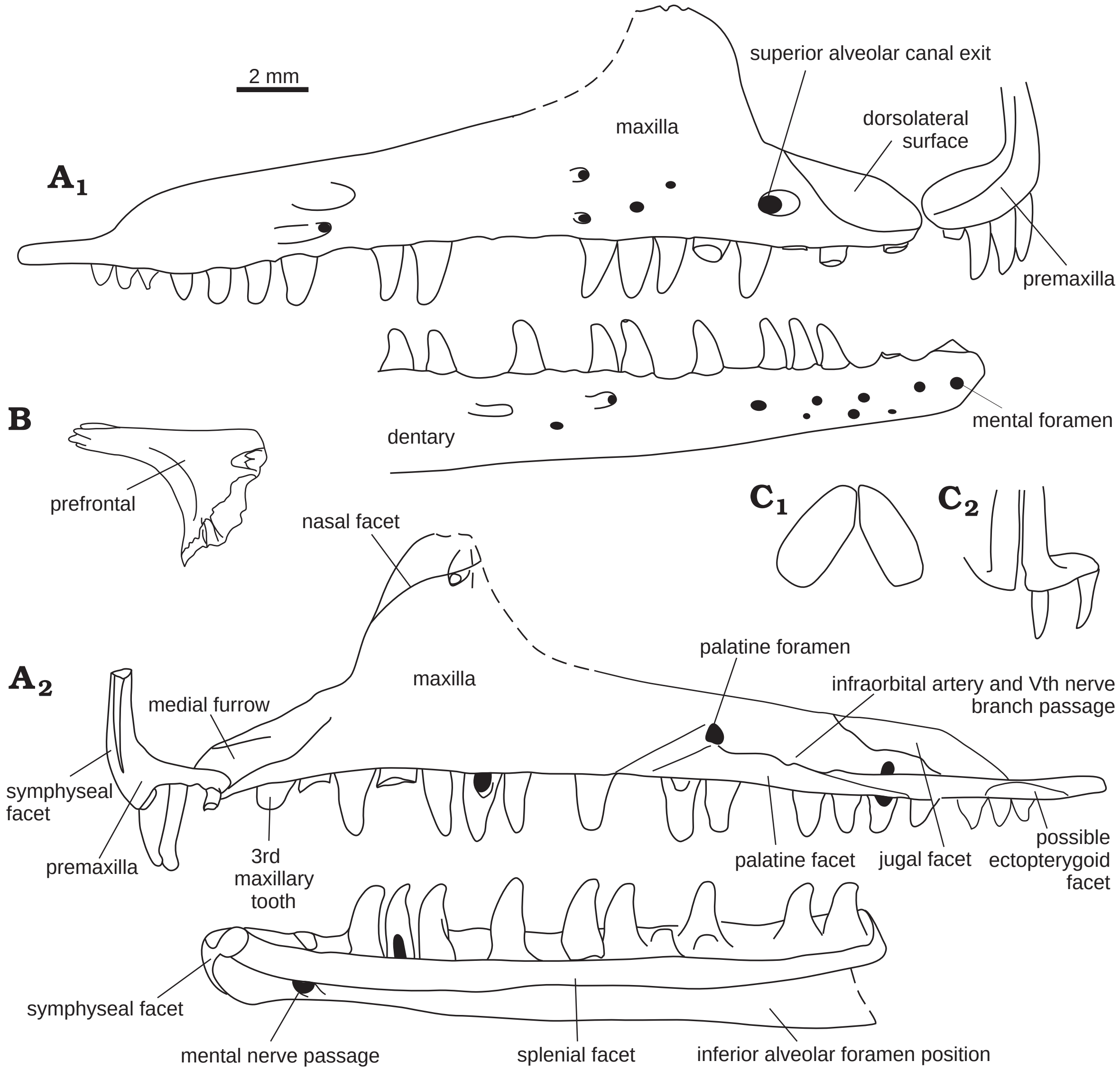


Fig. 2. *Czatkowiella harae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Reconstruction of the jaws based on ZPAL RV/5, 100, 101, 102, 471, in labial (A_1) and lingual (A_2) views. **B**. Left prefrontal, ZPAL RV/466 reversed, in lateral view. **C**. Praemaxillae, the outline of articulated bones, in ventral view (C_1) and anterior view of the articulated bones (C_2).

Below the palatine foramen, the medial border of the supra-alveolar shelf bears a shallow triangular palatine facet (Figs $2A_2$, $3C_3$). This extends between the 13th and 18th tooth position and tapers posteriad. The ectopterygoid position may not be determined from the posteromedial border of the juvenile specimen ZPAL RV/471, and is conjectural (Figs 1B, $2A_2$). The posterior process of the maxilla is low and of relatively constant height, but narrows abruptly in the posterior one sixth of its length. In this region, the medial surface of the lateral blade of the maxilla bears a furrow-like facet for the jugal (Fig. $2A_2$). This facet is rather short which suggests a significant contribution of the maxilla to the orbital border.

Frontal. — Several frontal types have been recognised amongst the Czatkowice 1 bones. They are all relatively similar, in being paired with only light sculpture, and differ mainly in the shape and size of the various facets for adjacent bones. Only one type, however, shows a range of sizes (*e.g.*, ZPAL RV/340–344, 480) within the single morphology and these elements are tentatively referred to *Czatkowiella*.

Each frontal (Fig. 5D, E, I) is relatively robust with the dorsal surface perforated by numerous vascular foramina. A sinuous midline suture, in which the contralateral frontals alternate in overlapping and underlapping one another (Fig. $5I_2$), with strong facets, demonstrates that the joint was strong. The prefrontal and postfrontal facets are separated by deep vascular foramina (Fig. $5A_2$). In dorsal view, the prefrontal facet is

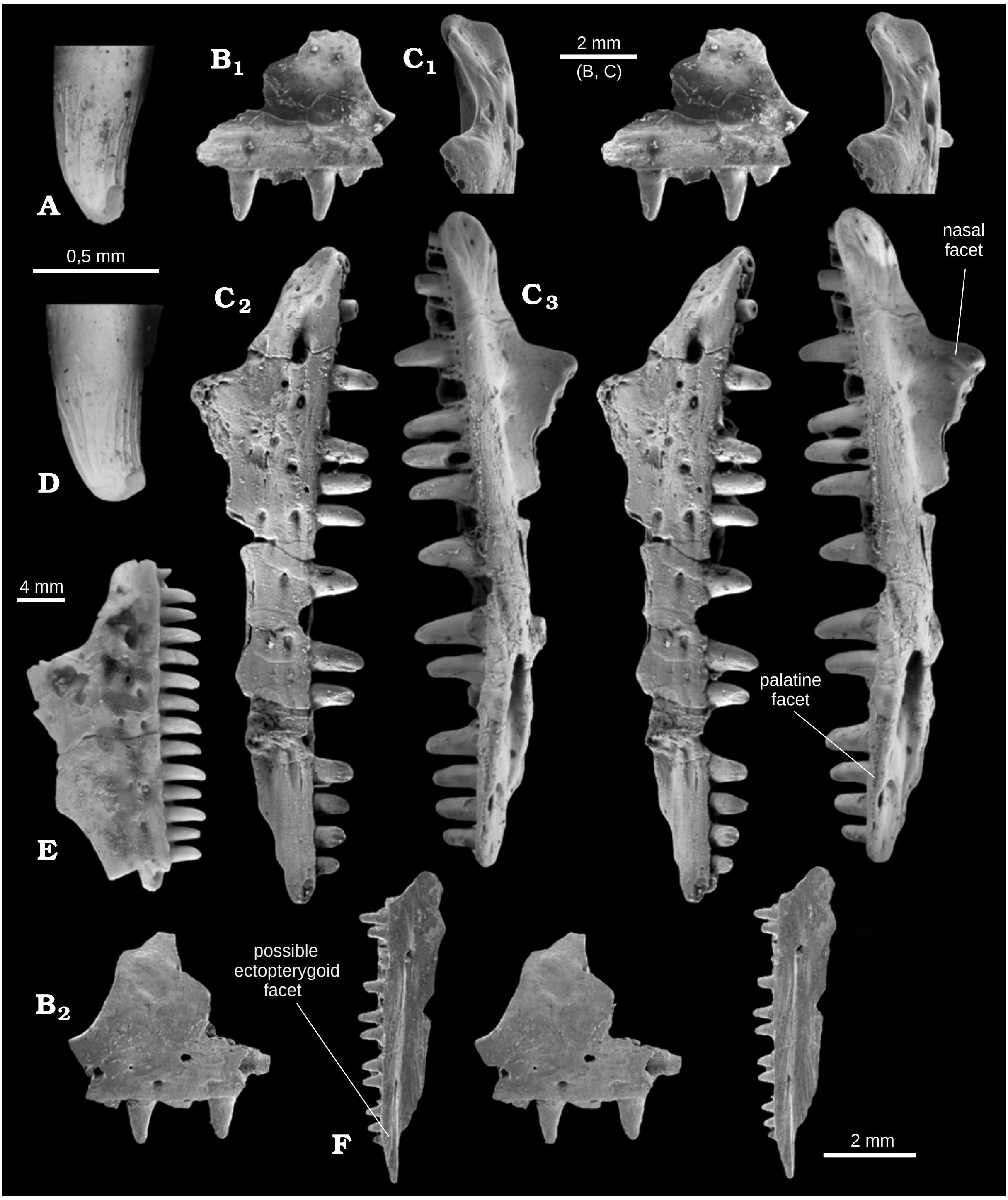


Fig. 3. *Czatkowiella harae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**, **D**. Two premaxillary teeth ZPAL RV/5, in lingual view. **B**. A fragment of left maxilla ZPAL RV/101, in lingual (B_1) and labial (B_2) views. **C**. Anterior part of right maxilla ZPAL RV/100, in dorsal (C_1, anterior fragment), labial (C_2), and lingual (C_3) views. **E**. A fragment of an old adult specimen of maxilla ZPAL RV/1126, in labial view. **F**. Posteriormost part of right maxilla of small individual ZPAL RV/471, in lingual view. SEM micrographs; all but A, D, E stereo-pairs.

visible only as a narrow slot facet winding around the anterolateral margin of the bone although it comes onto the dorsal surface anteriorly where it grades into the nasal facet (Fig. 5D, E_2).

In ventral view, a relatively wide central part of the bone is divided into a deeper anterior concavity for the olfactory bulbs and a shallower, longer posterior surface which roofs the olfactory tracts as they pass forward to the nose. The central concavities are bordered by low sharp subolfactory crests (*cristae cranii*). About the

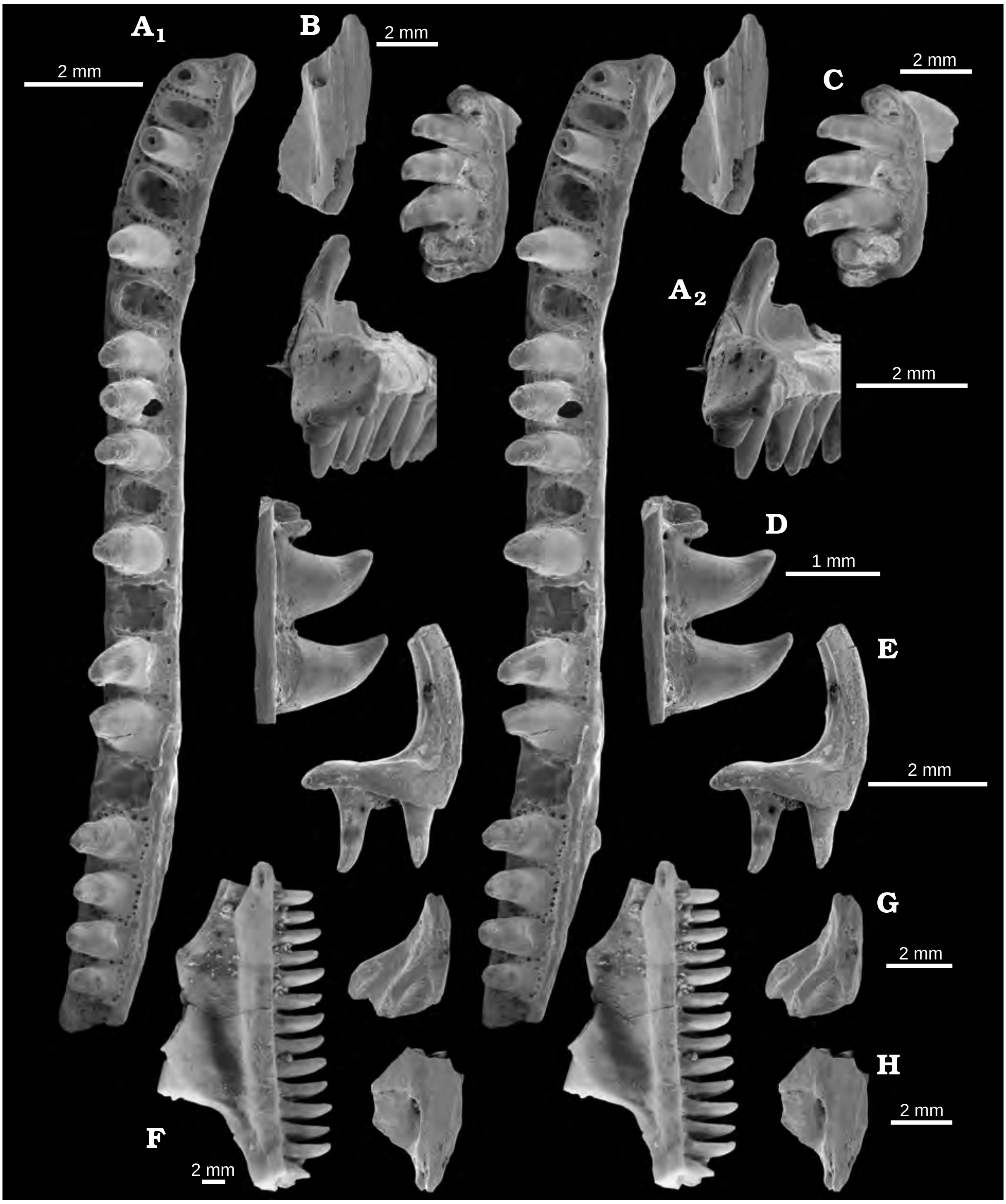
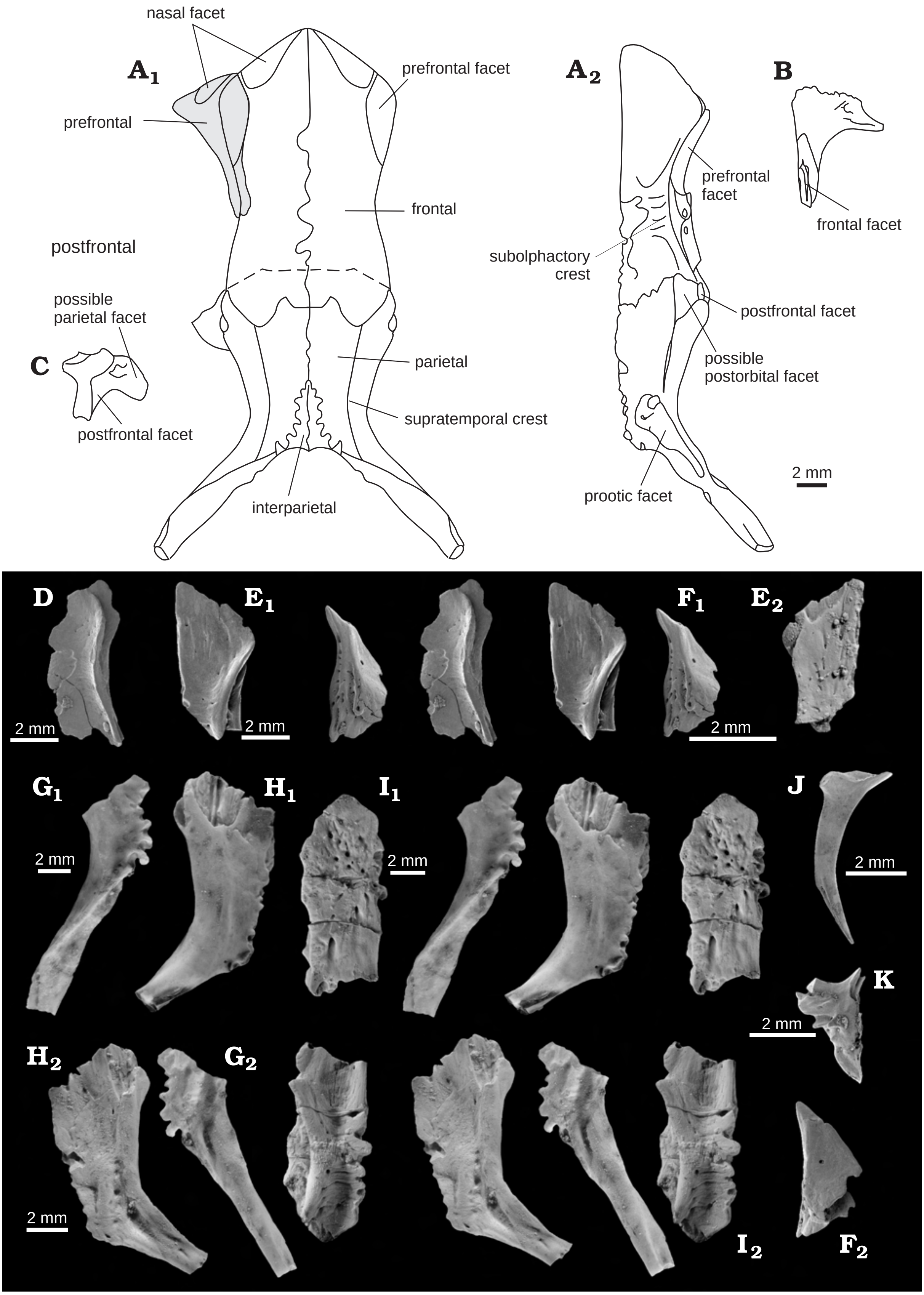


Fig. 4. *Czatkowiella harae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Maxilla ZPAL RV/100, in occlusal (A_1) and anterior (A_2) views. **B**. Anterior part of right lacrimal ZPAL RV/224, in medial view. **C**. Premaxilla ZPAL RV/5, in ventral view. **D**. Posterior maxillary teeth ZPAL RV/1119, in lingual view. **E**. Premaxilla ZPAL RV/111, in medial view. **F**. Maxilla fragment of old adult specimen ZPAL RV/1126, in lingual view. **G**. Supratemporal ZPAL R.V/1076. **H**. Posterior part of the right lacrimal ZPAL RV/225, in lateral view. SEM stereo-pairs.

Fig. 5. *Czatkowiella harae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Reconstruction of a partial skull roof, in dorsal view (A_1) and ventral view of the left part of the same (A_2). **B**. Left prefrontal in medioventral view with the anterior part damaged. **C**. Postorbital, in direct dorsal view. **D**. Central part of the left frontal ZPAL RV/994, in ventral view. **E**. Anterior part of the left frontal ZPAL RV/995, in ventral (E_1) and dorsal (E_2) views. **F**. Right postfrontal ZPAL RV/1075, in ventral (F_1) and dorsal (F_2) views. **G**. Posterior part of the left parietal ZPAL RV/820, in dorsal (G_1) and ventral (G_2) views. **H**. Left parietal ZPAL →



RV/724, in dorsal (H_1) and ventral (H_2) views. **I**. Central part of the right frontal ZPAL RV/342, in dorsal (I_1) and ventral (I_2) views. **J**. Left postorbital ZPAL RV/1072, in medial view. **K**. Left interparietal ZPAL RV/1065, in ventral view. All but A–C SEM micrographs; all but E_2, F_2, J, K stereo-pairs.

mid-length of the bone the crests lie at roughly one quarter of the frontal width from the orbital margin, and slope very steeply toward the orbit (Fig. 5D, I_2). There is variation in this feature, as shown by specimens ZPAL RV/994 and 995, and the frontal table may have extended further over the orbit with age as the olfactory crests became thicker (Fig. 5D, E_1, I_2). The crests diverge anteriorly and posteriorly. Anteriorly, they bear complex prefrontal facets. Posteriorly, each postfrontal facet is subdivided into two concavities, the anterior one almost touching the prefrontal facet. Medial to the rear of the subolfactory crest is a parietal facet. It extends across towards the midline and shows that the frontoparietal overlap was extensive.

Parietal. — As with the frontal, there are several diapsid parietal types at Czatkowice 1. Of these, only one type fits the morphology of the designated frontal, reaches a corresponding adult size to other bones attributed to this taxon, and comes in a range of sizes. It is represented by specimens ZPAL RV/373, 367, 444, 724, and 820, the most complete of these being the latter two (Fig. 5G, H). ZPAL RV/724 is a nearly complete left bone missing only the distal end of the postparietal process; ZPAL RV/820 is another left bone preserving the rear end of the skull table and an almost complete postparietal process. The description that follows is based on these two specimens.

The parietals are paired. Each bone is elongate, with a long skull table and a long posterolaterally directed postparietal process. The anterior margin bears a rugose dorsal facet for the frontal (the total suture being W-shaped) and a smaller lateral slot facet for the postfrontal (Fig. 5H). On the ventral surface, there is another frontal facet (suggesting the two bones slotted firmly into one another) and a shallower facet, possibly for the postorbital. The anterior margin of the parietal is wider than the rest of the bone but there is no marked anterolateral parietal wing. The parietal plate is rather flattened, with the lateral adductor shelf lying at only a shallow angle to the dorsal surface. The concave lateral edge formed the margin of the upper temporal fenestra, with the greatest embayment towards the rear end of the bone — just anterior to the origin of the postparietal process. Medially, the interparietal suture is slightly sinuous anteriorly and then becomes more interdigitated posteriorly (Fig. 5G, H). There is no parietal foramen. In ZPAL RV/724, the medial border is straight from front to back, but in smaller specimens, including ZPAL RV/444 and 820, the borders diverge leaving a triangular gap in the back of the bone (Fig. $5A_1$). This is particularly striking in ZPAL RV/820, where edge is strongly interdigitated both medially and then for a short distance posteriorly. This gap accommodates a pair of postparietal/interparietal elements (see below), but in more mature specimens (*e.g.*, ZPAL RV/724), the postparietal has become fully incorporated into the body of the bone. The postparietal process is long, running out almost horizontally from the parietal plate but at an angle of about 45°. From proximal to distal, the orientation of the process changes from horizontal to vertical, with the dorsal plate tapering sharply and the development of a ventrolateral flange. At the tip of this is a vertical slot facet for the supratemporal.

Postparietal/interparietal. — ZPAL RV/1065 (Fig. 5K) is a right postparietal bone that fitted into the triangular cleft described above in the back of the parietal plate. The bone has a rough ventral surface and a smoother dorsal surface. The posterior edge is sharp and curved, the medial margin bears an extension of the interparietal suture, and the lateral edge bears deep digitations matching those of the parietal.

Prefrontal. — Several types of small prefrontal have been recovered, differing in the length and robusticity of the orbital process and the size and position of facets for surrounding bones. The commonest and morphologically most consistent type of prefrontal, exemplified by specimens ZPAL RV/410 and 466 (Figs $5A_1$, 6B, F), is found in a range of sizes. It has a frontal process and frontal facet that most closely fits the frontal type referred to *Czatkowiella*.

The bone is strongly curved with a long, relatively slender orbital (frontal) process and a broad, medially concave body that contributes to the lateral wall of the nasal chamber. The frontal process tapers posteriorly. On its medial surface (Fig. 6F) it bears a complex interlocking facet that wrapped around the anterolateral margin of the frontal. Anteromedially, this process expands horizontally into a facetted flange that could have supported the posterolateral part of the nasal. Whether the prefrontal met the maxilla anterodorsally is not known as this very thin region of the bone is generally broken. The remainder of the bone then curves anteroventrally to form the anterior margin of the orbit. The orbital flange is narrow and tapers at its tip into a relatively narrow curved process that met the palatine, but probably was not strongly sutured to it (if at all). The flange supports a broad facial region with a large anterolateral facet that is in two parts with a slight step between them. This large double facet is for the lacrimal (Fig. $6B_1$).

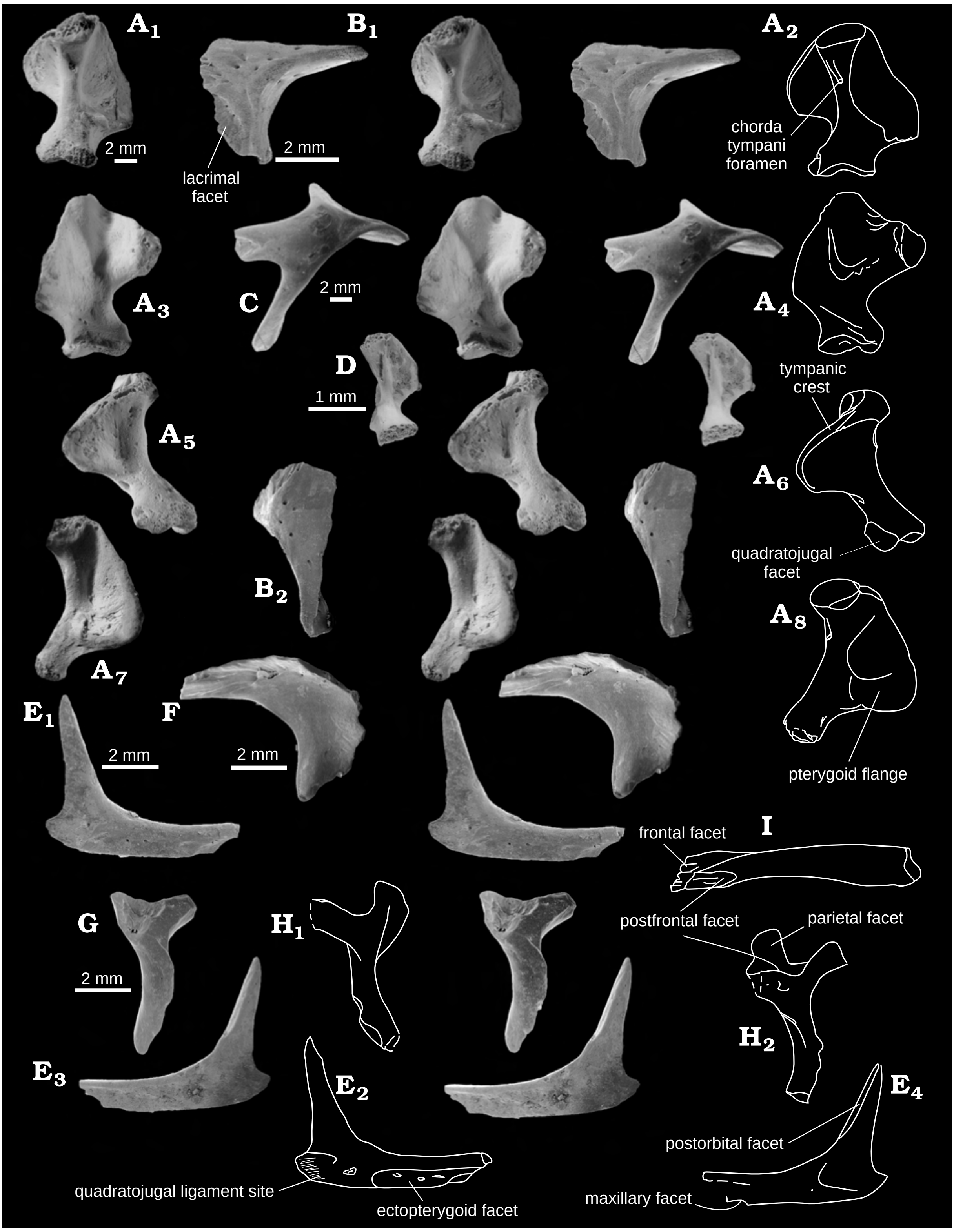


Fig. 6. *Czatkowiella harae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Left quadrate ZPAL RV/375, in posterior (A_1, A_2) anterior (A_3, A_4), lateral (A_5, A_6), and medial (A_7, A_8) views. **B**. Left prefrontal ZPAL RV/466, in lateral (B_1) and dorsal (B_2) views. **C**. Left squamosal ZPAL RV/27 possibly belonging to *Czatkowiella harae*, in lateral view. **D**. Small left quadrate ZPAL RV/192, in posterior view. **E**. Left jugal ZPAL RV/113, in medial (E_1, E_2) and lateral (E_3, E_4) views. **F**. Left prefrontal ZPAL RV/410, in medial view. **G**. Left postorbital ZPAL RV/284, in lateral view. **H**. Left postorbital ZPAL RV/355, in medial (H_1) and lateral (H_2) views. **I**. Parietal ZPAL RV/724, in left side view. All but A_2, A_4, A_6, A_8, E_2, E_4, H_1, H_2, I SEM stereo-pairs.

Lacrimal. — The lacrimal of *Czatkowiella* is represented by several specimens (*e.g.*, ZPAL RV/1051, 1052; Fig. 4B, H respectively) attributed on the basis of size (too large to belong to the smaller diapsids) and fit. The lacrimal has a double facet on its medial surface that closely fits the facet morphology on attributed prefrontals in size and orientation. The lacrimal is an elongate and roughly triangular bone with a straight ventral maxillary edge, a curved posterior margin that was excluded from the orbit by the prefrontal, and a bilobed dorsal edge that curved downward and forward to meet first the prefrontal and then the maxilla. The opening of the lacrimal canal is set well forward on the face (Fig. 4H), requiring the presence of a deep groove to carry the duct from the orbital margin to the foramen. From here, the duct canalises the bone and presumably opened from the apex to cross the inner surface of the maxilla, but this region is not preserved in any specimen.

Postfrontal and postorbital. — The postorbital specimens ZPAL RV/284, 355, 377, 508, 1071–1074, 1084 are attributed to *Czatkowiella* on the basis that they are, on average, smaller than those of *Osmolskina* (Borsuk-Białynicka and Evans 2009), and display a range of sizes. The bone is a distinctive element that is bi- rather than triradiate (Fig. 6G, H), with a long, curved jugal process and a long straight squamosal process. The postorbital completed almost the entire posterior orbital margin *via* the elongated jugal process. The squamosal process is long and slender, and has a facetted posterior tip that slotted into a facet on the lateral surface of the squamosal. The dorsomedial process of the postorbital is very short and inclined medially. It bears a deep concavity that accommodated a small postfrontal. The concavity is extended by a median tongue-shaped process that turns posteromedially, possibly to contact the parietal (Fig. 5A_2, C).

Only one incomplete postfrontal bone (ZPAL RV/1075,) has been identified. It must have straddled the frontoparietal suture. Its slender anteromedial end is mediodorsally and laterodorsally faceted (Fig. 5F_1) and was thus overlapped by the frontal. Only posteriorly, does the postfrontal bear a postorbital facet (Fig. 5F).

Jugal. — Jugals are usually rather common and easily recognised elements in microvertebrate deposits of this type, but relatively few non-archosaurian jugals have been recovered. Of these, most are very small and belong either to the small lepidosauromorph or to juveniles of other taxa. However, one subset is larger and flatter, with weak ectopterygoid facets (*e.g.*, ZPAL R V/113; Fig. 6E_2). These bones have a strap like ventral component and a dorsal process rising subvertically at only a slight angle to the main axis of the bone. This dorsal process bears a strip facet along its anterior margin for the postorbital. The main body extends posteriorly into a short, rounded posterior process, and anteriorly into longer anterior maxillary process that fitted into a groove on the dorsomedial surface of the maxilla. The posterior process bears no articular facet for the quadratojugal. Instead, it is roughened for the attachment of a quadratojugal ligament that was the only structure closing the lower temporal fenestra ventrally.

Squamosal. — The squamosal is another problematic bone. While archosaurian squamosals are abundant, very few small reptile squamosals have been identified. None of these has a size range that matches other elements of *Czatkowiella*. However, two morphs exist for the squamosal of *Osmolskina* (Borsuk-Białynicka and Evans 2009) one with a narrow body and long anteroventral ramus, and one with a thicker (dorsoventrally) body and a shorter more ventrally directed ramus. Both display the same quadriradiate type with a lozenge-shaped body, anteriorly faceted postorbital process, and a bifid parietal process with its posterior part (*i.e.*, posteromedial process of the squamosal) overhanging the quadrate head. It seems likely that one or other of these squamosal types pertains to *Czatkowiella*. The finer outline and more open angle between the posterior and ventral processes of the longer type match the anterodorsal border of the *Czatkowiella* quadrate better than that of *Osmolskina* which is anteriorly less extensive and is directed more vertically (Borsuk-Białynicka and Evans 2009). The longer squamosal type (Fig. 6C) is therefore provisionally attributed to *Czatkowiella*.

Supratemporal. — Whichever squamosal morphology is referred to *Czatkowiella*, the angle and shape of the posteromedial process is such that it would not have fitted into the slot at the tip of the postparietal process. This suggests the presence of an intervening supratemporal bone. ZPAL RV/1076 (Fig. 4G) is a partial supratemporal tentatively attributed to *Czatkowiella*. It comprises a small curved body bearing a concavity that accommodated the medial tip of the squamosal and a posterodorsal sheet of bone that maintained the posterior edge of the upper temporal fenestra. The medial facet for the parietal is not preserved.

Quadrate and quadratojugal. — The quadrate is strongly arched (Fig. 6A_5–A_8) Its contact with the squamosal is fairly long. The cephalic condyle and the mandibular condyle are connected by a strong posterior pillar. A small foramen for the chorda tympani perforates the posterior face of this pillar at about one third of the distance from the cephalic condyle (Fig. 6A_1, A_2). Both the pterygoid flange and tympanic crest diverge anteriorly from the pillar, so that the proximal half of the bone is very large and its anterior face is concave. The medial surface of the pterygoid flange bears a clear pterygoid facet (Fig. 6A_7, A_8). The ventral extremity of the quadrate projects laterally to contact the quadratojugal. Between it and the tympanic crest, the margin is deeply incised by a quadratojugal foramen. This was framed laterally by a reduced quadratojugal. A small oval quadratojugal facet lies on the ventrolateral margin of the quadrate (Fig. 6A_5, A_6), but the quadratojugal itself has not been recognized itself. Medial to this, the mandibular condyle bears an articular facet for the lower jaw. This articular facet extends onto the anterior surface of the bone. If this joint surface was horizontal in life, then the ventral half of the quadrate sloped posteriorly at an angle of about 45° (Fig. 1C). The lower margin of the pterygoid flange would then have extended subhorizontally (Fig. 6A_7, A_8) to contact the quadrate ramus of the pterygoid.

PALATAL COMPLEX

Vomer. — The vomer of *Czatkowiella* is attributed on the basis of size and fit between the anterior end and the maxilla. The anterior and middle parts of the bone are well represented (*e.g.*, ZPAL RV/159, 485, 518, 519, 753) but the posterior region is thin and tends to fragment. The anterior tip of the bone is bifid (Fig. 7F, L), the anterolateral lobe fitting into the posterior part of the medial furrow on the maxillary tip (Fig. 2A_2), and the anteromedial lobe directed forward, perhaps with a ligamentous attachment to the premaxilla. The medial edge of the bone is straight and bears a rugose sutural surface for the contralateral vomer (Fig. 7I_1), deep in the anterior quarter, very deep and forming a raised dorsal ridge in the second quarter, and shallower and grooved further posteriorly. The lateral edge is concave anteriorly (forming the narrowest part of the bone) and convex posteriorly as the bone widens out. The dorsal surface of the bone is guttered anteriorly between the raised medial and lateral edges, and then expands into a wider shallower concavity posteriorly (Fig. 7F, J). A small foramen consistently perforates the anterolateral edge in the second quarter of the bone (Fig. 7E, F), but it does not go through onto the palatal surface of the bone. It was probably for an emissary vein. In *Sphenodon* (O'Donaghue 1921), a large venous sinus occupies the dorsal concavity on the vomer and it is likely the same was true of *Czatkowiella*. The palatal surface of the vomer has a covering of small rounded denticles. A double row begins on the anteromedial edge (Fig. 7I_2, L), crossing the bone to the anterolateral edge and then running along this margin until the bone expands in its posterior half. At this point the rows divide, a single row continuing along the lateral margin with a double row extending into the central area. This double row continues backward and medially to the edge of the bone. In ZPAL RV/753, the dorsal surface bears facets for the palatine and pterygoid, although this thin region is not complete. The anterolateral tip of the palatine fitted into a slot facet on the dorsolateral edge of the vomer (Fig. 7F, J). Medially, at about the same level, the intervomerine suture thins abruptly creating a grooved shelf that accommodated the anterior tip of the pterygoid Fig. 7F, J).

Palatine. — The palatine of *Czatkowiella* is represented by numerous bones in a range of sizes. It is a large elongated sheet of bone bearing a strong lateral maxillary process. The maxillary process is separated from the main body of the bone by two U-shaped incisions, the anterior one corresponding to the choana, the posterior one to the suborbital fenestra. The process is perforated centrally by an infraorbital foramen that lay adjacent to the palatine foramen of the maxilla (see above). The dorsal surface (Fig. 7A_2, C) of the bone is subdivided into two parts separated from each other by a transverse step. The anterior part is relatively flat, while the posterior one is concave. The anterior part has a low surface that may have had a ligamentous connection to the orbital process of the prefrontal but there is no prefrontal boss. A groove crosses the bone from medial to lateral. It carried branches of the palatine nerve towards the infraorbital foramen (joining the maxillary nerve). Lateral to the maxillary process, the ventral surface (Fig. 7A_1, D, G) is also divided into two, but medially and laterally. The lateral surface runs along the margin of the bone and carries a tooth row posteriorly but none anteriorly. The medial edge is covered by a large facet for the pterygoid, grading anteriorly into a shorter facet for the vomer. It is clear from the facet pattern that the pterygoid met the vomer anteriorly, separating the palatines for their complete length and excluding them from the interpterygoid vacuity.

Pterygoid. — Pterygoids are common in the material (*e.g.*, ZPAL RV/70, 71, 75, 76), but none is complete. Judging by eye, the variability range of the pterygoids attributed to *Czatkowiella* is larger than that of *Osmolskina* (Borsuk-Białynicka and Evans 2009). In this respect the *Czatkowiella* pterygoids correspond to the *Czatkowiella* braincase material (see p. 205).

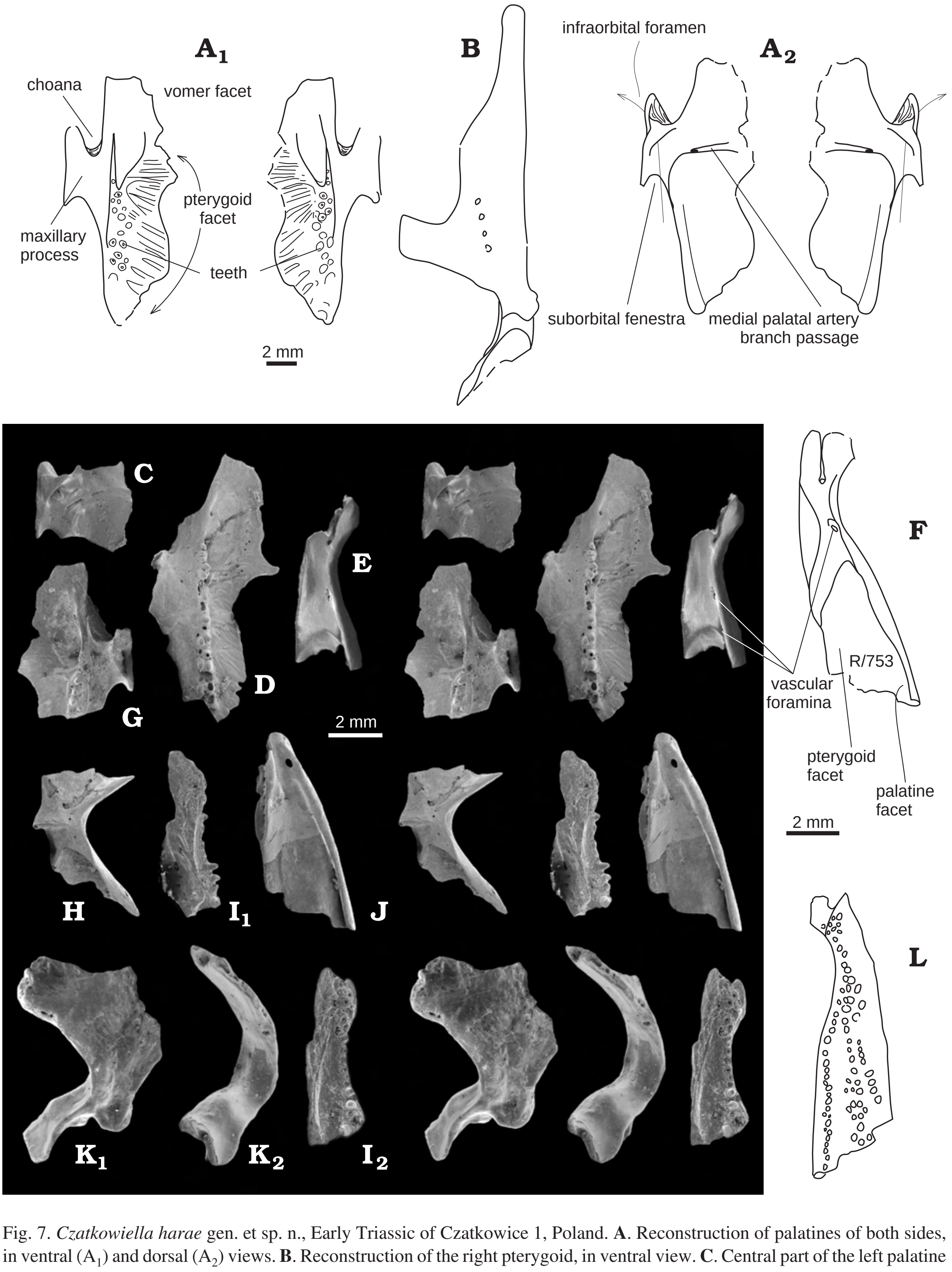


Fig. 7. *Czatkowiella harae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Reconstruction of palatines of both sides, in ventral (A_1) and dorsal (A_2) views. **B**. Reconstruction of the right pterygoid, in ventral view. **C**. Central part of the left palatine ZPAL RV/202, in dorsal view. **D**. Right palatine ZPAL RV/997 without maxillary process, in ventral view. **E**. Anterior part of the right vomer ZPAL RV/518, in dorsal view. **F**. Reconstruction of the right vomer, in dorsal view. **G**. Central part of the left palatine ZPAL RV/203, in ventral view. **H**. Central part of the left pterygoid ZPAL RV/334, in ventral view. **I**. Anterior part of the left vomer ZPAL RV/519, in medial (I_1) and ventral (I_2) views. **J**. Posterior part of the right vomer ZPAL RV/753, in dorsal view. **K**. Right pterygoid ZPAL RV/76, in ventral (K_1) and lateral (K_2) views. **L**. Reconstruction of the right vomer, in ventral view. All but A, B, F, L SEM stereo-pairs.

The palatal flange may be confidently reconstructed as a rather narrow triangle, its medial and lateral borders enclosing an angle of no more than 60° (Fig. 7H, K). The palatal surface of the wing bears a longitudinal concavity that turns gradually into a dentigerous field extending along the medial border (Fig. 7H, K_1). The dorsal surface of the wing is folded transversely, the main fold extending as a longitudinal convexity bordered medially and laterally by concavities. The anterior extent of the bone is reconstructed (Fig. 7B) on the basis of the rest of the ventral aspect of the skull but it is clear from the facets on the vomer that the pterygoids met in the anterior midline (Fig. 1B). Posteriorly, the ventral surface of the bone passes gently into the quadrate ramus without the bordering crest that occurs on the archosauriform pterygoids (Borsuk-Białynicka and Evans 2009). There is also no ligament tuberosity in this region. In these two respects, the pterygoids are similar to those of *Prolacerta broomi* (Gow 1975, fig. 11). At the junction between the palatal plate and the quadrate ramus is the medial basipterygoid fossa. As a whole the pterygoid is dorsally concave (Fig. $7K_2$). The quadrate ramus is angled laterally at roughly 90° to the lateral border of the palatal wing. At the base, the quadrate ramus is hemi-cylindrical in cross-section, and dorsally convex. It expands posteriorly into a bony blade, with thickened dorsal and ventral margins, although this region is usually broken.

BRAINCASE

The braincase bones are mostly disarticulated. In the Czatkowice 1 assemblage *Czatkowiella* is the second largest reptile after the archosauriform *Osmolskina*. Among the basioccipitals, the specimens more delicately built are always fused with the exoccipitals, and never with the opisthotic. The opisthotics with no conjoined exoccipital clearly belong with them. In *Osmolskina* the reverse is true: the exoccipital is always completely integrated with the opisthotic, and these bones are thus readily discriminated from those of *Czatkowiella*. The assignment of other braincase bones is mainly based on a size criterion. The braincase base of *Czatkowiella* is basically horizontally aligned, the parasphenoid rostrum extending in the same plane as parasphenoid ventrolateral crests. The angle between the basisphenoid and the basioccipital is more or less open depending on the amount of cartilage in the basisphenoid-basioccipital contact, which is unknown. All specimens display a well-ossified neurocranial surface.

Basioccipital and exoccipital. — The exoccipitals are tightly fused with the basioccipital (Fig. 8A, D), except in juveniles. The tripartite structure of the occipital condyle is evident only in eroded specimens. The exoccipital shafts first diverge dorsally, then they converge, but do not meet, above the large circular foramen magnum (Figs $8A_1$, 9A). The exoccipitals are subtriangular in transverse section, with the surfaces facing medially, posterolaterally and anterolaterally. Their upper ends are only rarely preserved. Roughly level with the dorsal margin of the condyle, the exoccipital is perforated by the main hypoglossal nerve foramen, with one or two much smaller accessory foramina below it (Figs $8A_1$, 9A). Ventrally, the exoccipitals are separated in the midline by a narrow strip of basioccipital (Figs 8D, 9D). This zone expands a little towards the occipital condyle and much more so anteriorly where the basioccipital becomes the only element of the braincase floor. It bears a sagittal crest that protrudes anteriorly. On either side of the protruding part, inclined slightly laterally, the anterior margins of the basioccipital fit the posterior surfaces of the basisphenoid, although the bones may have been separated by cartilage in life. Ventrally, the gap was bridged by the posterior lamina of the parasphenoid (Figs 8H, 9G). This overlapped the basioccipital and left a parabolic trace on its ventral surface. Anterior to the base of each exoccipital, and below its suture with the basioccipital (ZPAL R.V/423), there is a transverse furrow corresponding to the floor of the metotic fissure (cranial nerves IX and X). The braincase floor is covered by finished bone which evidently appeared early in ontogeny. Together, the basioccipital and exoccipitals form a sub-quadrangular occiput (Fig. 8A) the ventral corners of which bear strong basal tubera for the attachment of hypaxial muscles, most notably *m. longus colli ventralis*. These tubera are laterally flattened and are united ventrally by a concave crest. The crest separates the neck of the occipital condyle from the anteroventral concavity that continues onto the parabasisphenoid.

Supraoccipital. — The supraoccipital attributed to *Czatkowiella* is a subhexagonal blade of bone, wider than long, with the opisthotic and prootic borders enclosing an angle of approximately 90°, and separated from each other by a small incision (*e.g.*, Fig. $8B_1$). The concave posterior border of the supraoccipital is laterally incised by small exoccipital facets that do not meet each other. Between them, is the fairly long supraoccipital border of the foramen magnum. The anterior border is sinuous (Fig. $8B_2$), with bilateral con-

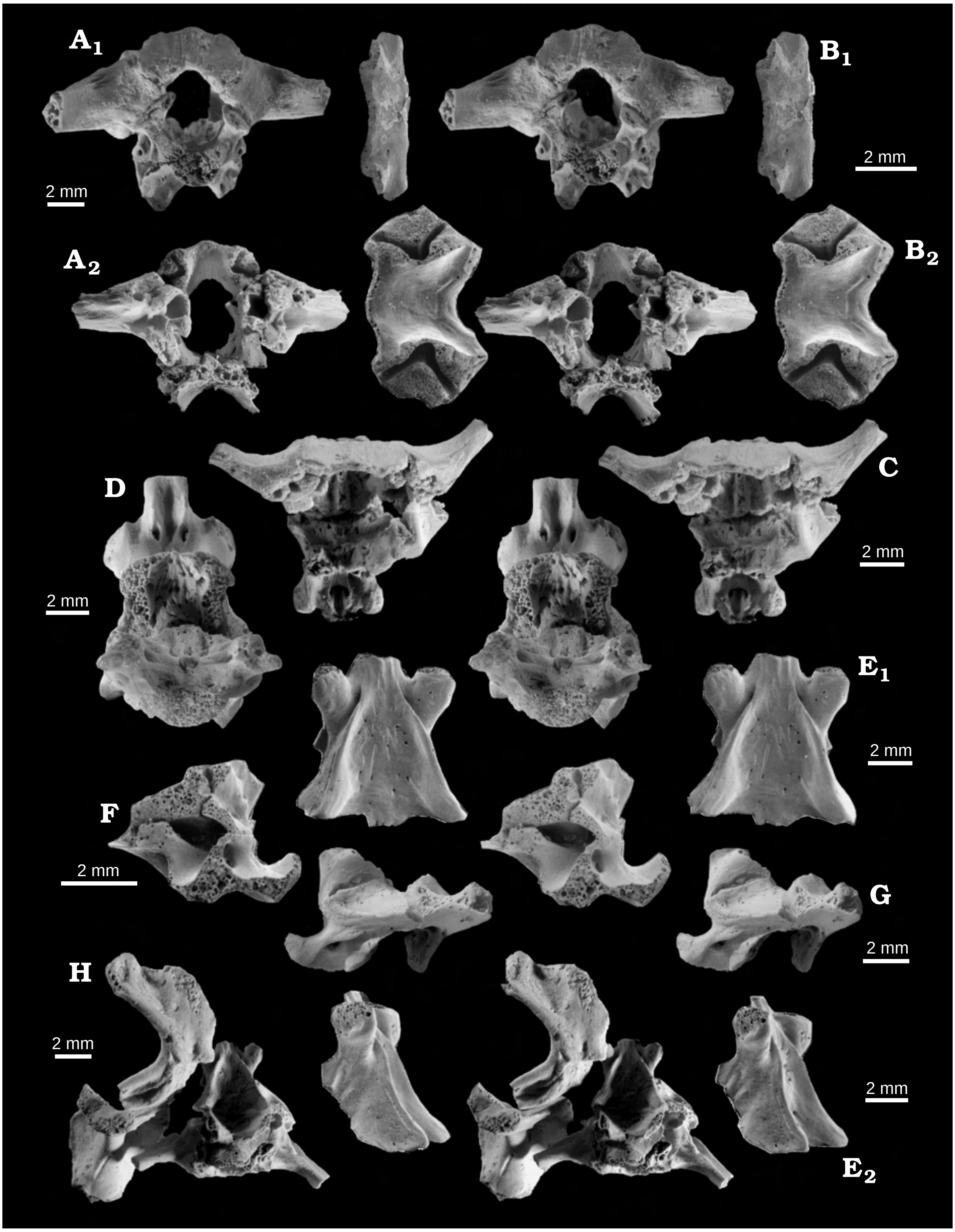


Fig. 8. *Czatkowiella harae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Braincase ZPAL RV/433 combined from different individuals, in posterior view (A_1), the same in anterior view with the parabasisphenoid and prootics omitted (A_2). **B**. Supraoccipital ZPAL RV/126, in anterior (B_1) and ventral (B_2) views. **C**. Braincase ZPAL RV/433 combined from different individuals with the parabasisphenoid and the left prootic included, in anterior view. **D**. An incomplete braincase ZPAL RV/430 in dorsal view combined from different individuals, with the supraoccipital and prootics omitted. **E**. Parabasisphenoid ZPAL RV/433, in ventral (E_1) and lateral (E_2) views. **F**. Left prootic ZPAL RV/119, in medial view. **G**. Left prootic combined with opisthotic ZPAL RV/432, in lateral view. **H**. A braincase ZPAL RV/999 combined from different individuals with a quadrate and a pterygoid ZPAL RV/76 added, in ventral view. All stereo-pairs; B, E, F, G SEM micrographs.

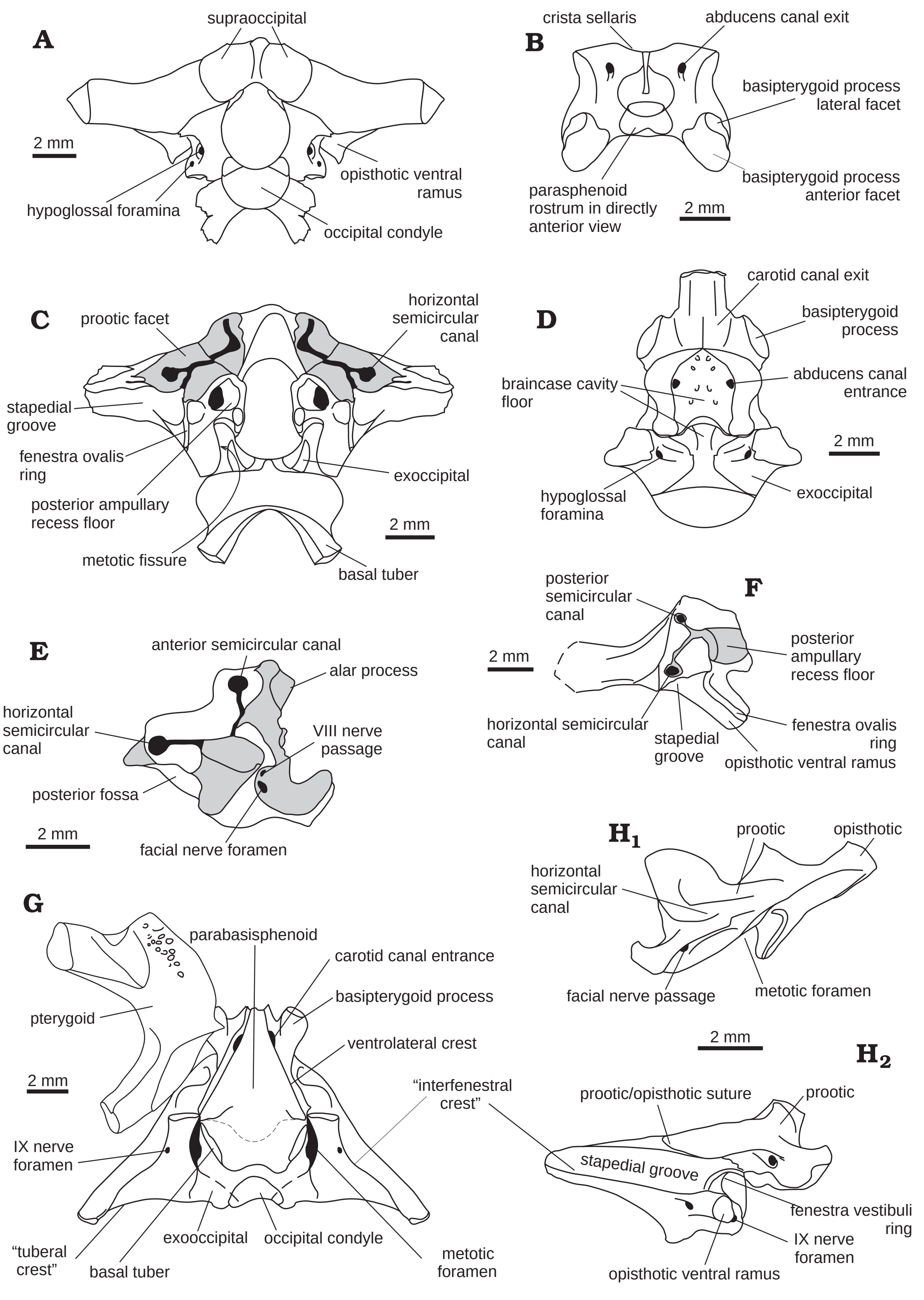


Fig. 9. *Czatkowiella harae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Explanatory schemes to Fig. 8. **A**. Braincase, in posterior view. **B**. Parabasisphenoid, in anterior view. **C**. Posterior part of the braincase, in anterior view with parabasisphenoid and prootics omitted. **D**. Partial braincase, in dorsal view with supraoccipital and prootics omitted. **E**. Left prootic, in medial view. **F**. Left opisthotic, in anteromedial view. **G**. Braincase with pterygoid articulated, in ventral view. **H**. Left prootic and opisthotic articulated, in lateral (H_1) and ventral (H_2) views.

cavities separating the anteriorly protruding central part from the prootic facets. The thin anterior surface of the bone was probably continued forward in cartilage and bears no special cavities for venous sinuses. Instead, the dorsal surface of the bone is grooved by two concavities extending posteriad from the anterior border, and two extending laterad towards the notch between the prootic and opisthotic facets. Further furrows, perhaps associated with veins, run on the ventral surface of the bone (Fig. $8B_2$), parallel to the posterior border. The whole plate is well ossified even at a small size, matching the condition of other parts of the cranium attributed to *Czatkowiella*. The facets for neighbouring bones and for the internal labyrinthine walls are very distinct. Bilaterally, the supraoccipital provides the dorsal components of the otic capsules. The prootic and opisthotic margins are perforated by entrance foramina of the anterior and posterior semicircular canals respectively. On each side of the bone, the internal surface of the capsule is grooved by the semicircular canals.

Parabasisphenoid. — In ventral view, the parabasisphenoid forms a long triangle of bone (Figs 8E, 9G). Two straight blunt ventrolateral crests converge anteriorly from the posterolateral parasphenoid wings towards the bases of the basipterygoid processes, and then run in parallel along the ventral surface of the parasphenoid rostrum (cultriform process). Between the crests, the ventral surface is concave, deep posteriorly but becoming shallower towards the rostrum. The surface then becomes convex rostrally. A possible parasphenoid component is long, its posteromedial part overlapping the ventral surface of the basioccipital almost to the level of the basal tubera.

The basipterygoid processes are short, broad and somewhat dorsoventrally flattened. They are widely separated from each other by the base of the parasphenoid rostrum. Seen in anterior view, they are also ventrally deflected with the articular surfaces for the pterygoids on the anteroventral and ventrolateral surfaces. In anterior view, the rostrum seems tripartite — the dermal parasphenoid ossification (or ossifications) underlying the paired trabeculae cranii, represented by their ossified ovoid bases. Between the basipterygoid processes and the ventrolateral crests, there are distinct furrows that transmitted the internal carotid arteries and the palatine branches of the facial nerve (VII). At the base of the parasphenoid rostrum and lateral to the ventrolateral crests are paired carotid foramina (Figs 8E, 9G). At the level of these foramina, each artery must have divided. A palatine branch accompanied the nerve forward along the ventrolateral edge of the rostrum, while the cerebral branch entered the carotid foramen and ran through a short vertical canal to reach the dorsal side of the cultriform process just anterior to the hypophysial fossa (Figs 8C, 9B). The fossa which is an excavation of the anterior wall of the basisphenoid is divided by a, vertical, sagittal crest into two concavities, which give the surfaces of origin for retractor muscles of the eye. Each surface is perforated by a short canal for the abducens nerve (Figs 8C, 9B). The intracranial surface of the basisphenoid is subrectangular in outline, concave, and covered by finished bone. The lateral walls of the parabasisphenoid (Fig. $8E_2$) are fairly deep but horizontally aligned. They bear elongated facets for the prootic. These extend towards the midline along the crest of the dorsum sellae but it is not clear whether or not they met.

Posteriorly, the basisphenoid bears oblique, more or less finished, posterior surfaces for the basioccipital, whereas a ventral sheet of finished bone, roughly corresponding to parasphenoid, extends onto its ventral surface. When articulated, the parabasisphenoid and basioccipital together form a longitudinally concave neurocranial cavity floor. The ventral ramus of the opisthotic probably entered the space left between the basioccipital and parabasisphenoid on each side.

Opisthotic. — The opisthotic attributed to *Czatkowiella* is represented by a number of specimens (*e.g.*, ZPAL RV/179–182, 432, 449) permitting an accurate reconstruction. The main body of the opisthotic extends into a slightly bilaterally flattened paroccipital process. In life, the contralateral processes extended directly laterad, while changing posterolaterally in the distal parts only. The exoccipital facet faces ventromedially, and the supraoccipital facet dorsomedially. The supraoccipital facet bears the circular opening of the posterior semicircular canal. The prootic facet cuts obliquely through the anterolateral edge of the bone (Figs $8A_2$, 9C). It contains the opening for the horizontal semicircular canal, and below it lies the wide entrance of the vestibular cavity containing the posterior ampullary recess. Posteroventral to the prootic facet, the surface of the paroccipital process is flattened and sculptured by heavy longitudinal crests. A still more ventral wall of the opisthotic bears a longitudinal stapedial groove directed towards the fenestra vestibuli. The groove is bordered anterolaterally by a distinct crest extending in line with the prootic crest, posteriorly by another crest, (roughly corresponding to the intertuberal crest, Oelrich 1956), that continues proximally onto the ventral ramus of the opisthotic (Figs $8A_2$, 9F, H_2), and still more medially by a crest analogous to the crista tuberalis of lizards.

A circular convexity or ring (Figs 8A$_2$, 9C, F, H), that cuts transversely through the stapedial groove, demarcates the attachment area of the membrane covering the fenestra vestibuli. The ring continues onto the anterior surface of the ventral ramus of the opisthotic.

The ventral ramus of the opisthotic is a fairly long, subvertically oriented, blade (Figs 8G, 9F, H). It extends into a large anteromedially directed flange (denoted as the posterior ampullary recess floor in Fig. 9C, F), that protrudes from the ventral corner of the posterior ampullary recess. The ventral ramus also forms the anterolateral border of the metotic foramen, with the exoccipital providing its posteromedial wall. Close to its base, the ventral ramus is perforated by a short, superficially placed, lateral canal (Fig. 9G).This may have carried the glossopharygeal nerve (IX), or one of its branches, while the vagus (X) passed through the main part of the foramen. This is not, however, homologous to the condition in lizards where a separate ventral channel is created for the glossopharyngeal nerve and perilymphatic duct by the apposition of the opisthotic (posterior ampullary prominence) and exoccipital below the vagus foramen. A similar small canal can be found on the opisthotic of the basal rhynchocephalian, *Gephyrosaurus* (SEE unpublished data).

Prootic. — The prootic is exemplified by specimens ZPAL RV/119–121, 461, 462. These are attributed mainly on the basis of their subhorizontal alignment, as determined by the course of the horizontal canal (Fig. 8F). This matches the basically horizontal alignment of the braincase floor in *Czatkowiella*. The lateral surface of the main body has distinct elongated convexities covering the anterior and horizontal semicircular canals. Above the anterior canal, there is a small but distinct triangular alar process. A well-developed anterior inferior process extends anteriad, separated from the main part of the bone by the wide incisura prootica marking the position of the trigeminal nerve ganglion (V). This contains a small, subtriangular supratrigeminal process. In its upper part, a small notch marks the exit of the *vena cerebralis media* from the interior of the brain case. The lateral face of the prootic (Figs 8G, 9H$_1$) is partially divided by a weak *crista prootica* that extends posterodorsally from the lower margin of the anterior inferior process. It converges posteriorly with the ventral margin of the bone as it passes into the lateralmost crest of the opisthotic, but gradually fades out. The *crista prootica* overhangs the small facial foramen and the grooves into which the anterior (palatine) and posterior (hyomandibular) branches of the nerve pass.

In medial aspect, the prootic (Figs 8F, 9E) is excavated for the inner ear structures. The main cavity, the *cavum vestibulae*, receives the anterior semicircular canal dorsally, horizontal semicircular canal posteriorly where it contacts the opisthotic, and is open posteroventrally. Anterodorsal to the anterior semicircular canal is a funnel-shaped excavation, the subarcuate fossa, for the cerebellar flocculus and part of the dural venous sinus system. Anteroventral to the fossa, and posterior to the incisura, a third excavation housed the ganglia of the facial and vestibulocochlear nerves. The excavations are separated from one another by flat surfaces of unfinished bone representing internal sutures or divisions continued in cartilage. The openings of the anterior and horizontal semicircular canals are located within the supraoccipital and opisthotic surfaces respectively. Ventral to the base of the posterior process, and posterior to vestibular cavity, is a triangular shelf labelled as posterior fossa in Fig. 9E, that provides the anterolateral wall of the stapedial fossa.

MANDIBLE

The lower jaw of *Czatkowiella* is known from the dentary, surangular, and less certainly, parts of the angular and perhaps splenial.

Dentary. — The dentary of *Czatkowiella* is represented by a large number of specimens, including adult and juvenile examples (Fig. 10). None is complete and we can therefore only estimate the tooth count but it was probably between 20 and 30 in adult animals. The anterior teeth are elongate cones with a slight curvature and apical striae, as in the upper teeth (Fig. 3A, D), but the teeth become more robust and more recurved (*e.g.*, Fig. 4D) towards the posterior end of the dentary, especially with age. The jaw ramus is shallow. In lateral view, the bone is lightly sculptured, at least in adults, and bears a series of neurovascular foramina, that are particularly numerous at the anterior end of the bone, below the first 6–8 tooth positions. This region of the bone is also somewhat unusual in that the dorsolateral and ventrolateral surfaces meet at an angle to form a slight crest. In medial view, the tooth row lies above a strong, slightly rounded subdental ridge that thickens anteriorly and contributes to a strong rugose symphysial surface in adult animals. This surface is less rugose in immature specimens. Below tooth position 6–7 (depending on the age of the animal and the size of the

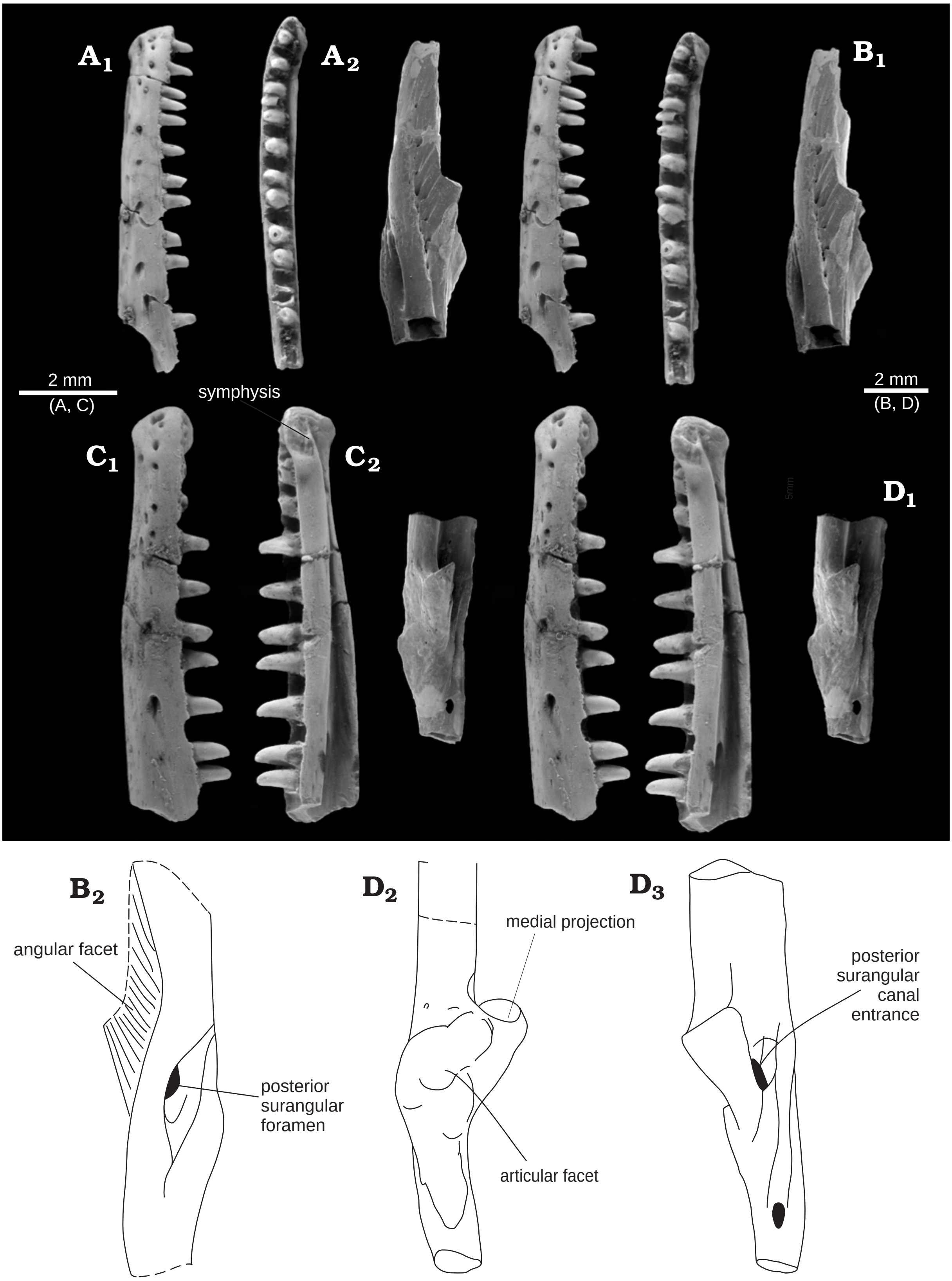


Fig. 10. *Czatkowiella harae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Left dentary ZPAL RV/107, in labial (A_1) and occlusal (A_2) views. **B**. Posterior fragment of the right surangular ZPAL RV/486, in ventrolateral (B_1) view; morphological diagram of the same (B_2) reversed. **C**. Left dentary ZPAL RV/106, in lateral (C_1) and lingual (C_2) views. **D**. Posterior fragment of the left surangular ZPAL RV/166, in mediodorsal (D_1) view; morphological diagram of the same in dorsal (D_2) and medial (D_3) views. All but B_2, D_2, D_3 SEM stereo-pairs.

teeth), the subdental ridge develops a facet, more obvious in the juvenile than the adult, which clearly supported the splenial. This suggests that the splenial did not reach the symphysis, leaving the Meckelian fossa open for a short distance anteriorly. In this region, roughly at the level of the second or third tooth position, the medial wall of the fossa is perforated by a conspicuous nutrient foramen. The Meckelian fossa is generally deep but low. It is open ventrally in young animals although the ventral margin shows a slightly incurving in more mature individuals. Further posteriorly, at around the level of tooth position 15–16, the fossa is perforated by a small foramen representing the opening into the inferior alveolar canal, carrying branches of the mandibular division of the trigeminal nerve (Viii) and accompanying blood vessels. There were at least four tooth positions behind this point, but the posterior end of the bone is not preserved in any specimen.

Surangular. — The surangular is represented by several fragments (Fig. $10B_1$, D_1) distinguished by their narrow proportions. They show a size range corresponding to those of other *Czatkowiella* bones. A thick dorsal ridge passes posteriorly into a hook-like medial projection. On its posterior surface, this projection bears a rather poorly determined dorsomedial facet for the articular. The large canal, for the mandibular division of the trigeminal nerve and associated blood vessels, enters at the base of the hook-like projection (posterior surangular canal entrance Fig. $10D_3$), and exits by a large posterior surangular foramen situated further posteriorly within a furrow on the ventrolateral face of the posterior process (Fig. $10B_2$). A smaller foramen, of unknown function, opens on the medial surface of the bone, still further posteriorly, at the end of a furrow that parallels the medioventral border of the facet for the articular bone.

Dentition. — The marginal teeth of the adult animal are large and recurved with a slight labiolingual compression. Under Scanning Electron Microscopy, the teeth (premaxilla, maxilla, dentary) are shown to have finely striated tips (Figs 3A, C_1, D, 4A, E), but the striation becomes less obvious with age (*e.g.*, Figs $3C_2$, 4F). The labial margin of the jaw is higher than the lingual one giving a subpleurodont implantation in smaller individuals, but in larger individuals the teeth approach a subthecodont condition. Tooth replacement occurs from the lingual side of the tooth. It is active in small animals but may have slowed down in adults (*e.g.*, ZPAL RV/1126; Fig. 4F).

VERTEBRAE

The vertebrae of *Czatkowiella* range in size but are characterised by having very dense bone (much heavier and denser than that of either of the smaller diapsids), bicipital cervical ribs and three-headed ribs in the anterior part of the trunk. Further posteriorly, the two ventral rib facets consolidate into a single parapophysis that eventually merges with the diapophysis towards the end of the dorsal vertebral series. The cervical vertebrae attributed to *Czatkowiella* are much elongated whereas the dorsal vertebrae overlap to some degree in their proportions and centrum shape with those of the basal kuehneosaurid from the same material (Evans 2009, see also Fig. 16 herein), but they differ in having a shorter and wider neural arch, shorter wider spine (Fig. 11B), and more strongly divergent zygapophyses separated by a deep V-shaped triangular cleft posteriorly.

Axis. — There is a single common axis type (*e.g.*, ZPAL RV/615; Fig. 11E) and, logically, this should belong to *Czatkowiella*, given the robusticity of the bone and the shape and position of the anteriorly placed rib facets. The bone has a long neural spine with a horizontal dorsal margin that extends forward beyond the anterior tip of the centrum to form a distinct anterior spur. The lateral faces of the spur are planar but the median part becomes more rugose so that it seems to form the posterodorsal limit to a small anterolateral surface. Conceivably this marks the attachment of a proatlas, an element reportedly present in *Prolacerta* (Gow, 1975). The flanks of the neural arch splay out ventrally and bear surfaces for the atlas arches on their anterior shoulders (Fig $11E_1$). Posteriorly, the zygapophyses are larger, longer, and divergent, with a ventrally shelved cavity between them. The axis centrum is much narrower than the arch with a strong midventral keel that renders the centrum triangular in cross-section (Fig. $11E_2$). The centrum is weakly amphicoelous but not notochordal, and its anterior face forms a planar attachment surface for the odontoid. The lateral surface of the axis is marked by three weak anteroposterior crests, one at the inferior margin of the arch which probably corresponds to the zygapophysial crest in later vertebrae, one at the neurocentral boundary, and one marking the lower limit of the centrum proper, below which is the keel. The central ridge bears a tubercle where it meets the anterior edge of the centrum and this must correspond to one head of an atlantal rib. Below it the

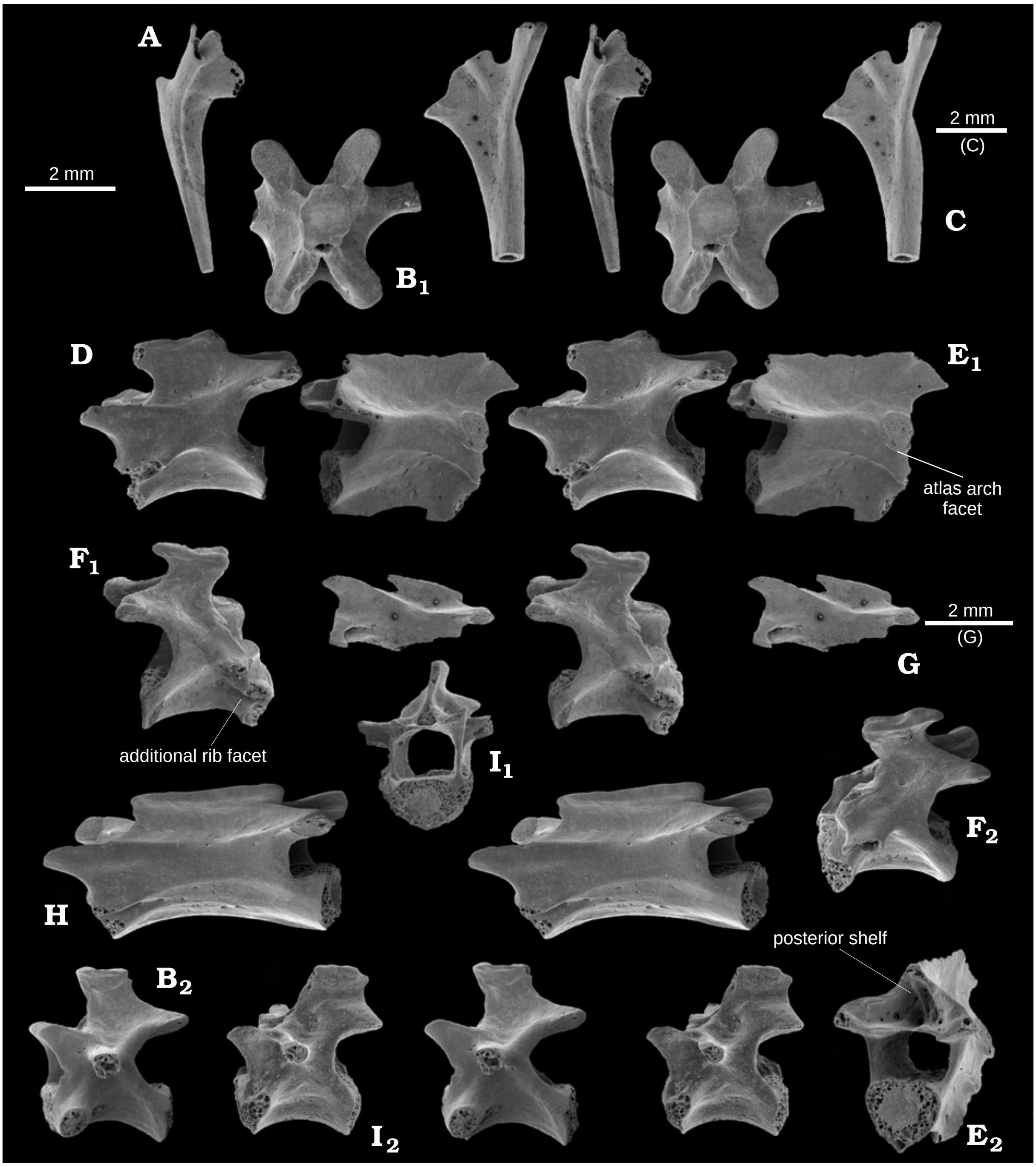


Fig. 11. *Czatkowiella harae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Right three-headed anterior dorsal rib ZPAL RV/934. **B**. Anterior dorsal vertebra ZPAL RV/618. **C**. Right three-headed dorsal rib ZPAL RV/1122. **D**. Anterior cervical vertebra ZPAL RV/613. **E**. Axis ZPAL RV/615. **F**. Dorsal vertebra ZPAL RV/619. **G**. Juvenile mid-cervical vertebra ZPAL RV/616 with proximal fragment of rib fused. **H**. ?Midcervical vertebra ZPAL RV/616. **I**. Posterior dorsal vertebra ZPAL RV/221. Right lateral view (A, E_1, F_1), left lateral view (D, F_2, G, H, I_2), dorsal view (B_1), posterior view (E_2), and anterior (I_1) views. SEM micrographs; all but E_2, I_1 stereo-pairs.

edge of the centrum is usually damaged, but there is a hint of a second, weaker tubercle, suggesting the axial rib was dichocephalous with the two heads close together.

Atlas intercentrum. — This is a small compact, transversally enlarged, body that is trapezoid in outline (ZPAL RV/1100; Fig. 12C). The shorter side bears a concave articular surface that probably met the occipital condyle, and the anterolateral sides bear facets for the atlantal arches. The dorsal surface is convex and spongy and probably contacted the atlas centrum. The fully ossified ventral surface is sculptured and concave in longitudinal section. The bone is smaller than the atlantal intercentra attributed to *Osmolskina* (Borsuk-Białynicka 2009) and displays a more elaborate morphology, but it is too large to belong to any of the smaller Czatkowice 1 taxa.

Postaxial cervical vertebrae. — The cervical vertebrae of *Czatkowiella* are well represented in the collection. There is a common morphology, with some differences in vertebral length in relation to height, centrum shape, and the shape of the neural spine.Vertebral number cannot be reconstructed, but there is a limited number of cervical morphotypes and it seems likely that the neck was fairly conservative (7–9 segments).

A typical cervical vertebra (*e.g.*, ZPAL RV/616; Fig. 11H) is roughly twice as long (anterior to posterior length of the centrum) as it is high (lower margin of centrum to tip of neural arch midvertebrally). The centrum is solid with weakly convex anterior and posterior surfaces (amphiplatyan). It is subcircular in transverse section with a small ventral angulation when the ventral crest exists, but this is usually absent or very weak. The ventral margin of the centrum slopes posteroventrally, so that the posterior articular surface is lower than the anterior one. The ventral surface is concave, a shape that is accentuated by the anteroventral protrusion of the facets for dichocephalous cervical ribs. These facets are situated bilaterally on the anteroventral borders of the centrum, and are joined to the posterior margin of the centrum by weak curved anteroposterior ridges (see *e.g.*, Fig. 11D, H). Neurocentral sutures are always fully closed. The arch is elongate with a low more or less horizontal spine that has a very long base extending over the whole length of the vertebra. The anteroposterior length of the spine is slightly greater at its apex than at its base, creating a slight overhang at each end (Fig. 11D, G), which is most evident in the anterior dorsals (Fig. 11F). Both zygapophyses extend slightly beyond the end of the centrum. Laterally, the zygapophyses are joined by an anteroposterior crest, although this may be disjunct in some of the longer elements. Seen in dorsal view, the median edge of the cervical neural spine is narrow but it becomes wider in dorsals, particularly so in the anterior part of the dorsal series (Fig. 11B). The triangular recesses between the zygapophyses are shelved with bone. Between the postzygapophyses the shelf extends well back, creating a deep posterior recess that extends below the spine and forms one of the most consistent features of *Czatkowiella* vertebrae (Fig. 11E$_1$). Between the prezygapophyses the corresponding shelf is very short and bears a slight longitudinal furrow, probably a trace of ligament. No accessory articulations (*e.g.*, like the zygosphene-zygantrum system of lepidosaurs) are developed between successive vertebrae.

In other long necked taxa, and particularly in the articulated neck of *Malerisaurus langstoni* (Chatterjee 1986), the most anterior cervicals are shorter than those in the middle of the neck, with vertebral length increasing backwards, before shortening again towards the beginning of the trunk. This pattern is supported by *Amotosaurus rotfeldensis* (Fraser and Rieppel 2006) in which the first cervical is about half the length of the next one and the midcervicals are the longest. This might be the case in *Czatkowiella* as well. The typical elongated cervicals (ZPAL RV/1132, 1133; Fig. 12) are thus considered middle neck vertebrae. However, how much shorter the anterior cervicals were than the middle ones is obscure. In the Alla Cascina specimen of *Macrocnemus bassani*, the third vertebra is more than 30% longer than the axis, while being only 10% shorter than the next cervical (Peyer 1937, p. 90). This means that the typically elongated cervicals in *Czatkowiella* (*e.g.*, ZPAL RV/1132) might have followed the axis directly. Among other criteria of vertebral position, the development of the ventral keel (similar to the axis keel) is the least useful, because the keel is weak at best, and might be size dependent. The position of rib facets, and the width of the neural spine barely change along the cervical series, except at the posterior end. The gradient of the neural spine along the vertebral column is most helpful. The neural spine forms a long narrow crest in mid-cervicals, then becomes anteroposteriorly shortened with an anterior spur (Fig. 11D), and finally develops an anterodorsal inclination (Fig. 11B$_2$) to become subvertical in the anterior dorsals Fig. 11F). At the end of the cervical series, the proportions of arch and centrum are more like those of the dorsal vertebrae, the centrum has become wider and somewhat dorsoventrally compressed, and the spine has a much shorter base but is taller. The diapophysis starts a posterior shift that becomes obvious only in dorsals. The parapophysis, that has the form of a thin crest in the anterior cervicals, becomes a conspicuous tuber on the anteroventral margin of the centrum (Figs 11, 12) at the transition to the dorsal series.

Dorsal vertebrae. — These can be divided roughly into anterior, middle, and posterior vertebrae, mainly on the basis of their rib facets and the robusticity of the centra. ZPAL RV/619 (Fig. 11F) probably represents a vertebra from the beginning of the dorsal series. This vertebra bears a third rib facet (Fig. 11F$_2$). between

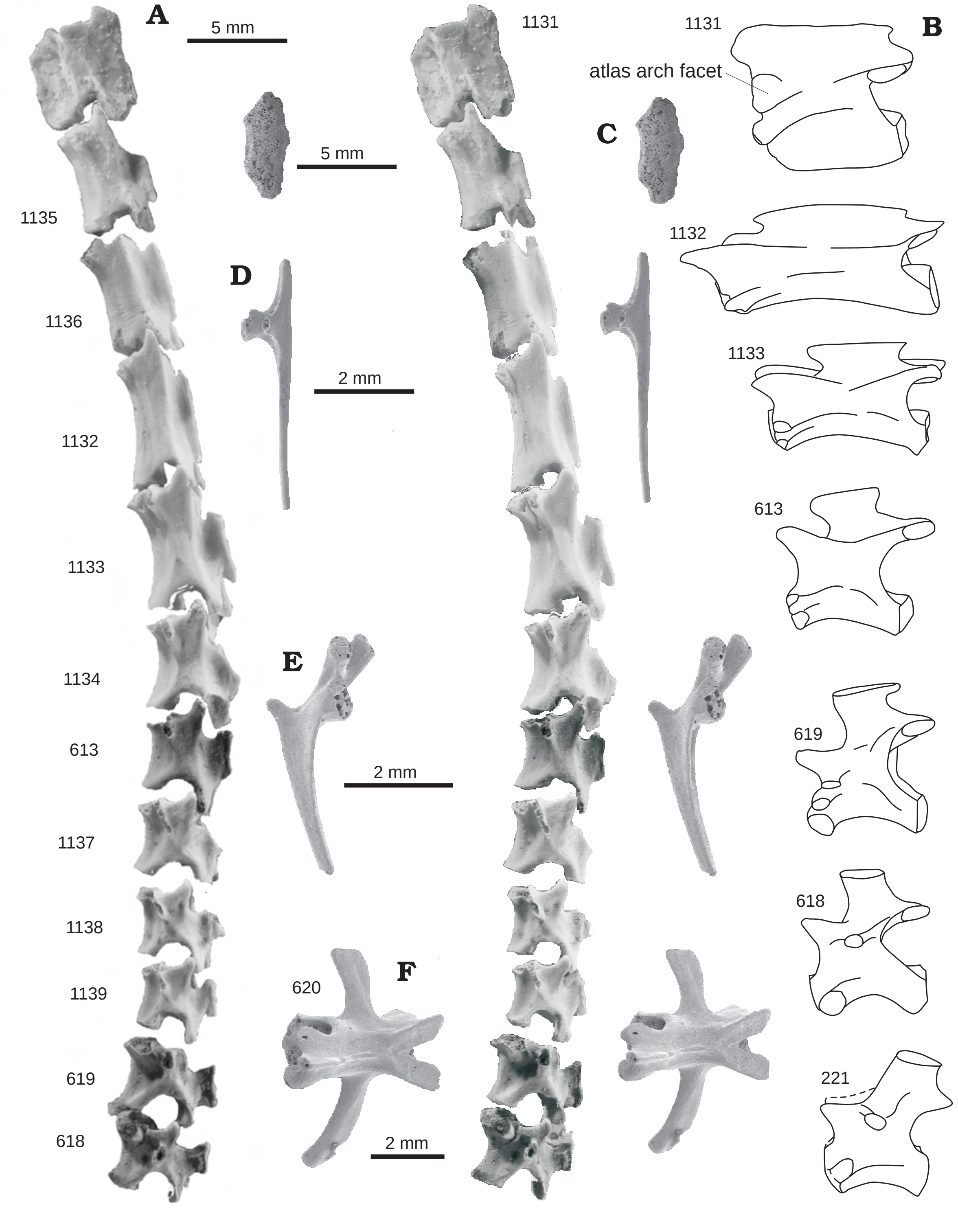


Fig. 12. *Czatkowiella harae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Disarticulated cervical and anterior dorsal vertebrae arranged in a possible anatomical sequence. **B**. Morphological diagrams of cervical and dorsal vertebrae. **C**. Atlas intercentrum ZPAL RV/1100. **D**. Cervical rib ZPAL RV/937. **E**. Left anterior dorsal rib. **F**. Anterior caudal vertebra. Left lateral (A, B), dorsal (C, F), and ventromedial (E) views. All but B stereo-pairs; C–F SEM micrographs. ZPAL RV/numbers alongside.

the main ones. The facet is preserved on the right side only, but the frequency of the three-headed ribs in the material suggests this was a normal feature of the *Czatkowiella* vertebral column. However, vertebrae with three rib heads are still rare and it seems likely that the three-headed ribs were limited to the transition between cervical and dorsal series in the living animal. The centrum is wider than in cervicals and somewhat dorsoventrally compressed. The spine is anteroposteriorly short with transversally broadened tip. Two rib facets are still present at the anterior margin of the centrum but the diapophysis has started to move posterodorsally. ZPAL RV/618 (Fig. 11B_2) probably followed ZPAL RV/619 (Figs 11F_2, 12) as shown by the more posterior position of the diapophysis.

Caudal vertebrae. — Caudal vertebrae are similar to the dorsals in terms of central shape, but they are longer, with longer neural spines. Anterior caudals have broad based transverse processes (Fig. 12F) that represent fused caudal ribs. The processes are supported anteriorly and posteriorly by horizontal crests. In more posterior caudals, the transverse process decreases in length until it is no more than a raised area on the anteroposterior crest. Behind that point, only the lateral crest remains. The neural spine similarly decreases in height until it is little more than a median ridge. At no point is there any trace of an autotomy septum.

RIBS

The ribs of the neck and anterior dorsal region have a distinctive morphology. ZPAL RV/937 is the anterior part of a cervical rib. The two small heads lie together, between a short tapering anterior process and a long, very slender horizontal posterior shaft (Fig. 12D). These slender shafts are solid in cross-section and the many fragments present in the sample suggest that the neck of *Czatkowiella* was supported by a series of overlapping ribs, as in other long-necked genera such as *Protorosaurus*, *Prolacerta*, *Macrocnemus*, and *Tanystropheus*. Further posteriorly the rib heads enlarge and begin to separate, but a small subset of vertebrae and ribs (*e.g.*, ZPAL RV/934 and 1122; Figs 11A, C, 12E respectively) show a three-headed morphology. In these ribs, the proximal head is divided into three parts — a large round upper facet, a second smaller facet, also rounded, and separated from the first by a shallow notch, and then a third smaller, offset facet, more sharply separated from the other two (Fig. 11C). A strong posteromedial crest runs from the smaller, lower, facet and curves back onto the shaft, which is much narrower. At the point of the angle there is a strong anterolaterally directed process. The angulation suggests this rib was directed as much backward as outward. Another subset of ribs shows a very similar morphology, but the two upper heads have coalesced. The three-headed ribs, and their vertebrae, are rare suggesting that there were only one or two such elements close to the neck-trunk boundary. Three-headed ribs also occur in this region in the Late Triassic kuehneosaurs and in a number of archosauriforms. Their distribution in the latter group is reviewed by Thulborn (1979) who suggests that these necessarily immobile ribs may have provided an important point of stability at the base of the neck.

LIMBS AND GIRDLES

There are a large number of limb and girdle elements in the Czatkowice 1 assemblage and these are more difficult to associate than skull remains. Work on this material is ongoing, but here we tentatively attribute a humerus and an ilium to *Czatkowiella*.

Humerus. — Among four humeral morphologies recognized to date from the Czatkowice 1 material, the type most safely attributable to *Czatkowiella* is a medium sized bone (*e.g.*, ZPAL RV/1146; Fig. 13C) with a strongly enlarged, rather flat distal end perforated by a large entepicondylar foramen. The slender shaft is strongly twisted, so that estimated angle of the distal upon the proximal plane is almost 90°. Only a slight furrow for the radial nerve grooves the lateral border of the distal head, but there is no enclosed ectepicondylar foramen. The bone ranges in length from roughly 10–30 mm (7 specimens), which is smaller on average than the limb bones of *Osmolskina* (Borsuk-Białynicka and Sennikov 2009). On the basis of a skull length/humerus length ratio of 7:4 in *Prolacerta* (Gow 1975), this humerus might fit *Czatkowiella*, given our reconstructed skull length (Fig. 1) of 40 mm. Morphologically, it is quite similar to that of *Petrolacosaurus* (Reisz 1981), and more primitive than that of *Prolacerta*, which shares the loss of entepicondylar foramen with Archosauriformes.

Ilium. — Five iliac morphologies have been identified amongst the Czatkowice 1 reptile remains: that of the euparkeriid *Osmolskina* (clearly identified on the basis of size, number and morphology); those of procolophonoids (identified by their short, broad vertical blades); those of the smallest lepidosauromorph (identified by its size, frequency and morphology: slender angled blade and prepubic process); and two other types of rather similar morphology but differing size range. Both have subhorizontal iliac blades, a supra-acetabular buttress less developed than in *Osmolskina*, and first sacral rib facets positioned anterior and

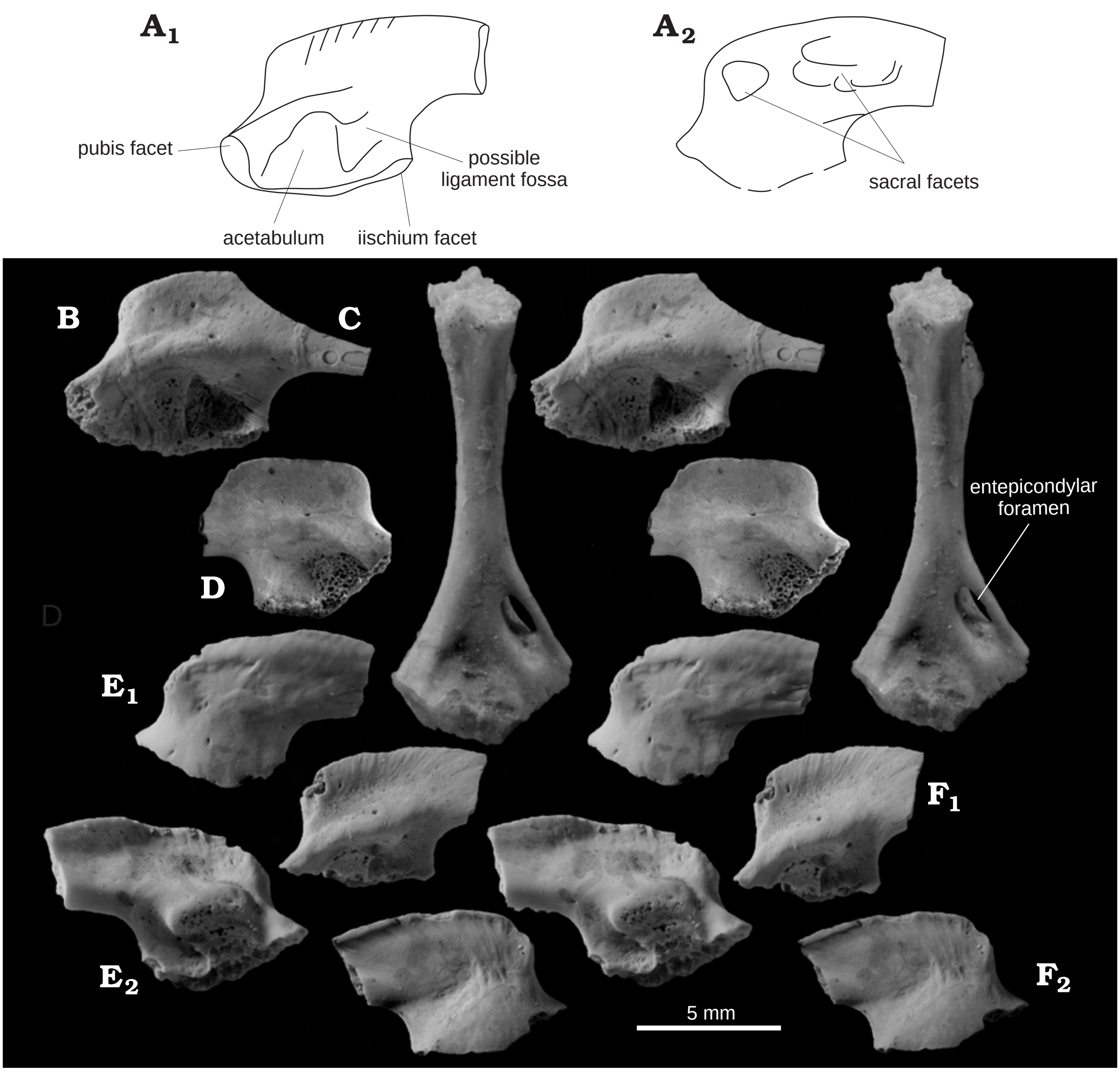


Fig. 13. *Czatkowiella harae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**, **B**, **D**–**F**. Ilia. **A**. Morphological diagrams. **B**. ZPAL RV/941. **D**. ZPAL RV/982. **E**. ZPAL RV/994. **F**. ZPAL RV/943. Left lateral (A_1, B, F), right lateral (D, E_2), right medial (A_2, E_1), and left medial (F_2) views. **C**. Left humerus ZPAL RV/1146, in dorsal distal view. All but A_1 and A_2 stereo-pairs.

just above the level of the acetabulum. However, although both types show a range of sizes, the largest examples of one type (Fig. 13), here referred to *Czatkowiella*, are much too large for the kuehneosaurid. The ilium referred to *Czatkowiella* is heavier than that referred to the kuehneosaurid, its acetabular part is relatively anteroposteriorly longer and less waisted, and its posterior process extends horizontally almost perpendicular to the posterior border of the acetabular part instead of ascending posterodorsally. Its anterodorsal part is obliquely cut off, the border descending anteroventrally with no anterior protrusion of any sort, in contrast to the smaller type that bears a conspicuous anterolateral tubercle in this region.

DISCUSSION

Czatkowiella shows a combination of features usually associated with basal archosauromorph reptiles — elongate neck vertebrae with closely associated dichocephalous ribs, cervical ribs with an anterior process, and strong transverse processes on the dorsal vertebrae. The long low cervical vertebrae are of a type traditionally associated with those described as "prolacertiforms", while differing from those of some long-necked archosauriforms in having more elongate and very low spines. The lack of a thecodont tooth implantation and the absence of an antorbital fenestra definitely preclude *Czatkowiella* from the latter group. In most recent phylogenies, "prolacertiforms" lie close to the base of Archosauriformes, whether as a monophyletic clade (*e.g.*, Jalil 1997) or a series of successive outgroups to the crown (Dilkes 1998; Rieppel *et al.* 2003; Müller 2004).

Dilkes (1998) included the five most completely known "prolacertiform" taxa in a phylogenetic analysis: *Prolacerta* (Early Triassic; South Africa, Antarctica, Australia), *Protorosaurus* (Late Permian; Europe), *Langobardisaurus*, *Macrocnemus* and *Tanystropheus* (Mid Triassic; Europe). Amongst these, he recognised a clade incorporating tanystropheids (*Tanystropheus*, *Langobardicus*) and *Macrocnemus*, to which the climbing non-"prolacertiform" *Megalancosaurus* and *Drepanosaurus* formed a sister clade. The Permian *Protorosaurus* formed the sister taxon to this heterogenous clade, while *Prolacerta* itself emerged as the sister taxon of Archosauriformes (Fig. 13). However, Dilkes' analysis was completed prior to new work on the Late Permian genus *Protorosaurus* (Gottmann-Quesada and Sander 2009). The skull of this genus has remained very poorly known because the skull of the holotype is badly damaged. A second, more complete skull has existed in the collections of the Naturkundemuseum Kassel for more than thirty years (Haubold and Schaumberg 1985, p. 184) but has only recently been fully studied (Annalise Gottmann, Bonn).

Czatkowiella has been coded into Dilkes' data matrix and the codings for *Protorosaurus* (Dilkes, 1998) have been updated, using information and photographs supplied by Annalise Gottmann (personal communication 2002, 2005). One of the most important changes is in Dilkes (1998) character 8. Like *Czatkowiella*, the new material shows that *Protorosaurus* lacks a posterolateral process on the premaxilla. We first ran a heuristic search using the full matrix (PAUP 3.1: random addition sequence, Tree-bisection-reconnection [TBR], multistate characters treated as polymorphism) and obtained four equally parsimonious trees (Length = 399, consistency index [CI] = 0.439, rescaled consistency index [RC] = 0.268). The strict consensus tree placed *Czatkowiella* as the sister group of *Protorosaurus*, with the two forming a small clade at the base of Archosauromorpha (Fig. 14A). The original matrix is too large for a more rigorous Branch-and-Bound search, so its size have been reduced by removing the archosauriform *Euparkeria*, the long-necked *Langobardisaurus* that always groups with *Macrocnemus* and *Tanystropheus*, and all of the rhynchosaur taxa (the main focus of Dilkes' 1998 study) except the basal *Mesosuchus*. The analysis yielded two Maximum Parsimony Trees (MPT) (L = 289, CI = 0.554, RC = 0.288) that differed only in the placement of the archosauromorph *Trilophosaurus* (as a sister taxon to the *Macrocnemus*/*Tanystropheus*/drepanosaurid clade or as the sister taxon of all archosauromorphs crownward of *Protorosaurus*). The strict consensus of these trees is shown in Fig. 14B.

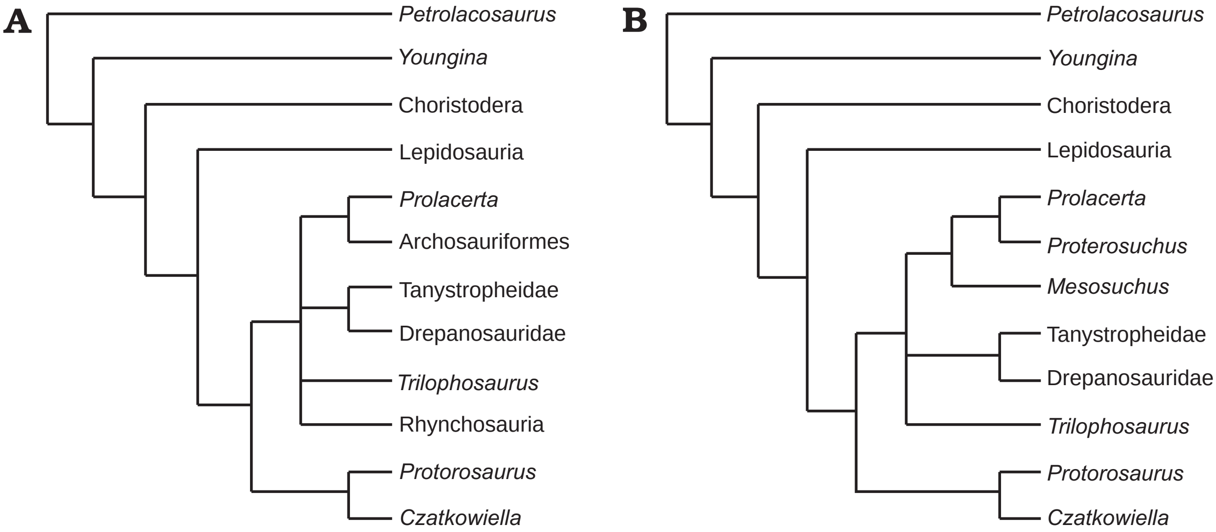


Fig. 14. Cladograms resulting from analyses using the matrix of Dilkes (1998) with data for *Protorosaurus* updated and with the inclusion of *Czatkowiella*. **A**. Strict consensus of four equally parsimonious trees resulting from a heuristic search using the full matrix (but with smaller clades grouped subsequently where appropriate to simplify the tree). **B**. Strict consensus of two maximum parsimony trees obtained from a branch-and-bound analysis using a reduced version of the Dilkes (1998) matrix (see text for details).

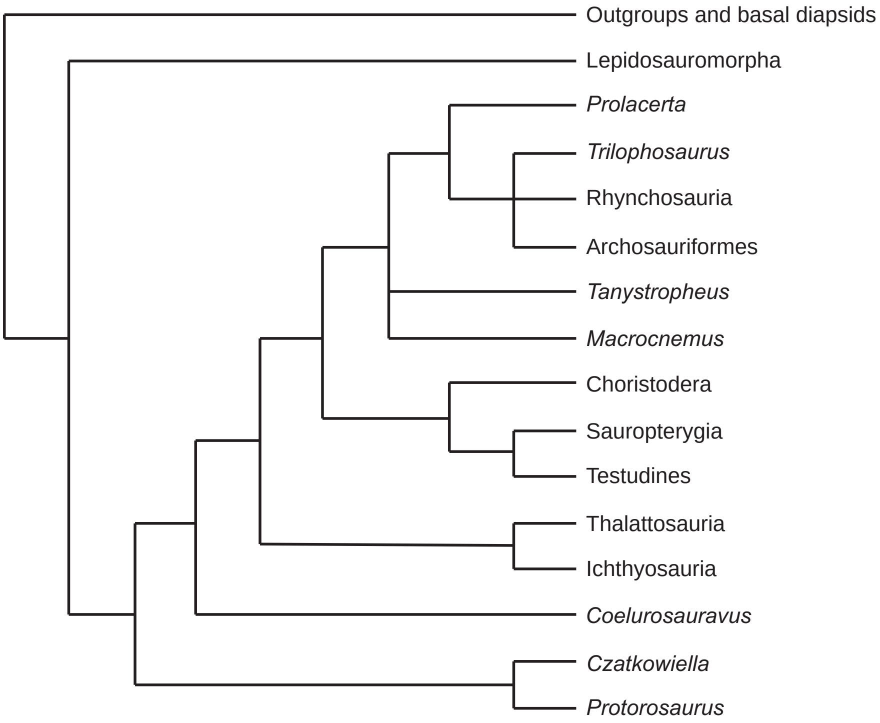


Fig. 15. Strict consensus of three equally parsimonious trees resulting from a heuristic search using the data matrix of Müller (2004), with *Czatkowiella* added and *Protorosaurus* updated.

A second, more general, diapsid analysis has recently been published by Müller (2004). Again, *Czatkowiella* has been coded into this data matrix, the codings for *Protorosaurus* updated, and an analysis run using the same format as the original analysis (heuristic search option, random addition sequence — 100 replicates, TBR branch swapping, trees rooted by outgroup [Synapsida, Seymouriidae], and with multistate characters interpreted as polymorphism). The analysis produced 3 equally parsimonious trees (TL = 1008; CI = 0.425; RC = 0.232), the strict consensus of which (Fig. 15) again places *Czatkowiella* and *Protorosaurus* as sister taxa, but at the base of a clade that incorporates Archosauromorpha, Sauropterygia, Testudines, ichthyosaurs, and the Permian glider *Coelurosauravus*, but not Lepidosauromorpha.

These two taxa (*Protorosaurus* and *Czatkowiella*) may thus represent a small clade of basal Permo-Triassic diapsids (Protorosauria *sensu stricto*) that are not closely linked to long-necked archosauromorphs like *Prolacerta*, *Tanystropheus* and *Macrocnemus*. Vertebral elongation would thus be a primitive rather than a derived trait within diapsids, reversed in several subsequent lineages (*e.g.*, rhynchosaurs, trilophosaurs). *Protorosaurus* and *Czatkowiella* share a similar skull morphology (long nasals, large lacrimal fully or partially excluded from the orbit by the prefrontal, maxillary tooth row not extending far beyond the anterior margin of the orbit, jugal with only a short posterior process, loss of the parietal foramen, reduction of the quadratojugal, slender dentary), but most of these features are not unique and occur in other diapsids of this grade (*i.e.*, around the base of Neodiapsida). Images of the Kassel skull (Annalise Gottmann, photograph) suggest that *Protorosaurus* may share the unusual premaxillary morphology of *Czatkowiella* in that in both the articular surface between the premaxillae appears weak. However, they differ in parietal morphology (fused with a sagittal crest in *Protorosaurus*, no evidence that the postparietals were incorporated). The teeth of both taxa have a similar shape and implantation. None of the teeth in the Kassel skull shows the mediolateral compression and grooving seen in mature teeth of *Czatkowiella*, but a partial dentition from a British *Protorosaurus* specimen (Evans and King 1993) has this morphology, and tooth shape may vary with age.

Postcranially, *Protorosaurus* and *Czatkowiella* share a long neck constructed of elongated cervicals with long, low spines, and slender, horizontally orientated cervical ribs. The cervical vertebrae of *Czatkowiella*, however, are more gracile and have much lower neural spines. In the trunk, the spines are also shorter while those of the caudal series lack the deeply bifid spines that characterise much of the tail in *Protorosaurus*. In its turn, *Protorosaurus* lacks the three-headed ribs found in the anterior trunk of *Czatkowiella* (Fig. 11A).

Thus *Czatkowiella* and *Protorosaurus s*hare few, if any, unique derived characters. They show similarities that may indicate relationship or may simply reflect a similar evolutionary grade. A more complete description of *Protorosaurus* (Gottmann-Quesada and Sander 2009) will help to resolve the issue.

CONCLUSIONS

Czatkowiella is relatively well known compared to other early diapsids but it has still proved difficult to classify. It shows skull and vertebral characters once thought diagnostic of the long-necked "prolacertiforms" (loss of the parietal foramen, distinct transverse processes on the dorsal vertebrae, double-headed ribs), but most recent cladistic analyses, including those presented here, have failed to support a monophyletic Prolacertiformes (Dilkes 1998; Rieppel 2002; Müller 2004). Our analysis using the matrices of Dilkes (1998) and Müller (2004) suggests a relationship between *Czatkowiella* and the Late Permian *Protorosaurus* at the base of Archosauromorpha. *Czatkowiella* is thus to be considered a survivor of the Permian stage of archosauromorph phylogeny (Fig. 16). However, this needs to be confirmed with a more detailed analysis at the new material of *Protorosaurus* (Gottmann-Quesada and Sander 2009). If this hypothesis of relationship is correct, then the similarities found between the cervical vertebrae and ribs of *Protorosaurus* (*sensu stricto*) and traditional "prolacertiforms" probably represent the retention of primitive character states, possibly synapomorphic for Archosauromorpha, or, given the cervical morphology of the basal diapsid *Petrolacosaurus* (Reisz 1981), for a more inclusive group. The challenge for the future will be to resolve the phylogenetic relationships of the other, more fragmentary, taxa previously classified as prolacertiform.

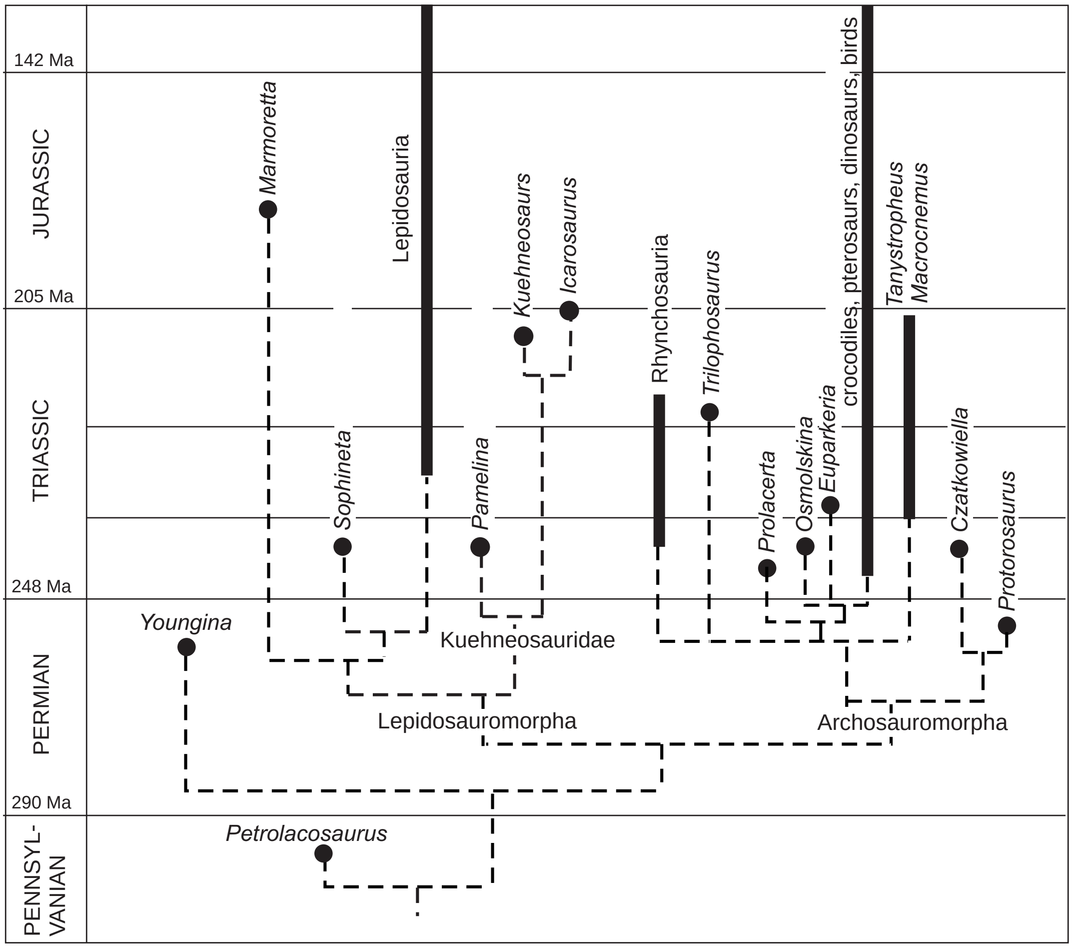


Fig. 16. Early diapsid phylogeny on a stratigraphic scale based on the current consensus, and present analysis of the Olenekian Czatkowice 1 taxa. Czatkowice stem kuehneosaur (Evans 2009); Czatkowice stem lepidosaur (Evans and Borsuk-Białynicka 2009).

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APPENDIX 1

Supplementary data matrix for *Czatkowiella* and *Protorosaurus*.

A. Codings for *Czatkowiella* and *Protorosaurus* in the data matrix of Dilkes (1998). Non standard entries: A = 1 or 2;

Czatkowiella	00010 00000 00??A 001?0 00??0 11011 010?1 1210? 0?011 01110 0??00 10100 00000 00?20 000?? 011?? 21101 0???1 ????? ????? ?1??? ????? ????? ????? ????0 00000 0001? 0A?01 ??00
Protorosaurus	01010 00000 000?1 00100 00001 210?1 ?101? 11??? ????? ????? 00?00 10000 00000 ????0 00010 0111? 21??0 102?3 21??? ???00 1???0 110?1 00?00 00000 11000 ?000? 00?01 0?000 0?00

B. Codings for *Czatkowiella* and *Protorosaurus* in the data matrix of Müller (2004). Non standard entries: A = 1 or 2, B = 1 or 3.

Czatkowiella	00010 10110 02101 02001 0?100 11?1? 1010? ?1011 0??00 001?? ?1??0 ????? ????? ?0??? ????? ????? ?0000 0?0?? 210?? 01?00 ?110? ????? ??1?0 000?? 00?00 10100 0???0 10?00 ????? ????? ?0001 11200 00200 0???? ???2? ?0010 00?1
Protorosaurus	00010 10110 22B?1 020?1 ?0?00 01??? ????1 0?011 0100? 0?10? 11?00 0??00 ??00? 200?0 ?0?00 01010 00000 0?010 1???? ????? 0100? 0?20? ?0??? 0000? 1100? 00??? ????? ????? ????0 11100 ?0001 ?100? ????? 00??? 0?12? ?0100 1011

CRANIAL AND MANDIBULAR OSTEOLOGY OF THE EARLY TRIASSIC ARCHOSAURIFORM *OSMOLSKINA CZATKOWICENSIS* FROM POLAND

MAGDALENA BORSUK-BIAŁYNICKA and SUSAN E. EVANS

Borsuk-Białynicka, M. and Evans, S.E. 2009. Cranial and mandibular osteology of the Early Triassic archosauriform *Osmolskina czatkowicensis* from Poland. *Palaeontologia Polonica* **65**, 235–281.

The basal archosauriform *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003 from the Early Olenekian karst deposits of Czatkowice near Kraków (southern Poland) shares a unique mosaic of skull character states with the African Anisian genus *Euparkeria*. This is considered, with reservation, as a basis for including them in the family Euparkeriidae Huene, 1920. A provisional diagnosis is given for this family, but no unique derived character states have been identified to support its monophyly. *Osmolskina* and *Euparkeria* differ primarily in snout structure. The vertical orientation of the basisphenoid, and the postero-ventral position of the entry foramina for cerebral branches of the internal carotid artery place both genera crownward of the proterosuchids. Lack of ossification of the medial wall of the otic capsule and the partial retention of pterygoid teeth exclude them from crown-group Archosauria, while they also lack erythrosuchid autapomorphies (including extremely short cervical vertebrae).

Key words: Early Triassic, Poland, basal Archosauriformes, euparkeriids.

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INTRODUCTION

Osmolskina is a small Early Triassic euparkeriid-grade archosauriform, known from the karst fissure deposits of Czatkowice near Kraków (southern Poland, Czatkowice 1 locality). *Osmolskina* is the largest and most common component of a diverse small vertebrate assemblage from these deposits including a small prolacertiform-grade reptile (Borsuk-Białynicka and Evans 2009), two basal lepidosauromorphs (Evans and Borsuk-Białynicka 2009a), including a basal kuehneosaurid (Evans 2009), procolophonids (Borsuk-Białynicka and Lubka 2009) and temnospondyls (Szyszkin and Sulej 2009). A tiny stem-frog, *Czatkobatrachus polonicus* (Evans and Borsuk-Białynicka 1998, 2009b; Borsuk-Białynicka and Evans 2002), and some fish, also belong to this fauna.

The Early Triassic archosauriforms are crucial to an understanding of the incompletely known section of phylogeny preceding the split between the crocodilian and dinosaur/avian lineages. Terrestrial faunas of this age have been recorded from all over the world, beginning with the most complete assemblages of eastern European Russia (Ochev and Shishkin 1985, 1989; Shishkin and Ochev 1993), through the Lower and Middle Germanic Buntsandstein (Induan-Olenekian in age), the North American Wupatki Member (the basal member of Moenkopi Formation, Morales 1987), the upper part of the Chinese Guodikeng Formation (Jimsarian, Fuguan, and probably Ordosian faunachrons, Lucas 1993), to the Gondwanan formations: the African Karoo (*Lystrosaurus* and *Cynognathus* zones), the Antarctic Fremouw, Indian Panchet, and Australian Arcadia formations.

The Early Triassic fauna was not as uniform over Pangaea as was that of the Permian. Therapsids were present in the Gondwanan assemblages along with large temnospondyls, basal archosauriforms, and procolophonians, but were absent from Laurasian assemblages, except for those of the Induan period (Battail 1993). Small non-archosauriform reptiles and other microvertebrates were distributed more randomly. If the Czatkowice 1 fauna is correctly dated to the earliest Late Olenekian (Szyszkin and Sulej 2009), this is the first terrestrial vertebrate assemblage of this age recorded from Euramerica outside the Cis-Urals and East European Platform.

The objective of the present paper is to give a detailed description of the cranial morphology of *Osmolskina czatkowicensis*. The systematic position of *Osmolskina*, its relationships with *Euparkeria*, and the status of the Euparkeriidae, as well as the information value of cranial characters at this stage of evolution, are also discussed.

Institutional acronyms. — BPS, Bayerische Staatssammlung für Paläontologie und Historische Geologie, München, Germany; GPIT, Institute und Museum für Geologie und Paläontologie, Universitat Tübingen, Germany; MZ, Museum of the Earth, Polish Academy of Sciences, Warsaw, Poland; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; SAM, South African Museum, Cape Town, Republic of South Africa; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

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GEOLOGICAL SETTING

Czatkowice 1 was the largest of several sediment infilled caves developed in the Early Carboniferous limestone quarry. (Paszkowski and Wieczorek 1982). Paszkowski (2009) gives a more detailed account of the geological setting of Czatkowice 1 locality. As a result of economic exploitation of the quarry, the Czatkowice 1 fissure no longer exists. The original age determination of the assemblage, as Early Olenekian on the basis of *Gnathorhiza* (Dipnoi) teeth and procolophonian material (Borsuk-Białynicka *et al.* 2003), has been revised to earliest Late Olenekian on the basis of temnospondyl material (Shishkin and Sulej 2009). This suggests Czatkowice 1 karst deposits are slightly younger than the upper part of the Vetlugian Superhorizon of the East European biozonation (Shishkin *et al.*1995, 2000; Shishkin and Ochev 1985; Ochev and Shishkin 1989). According to Ochev (1993), and Shishkin and Ochev (1993), the locality must have been within the xeric circumequatorial belt occurring at this latitude in Northern Pangaea. The vertebrate assemblage from Czatkowice 1, including both terrestrial and amphibious animals and some fish (Borsuk-Białynicka *et al.* 1999), indicates that the material was deposited primarily in a freshwater pool, probably developed within an oasis in an otherwise arid Central European Scythian environment. At a higher taxonomic level, the assemblage corresponds to others in Laurasia, but it differs dramatically in the size of the animals included (see below) and was probably taphonomically biased. The taphonomy of the Czatkowice 1 locality has recently been studied by Cook and Trueman (2009). The authors suggest that the diagenetic pathways included reworking of the skeletal remains, originally incorporated into sediments at the bottom of ephemeral lakes and pools, and their redeposition in nearby cave systems after a short fast transport during periods of stormy weather and flooding.

MATERIAL AND METHODS

General comments. — The material is completely disarticulated, and often broken into pieces, both before deposition and in preparation. Chemical breakdown of the matrix by acetic acid is the only method of preparation for this material. Freshly dissociated pieces may sometimes be matched with one another and glued together. The bones are mostly white, orange or dark brown, and are generally preserved three-dimensionally. Most of them show relatively little abrasion. To date, about 100 specimens have been catalogued, but there are hundreds of other specimens. The materials are stored at the Museum of the Earth and the Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

Attribution of osteological elements. — The primary criteria for the attribution of disarticulated bones to particular species are size ranges and relative frequency of particular morphotypes in the samples. Robustness of elements, sculpture, articular facet fit, and phylogenetically relevant characters are the next criteria. The composition of fossil assemblages is biased by the differential preservational potential of particular elements belonging to the same animal, and those of different animals. Nonetheless, the relative percentage of elements in a fossil sample seems to be fairly consistent for each member of the assemblage. The largest (20 mm dentary length) and most frequent remains belong to Archosauriformes and are generally considered conspecific. Some less common bones exceeding the normal variability range of the genus have been excluded as representing a separate taxon, their attribution being relegated to future studies. Next in size in the assemblage is a prolacertiform-grade reptile (Borsuk-Białynicka and Evans 2009a), but the dimensions overlap. The remaining material is a mixture of medium-sized procolophonids, and tiny bones (up to a few mm in length) including two rarer lepidosauromorphs (Evans and Borsuk-Białynicka 2009a; Evans 2009), tiny temnospondyls (Shishkin and Sulej 2009), and the stem frog *Czatkobatrachus polonicus* (Evans and Borsuk-Białynicka 1998, 2009b; Borsuk-Białynicka and Evans 2002). The dimensions of these animals do not overlap the range of *Osmolskina czatkowicensis*.

Reconstruction (Fig. 1A, B). — Based on counts of the best preserved bone fragments, such as frontals, quadrates and articulars, the number of *Osmolskina* individuals of the Czatkowice 1 taphocoenosis amounts to several hundred. Some more fragile bones are represented by single specimens. The reconstruction of the whole skull on the basis of such material requires some scaling of elements. The shape of paired premaxillae in the horizontal plane (Fig. $2A_1$) is conclusive for the horizontal outline of the skull as a whole, while the

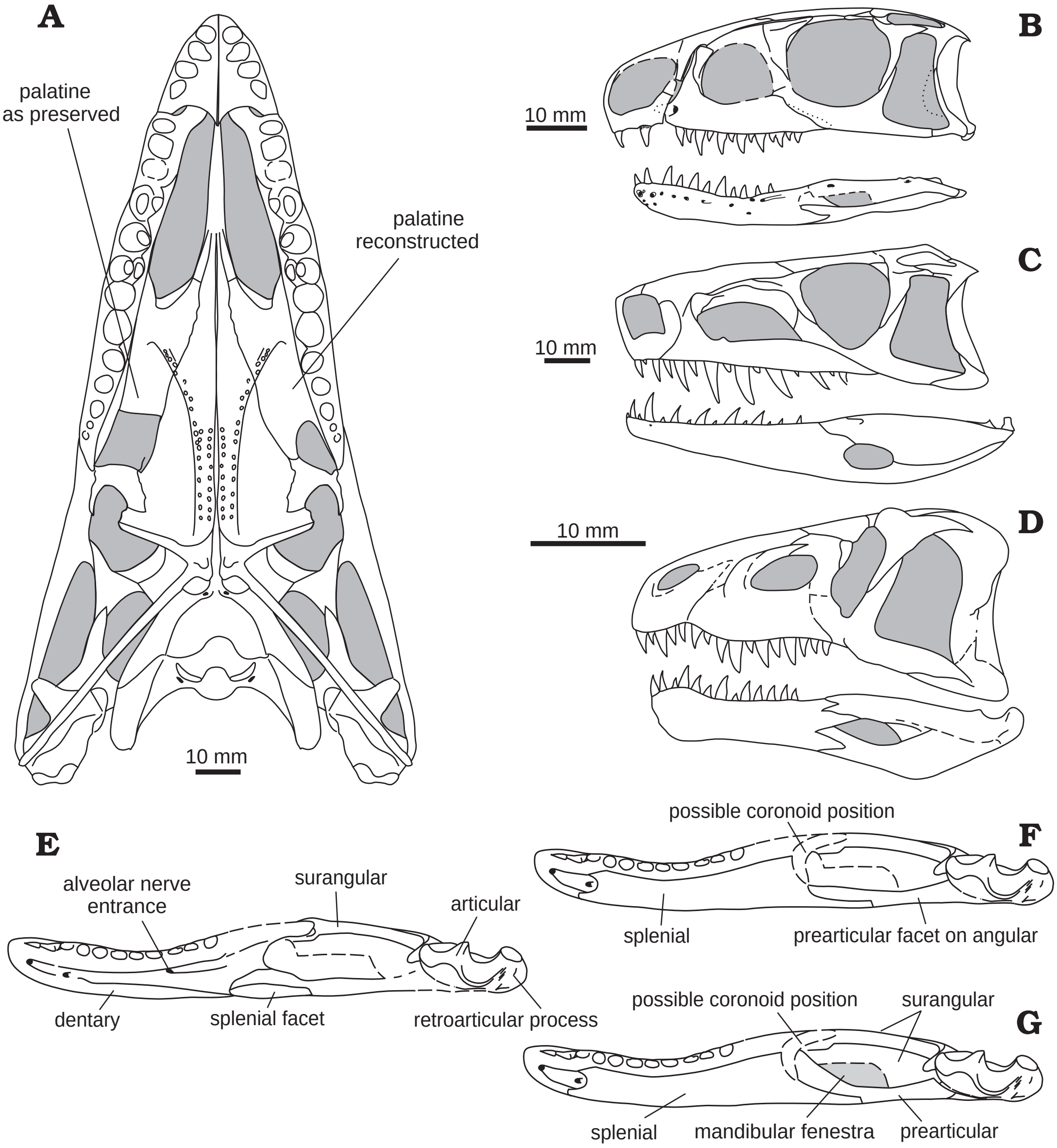

Fig. 1. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. Reconstructions: **A**. Skull. **B**. Skull with mandible. **E**–**G**. Mandibles, different views of mandibular bones; without splenial and prearticular (**E**), without prearticular (**F**), complete (**G**); out of scale. **C**. *Euparkeria capensis* Broom, 1913, skull with mandible (from Ewer 1965, fig. 2). **D**. *Erythrosuchus africanus* Broom, 1905, skull with mandible (from Gower 2003, fig. 1). Ventral (A), left lateral (B–D), and medial (E–G) views.

profile of the nasal process of the premaxilla (Fig. $2B_2$, D_1) affects that of the skull in a sagittal plane. The length of skull roof bones should correspond to that of the maxilla articulated with the jugal and quadratojugal, whereas the gap between the skull roof bones and the ventral profile of the skull should match the size of the quadrate, which closes the skull outline from behind. These interdependent dimensions help to correct the relative sizes of missing parts, especially those of the maxillae. There are no complete specimens of the maxilla. The posterior parts of the maxillae preserved as separate pieces (Figs 5B, 14D, E) are tentatively considered as belonging to the same species if they match the size and thecodont tooth implantation of the anterior fragments. The length of the maxilla has been deduced on the basis of the gap left between the jugal and the anterior part of the maxilla. Among other problematic elements, the pterygoids barely fit within the space outlined by the maxillae and jugals (Fig. 1A) unless aligned obliquely with the dentigerous fields descending ventro-laterad to produce a V-shaped concave palate open ventrally.

In spite of a poor ossification of the walls of the braincase, the component bones are fairly well preserved and allow a reconstruction of the whole element and of its details (Figs 17, 25).

The braincase structure of the basal archosauriforms *Sarmatosuchus*, *Erythrosuchus*, and *Euparkeria*, and of the basal crurotarsians *Batrachotomus* and *Stagonolepis* (Gower and Sennikov 1997, Gower 1997, Gower 2002, Gower and Weber 1998, and Gower and Walker 2002, respectively) has been used as a reference. Nonetheless, the complex nature of this part of the skeleton, and preservation problems, substantiate the use of extant comparative material. Lizards, although more distantly related to archosauriforms than crocodiles, have a less specialized skull structure than the latter group. Hence, lizard skulls have been used as the basis of structural interpretations, and the terminology of Oelrich (1956) has been applied.

Several points contribute to the reconstruction of the structure and the proper life position of the mandible. Most informative is the mandibular symphysis, which determines the alignment of the dentaries and their inclination to one another.

Individual age and size. — The braincase specimens show poor ossification of the internal surface, with almost no finished bone (except for the passage of nerve canals) suggesting that they are immature. The rarity of fully attached teeth may further suggest that much of the material is immature. However, cervical vertebrae, that match the size of the skull bones, have neurocentral suture closed which is a criterion of maturity in crocodiles and, most probably, in crocodilian relatives (Brochu 1996). The most abundant vertebrae of *Osmolskina*, with neural arches fused, are about the size of those of an adult individual of the lizard *Heloderma suspectum* (ZPAL RV/26) used for comparison. This specimen has a skull 60 mm in length, which corresponds to the average skull length reconstructed for *Osmolskina*. The closure of the neurocentral sutures does not necessarily mean a complete stoppage of growth (Brochu 1996).

The term “grade” used herein refers to taxa that share the same combination of primitive and derived characters but no unique synapomorphies.

SYSTEMATIC BACKGROUND

The Archosauriformes (*sensu* Gauthier 1986) correspond to what Romer (1956) designated as Archosauria. They belong to the diapsid subgroup Archosauromorpha (Gauthier, 1986) along with rhynchosaurs, “prolacertiforms” and a number of isolated genera which stand as plesions (Evans 1988). According to Gauthier’s definition, Archosauria is restricted to the two extant groups, Aves and Crocodilia, their most recent common ancestor and all its descendants, and thus correspond to the “crown group Archosauria” of *e.g.*, Benton and Clark (1988), or to Avesuchia of Benton (1999). Archosauriformes is a more-inclusive taxon encompassing a series of taxa on the archosaurian stem. Phylogenetic relationships within this assemblage have been studied by many authors (Benton and Clark 1988; Gauthier 1986; Sereno and Arcucci 1990; Sereno 1991; Parrish 1993; Juul 1994; Gower and Sennikov 1996; Gower 1997; Gower and Walker 2002). Gower and Wilkinson (1996) demonstrated a substantial agreement in the general topology of cladograms resulting from those studies, all supporting the monophyly of Archosauria *sensu* Gauthier (1986). The semistrict reduced consensus cladogram of those analyses (Gower and Wilkinson 1996, fig. 4) is a framework (Fig. 31) for discussion in the present paper. According to this tree, proterochampsids, euparkeriids, erythrosuchids, and proterosuchids are consecutive outgroups of Archosauria. The exclusion of these taxa from the Archosauria is based mainly on the retention of a palatal dentition (lacking in Archosauria *sensu* Gauthier 1986) and a virtually transverse construction of the tarsus, rather than the posteriorly deflected calcaneum of archosaurs (Juul 1994, p. 38). It is also supported by braincase data, most notably by a lateral position of the entrances of the cerebral branches of the internal carotid arteries into the parabasiphenoid (Gower and Weber 1998).

Proterosuchids are the most basal of the non-crown-group archosauriforms, including the medium-sized *Archosaurus* from the Late Permian of Russia (Tatarinov 1960; Sennikov 1995; Gower and Sennikov 2000), *Proterosuchus* from the Early Triassic (*Lystrosaurus* Zone) of South Africa (Cruickshank 1972), *Fugusuchus hejiapanensis* from the Early Triassic of China (Cheng 1980; Gower and Sennikov 1997), and the Mid Triassic Russian *Sarmatosuchus otschevi* (Gower and Sennikov 1997).

Erythrosuchids are large archosauriform predators recorded from the Late Olenekian through Ladinian of Russia, China, Argentina, and South Africa, and reviewed by Parrish (1992; see also Gower 2003). *Euparkeria* from the Anisian of the South African Karoo Formation (*Cynognathus* Zone), the only adequately known euparkeriid genus, was roughly contemporaneous with *Erythrosuchus* in South Africa (Mid Triassic, early Anisian, *Cynognathus* Zone; Hancox *et al.* 1995; Shishkin *et al.* 1995), but is much smaller in size.

Euparkeria capensis Broom, 1913 became the type genus of the family Euparkeriidae Huene, 1920. *Browniella africana* (Broom, 1913) from exactly the same site as *Euparkeria capensis* is currently considered conspecific with the latter (Haughton 1922; Ewer 1965). Among four Chinese genera assigned to the family, *Wangisuchus* Young, 1964, from the Upper Ehrmaying Formation (early Mid Triassic), *Xilousuchus* Wu, 1981 (Early Triassic, Heshanggou Fm), and *Halazhaisuchus* Wu, 1982 (Early Triassic, Lower Ermaying Fm; Lucas 1993) are of doubtful affinity (Gower and Sennikov 2000). Sennikov (1989) added a new possible euparkeriid, *Dorosuchus neoetus*, from the Anisian Donguz Formation to this list (Gower and Sennikov 2000). *Turfanosuchus* Young, 1973 from the late Early Triassic Lower Ehrmaying Formation, originally regarded as an euparkeriid (Young 1973), is more probably a crurotarsian (Parrish 1993 and Gower and Sennikov 2000, *contra* Wu and Russell 2001).

The Mid through Late Triassic Proterochampsidae (Sill 1967; Romer 1971, 1972a) includes medium-sized, lightly built semiaquatic crocodile-like animals from South and North America. Their highly distinctive anatomy is poorly documented.

SYSTEMATIC PALEONTOLOGY

Clade Archosauromorpha Huene, 1946

Clade Archosauriformes Gauthier, 1986

Family **Euparkeriidae** Huene, 1920

Provisional diagnosis. — Basal archosauriforms differing from crown-group Archosauria in the lateral orientation of the calcaneal tuber and the unossified medial wall of the otic capsule. They share a vertical orientation of the basisphenoid and the absence of an astragalocalcaneal canal with all archosauriforms except proterosuchids. They differ from erythrosuchids in the lighter construction of the skeleton, relatively smaller skull, and generally more elongate cervical vertebrae (centrum length/depth usually around 1.4–1.6 instead of 0.4–1.0 in erythrosuchids).

Generic composition. — *Euparkeria* Broom, 1913, *Osmolskina* Borsuk-Białynicka *et* Evans, 2003, most probably *Dorosuchus* Sennikov, 1989.

Occurrence. — Olenekian to Anisian of Pangaea (localities in Europe and South Africa).

Genus ***Osmolskina*** Borsuk-Białynicka *et* Evans, 2003

Diagnosis. — As for the species.

Osmolskina czatkowicensis Borsuk-Białynicka *et* Evans, 2003

Holotype: The fragmentary maxilla ZPAL RV/77 (Borsuk-Białynicka and Evans 2003, fig. 2A; and Fig. 5 herein).

Type horizon: Early Late Olenekian.

Type locality: Czatkowice 1, southern Poland.

Occurrences. — Type locality only.

Emended diagnosis. — An euparkeriid similar to *Euparkeria*, but smaller, having a modal skull length of about 60 mm, modal femur and tibia length about 40 mm and 30 mm, respectively. Differs from *Euparkeria* in having a slightly overhanging premaxilla (but less so than in proterosuchids) that has a deeper body (maximum length to depth 10:3 in *Osmolskina, versus* 10:4 in *Euparkeria*), a more oblique posterolateral process (sloping at an angle of 50° *versus* almost 90° in *Euparkeria*). The posterolateral process was weakly attached to the maxilla (with no peg and socket articulation developed), and was probably separated from it by a slit-like additional antorbital space. *Osmolskina* differs from *Euparkeria* in having a subquadrangular nasal process of the maxilla, and a barely recessed antorbital fenestra. The preorbital part of the skull is less elongated than in *Euparkeria.* The maximum maxilla length to depth is 5:1 in *Osmolskina czatkowicensis*, *versus* 7:1 in *Euparkeria capensis*. The estimated tooth count is 13 in both species, but the teeth are less compressed in *O.*

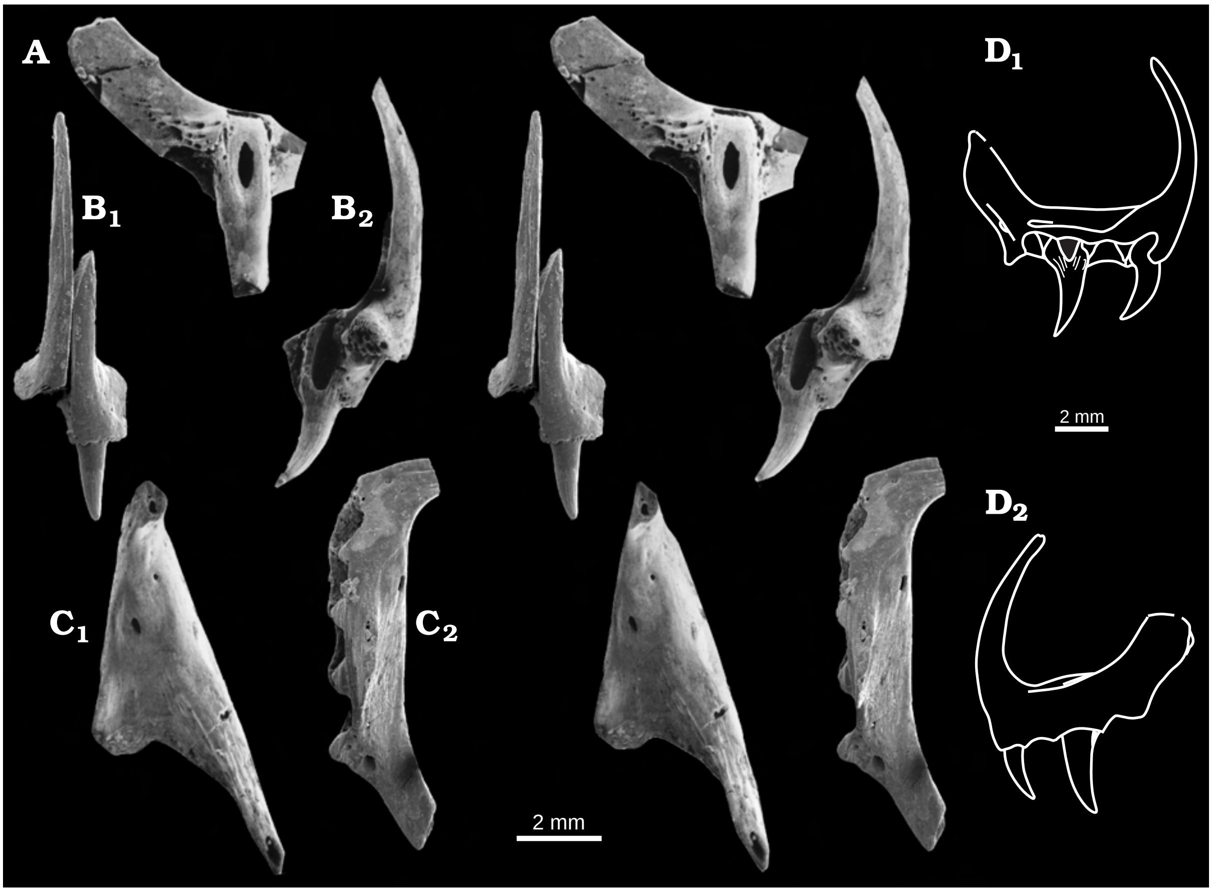

Fig. 2. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. Premaxillae. **A**. The posterolateral process ZPAL RV/83, in medial view. **B**. Articulated ZPAL RV/88a and 88b, in anterior (B_1) and right lateral (B_2) views. **C**. ZPAL RV/31, in dorsal (C_1) and medial (C_2) views. **D**. Reconstructions of premaxillae, in medial (D_1) and lateral (D_2) views. A–C, SEM stereo-pairs.

czatkowicensis. In *Osmolskina* the ventral bordering of the orbit is smoothly concave, and the orbit more rounded while tapering ventrally in *Euparkeria.* The mandible of *Osmolskina* does not increase in depth posteriorly unlike that of *Euparkeria*. *Osmolskina* differs from *Euparkeria* in the shorter humerus; more twisted femur (distal to proximal end angle is about 55° in *Osmolskina*, 32° in *Euparkeria*), and the extremely anterior position of the coracoid foramen or notch. Compared to *Dorosuchus* (femur about 90 mm, tibia about 70 mm in length, femur twist about 40°) *Osmolskina* is smaller and has the femur more twisted.

Material. — About 100 catalogued skull bones, including isolated braincase and mandibular elements, and several hundred less complete cranial elements.

SKULL ROOF

Premaxilla. — The premaxilla is robust and has three processes (Fig. 2). The main body is swollen to include four deep alveoli (Fig. $3A_2$, D) medially separated by interdental plates. A ventrally directed tubercle borders the tooth row. The posteriormost part of the bone is blunt, and more or less fits a concavity produced by the medially inclined anterior process of the maxilla (Fig. 3B, C_2) just anterior to the exit of the superior alveolar canal, but the contact is by no means precise. The posterolateral process passes obliquely backwards at an angle of about 50° to the long axis of the body. Distally, the medial surface of the process is sculptured by oblique (anteroventral) ridges (Fig. 2A) that are possibly for ligaments connecting the premaxilla to the nasal. The configuration of bones in this region suggests that the former overlapped the latter, but the overlapping parts are never preserved in the material. The posterior margin of the posterolateral process is acute and does not show any facets for the maxilla. The medial process of the premaxilla forms a triangular flange. Its medial border bears a symphyseal surface. The processes of both sides fill the space between the articulated premaxillae and

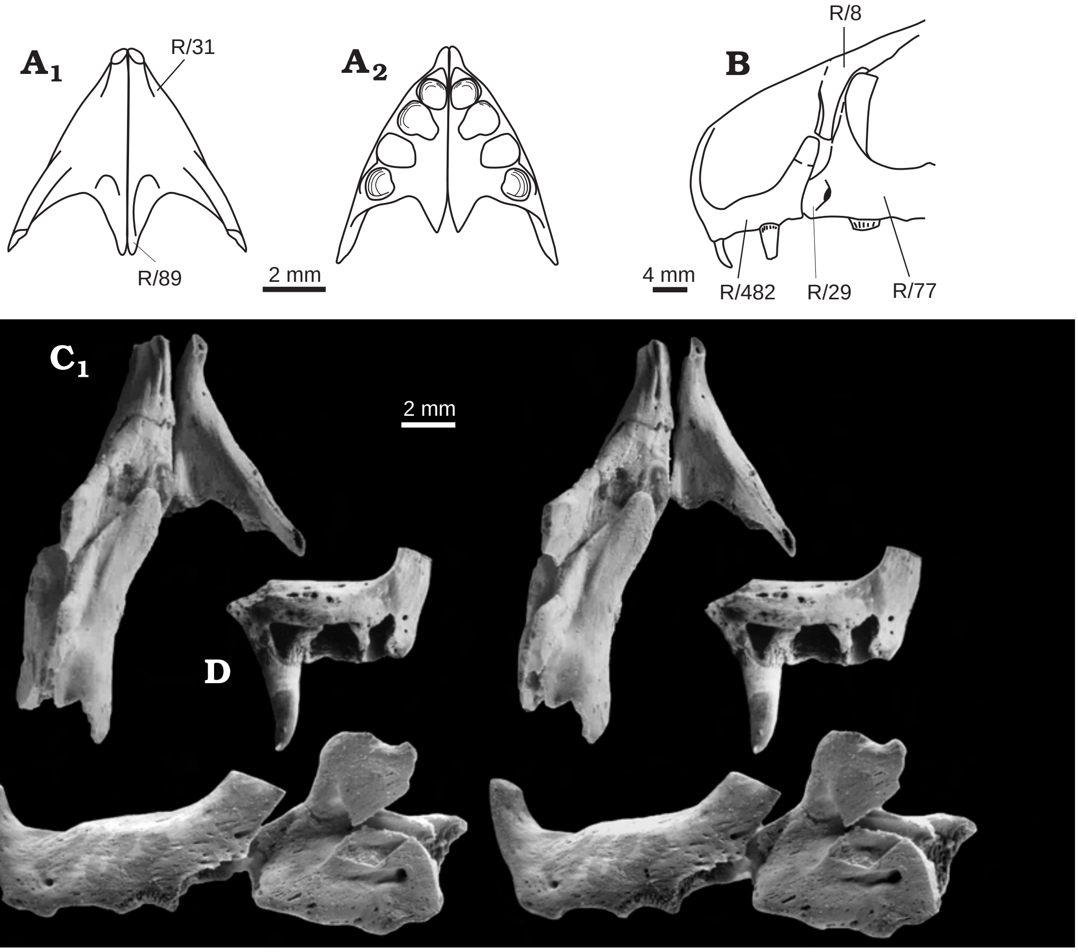

Fig. 3. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A**. Reconstruction of articulated premaxillae, in dorsal (A$_1$) and ventral (A$_2$) views. **B**. Reconstruction of anterior part of skull, in left lateral view. **C**. Premaxillae: ZPAL RV/30 (left) and 31 (right) combined with anterior part of maxilla ZPAL RV/29, in dorsal (C$_1$) and left lateral (C$_2$) views. **D**. Left premaxilla ZPAL RV/78, in medial view. C, D SEM stereo-pairs. Shortened catalogue numbers indicate the specimens on which the reconstruction is based.

protrude posteromedially. They leave no space for the entrance of the vomer (Figs 2C$_1$, 3A$_1$, A$_2$). On each side, a slight dorsal concavity received the underside of the anterior process of the maxilla (Fig. 3C$_1$). The premaxilla was probably held in place mainly by connective tissue.

The anterior (nasal) process is very tall, thin (Fig. 2B), and posteriorly concave. In transverse section, it is medially flat and laterally evenly convex. It suggests the external nares were fairly large. It tapers distally and becomes sub-tetrahedric at about 1/4 of its height, with the anterior and lateral surfaces flat, the former being narrower than the latter. The lateral surface probably served for the nasal contact. In anterior view, the articulated premaxillae are very slender. A longitudinal furrow follows the symphysis line on each side (Fig. 2B$_1$).

The length of the premaxilla body varies from ca. 7 to10 mm. Smaller specimens have more slender proportions and the angle of the posterior process to the horizontal is more acute. This variability is tentatively ascribed to allometric growth.

Maxilla. — There is no complete specimen. Usually, the maxilla breaks into four pieces that are difficult to match to one another. The central section (Fig. 4A) is usually sub-triangular but it develops dorsally into a tall, narrow sub-quadrangular nasal process (Fig. 6) and posteriorly into a horizontal tooth bearing ramus (ca. 30% the total height of the maxilla Fig. 6A, D–F). The borders of the nasal process are almost vertical, but become more oblique ventrally as the process broadens out. The lateral surface of the central portion is flat. Together with the curvature of the premaxilla (see above) and the position of the nasal (see below) it suggests that the snout was deep. Only the posterodorsal border of the maxilla curves slightly medially. The ventral border of the

Fig. 4. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. Anterior fragment of the holotype maxilla ZPAL RV/77 combined with a fragmentary nasal ZPAL RV/8, in lateral (A_1) and medial (A_2) views. SEM stereo-pairs.

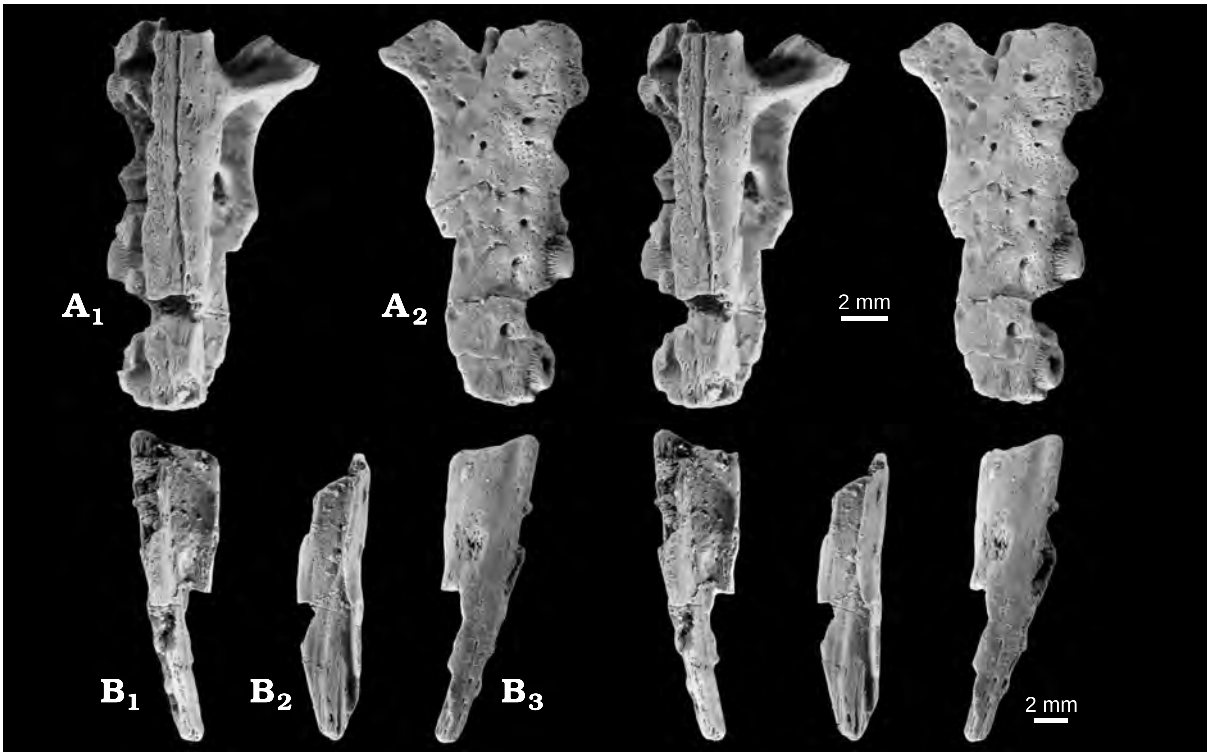

Fig. 5. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A**. Middle part of right maxilla ZPAL RV/81, in lingual (A_1) and labial (A_2) views. **B**. Posterior fragment of right maxilla ZPAL RV/160, in lingual (B_1), dorsal (B_2), and labial (B_3) views. SEM stereo-pairs.

maxilla is straight (Fig. 6A, C). A large exit foramen for the superior alveolar canal opens on the labial surface at the base of the premaxillary process (Figs $4A_1$, $6A_1$). The estimated number of alveoli is 13.

In the type specimen, ZPAL RV/77, the anterior border of the nasal process is damaged but the losses seem to be insignificant. The medial surface of the anterior border bears a longitudinal furrow descending almost half way down the total height of the maxilla. This groove is the posterior part of the nasal facet. Behind it the medial surface of the nasal process bears a pattern of sub-vertical ridges and furrows (Fig. $4A_2$) marking the position of the lacrimal. The posterior border of the nasal process crosses the dorsal margin of the maxilla to extend onto the medial surface. The dorsal margin of the horizontal ramus continues over the lateral face of the nasal process as an oblique crest ascending anterodorsally. The crest forms the anterior border of the weak antorbital recess.

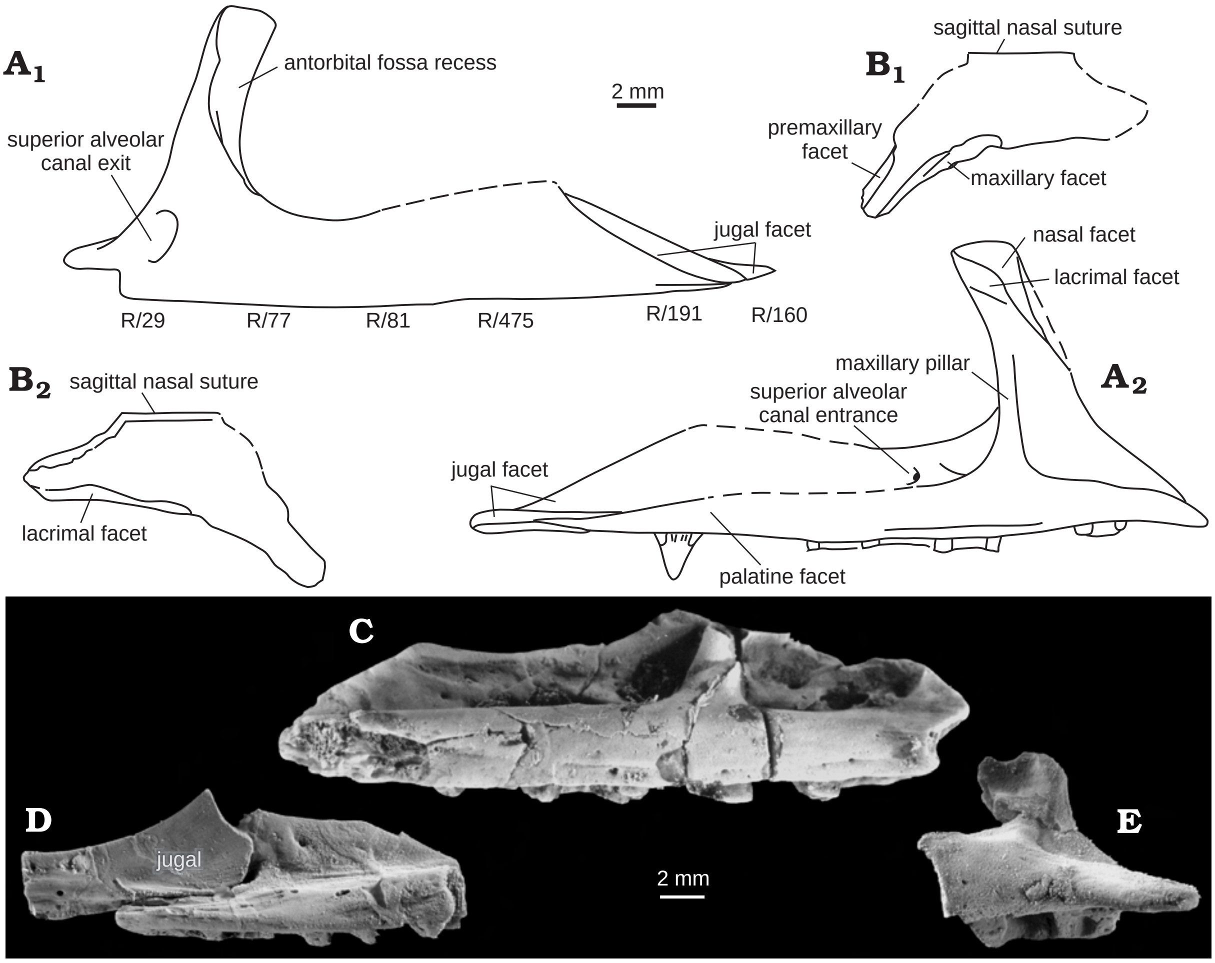

Fig. 6. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A**. Reconstruction of the left maxilla, in lateral (A_1) and medial (A_2) views. **B**. Left nasal ZPAL RV/8, in lateral (B_1) and medial (B_2) views. **C**. Central part of maxilla ZPAL RV/81, in medial view. **D**. Posterior fragment of maxilla ZPAL RV/484 combined with the anterior part of the jugal ZPAL RV/281, in medial view (right side bones reversed). **E**. Anterior part of maxilla ZPAL RV/29, in medial view. C–E SEM micrographs. Shortened catalogue numbers indicate the specimens on which the reconstruction is based.

The premaxillary process curves medially. It is an anteromedial pyramidal extension of the alveolar margin and corresponds to what Gow (1970) called an anterior median flange. There is no discrete articular facet for the premaxilla along the acute anterior border of the maxilla, nor is there any space between the nasal and maxilla for the posterior process of the premaxilla that probably fitted the anterior surface of the nasal. The contact between the processes of the premaxilla and maxilla was probably quite loose, possibly leaving an accessory antorbital fenestra. There are also no traces of a lateral overlap between the body of the maxilla and that of premaxilla. The bones probably only touched each other in this region, while the faintly sculptured ventral surface of the premaxillary process of the maxilla probably overlapped the dorsal surface of the medial process of the premaxilla in the anteriormost part of the palate (Fig. 3A). Articulated in such a way, the premaxilla slightly overhangs the maxilla (Fig. 3A_2, C), although the posterior premaxillary teeth are level with the maxillary tooth-row.

The medial face of the premaxillary process bears a sub-horizontal longitudinal furrow on the dorsal surface of the superior alveolar shelf. In articulated bones, this furrow is in line with the vascular foramen piercing the posterior margin of the premaxilla. It probably served for the neurovascular supply of the premaxilla from the superior alveolar canal. Faint sculpture on the lateral face of the premaxillary process, directly behind the anterior margin, may reflect the presence of ligaments that attached the premaxilla. Directly behind the nasal process, the dorsal border of the horizontal ramus is slightly concave, but the profile of the more posterior part is poorly known. It clearly sloped posteroventrally at the tip.

The medial surface of the main body of the maxilla (Figs $4A_2$, $5A_1$) displays a very deep, medially swollen alveolar part, and a sub-vertical pillar inclined anterodorsally and buttressing the fragile nasal process. Both the alveolar part and the pillar are sub-circular in transverse section, but the pillar is much smaller in diameter. The alveolar part is separated from the main lamina of the maxilla by a longitudinal furrow. A few millimetres posterior to the pillar base, and usually roofed by an oblique blade of bone (Fig. $6A_2$), is the entrance of the superior alveolar canal for the maxillary artery and superior alveolar branch of the maxillary nerve passing from the palatine. This opening (posterior alveolar foramen of Oelrich 1956) should correspond in position with the infraorbital foramen of the palatine. The palatine facet consists of a sub-perpendicular surface extending along the medial border of the alveolar edge between roughly the fifth to ninth alveolus, and tapering both anteriad (Figs $5A_1$, $6A_2$) and posteriad (Fig. 14D). The deepest part, facing obliquely dorsomedially at the level of about the sixth to seventh tooth, was probably received into a longitudinal concavity on the maxillary process of the palatine (see below). As a result, the anteromedial part of the palatine slightly overlapped the dorsal surface of the alveolar part of the maxilla.

As in the premaxilla, the maxillary alveoli are bordered by interdental plates situated slightly medial to the lingual side of the dentigerous margin. Labially the interdental plates pass into interdental septa. The alveolar part becomes flatter posteriorly (Fig. 6F), as the alveoli become shallower, and its dorsal wall bears numerous irregular perforations (possible reason for its poor preservation). The dorsal overlap of the jugal on the maxilla is fairly long (see *e.g.*, Figs $5B_2$, 6D).

Nasal. — The nasal is represented by a single damaged right specimen, ZPAL RV/8 (Figs 4, 6B), and some fragments. It is a transversally curved bone blade turning anterolaterally into a long process that descends obliquely down the lateral face of the snout. The posterior process, sub-triangular shape, allow for reconstruction of the U-shaped incision between joint nasals. The incision probably received the anteriorly protruding part of the frontal (Fig. 8B). An elongated wavy medial facet (Fig. $6B_2$) extending along approximately posterior one half of the preserved ventral border of the nasal should have received the lacrimal, but this bone has not yet been identified. The sagittal suture is straight and simple. The maxillary facet begins anterior to the lacrimal one and runs down the posterolateral border of the anterolateral process. As preserved, the process is rounded at the top and tapers ventrally. The anterior border of the process bears remnants of a premaxillary facet (Fig. $6B_1$).

Frontal. — The frontals (Fig. 7A–C) are represented by many specimens. They are flat, paired and strongly built, and ca. 3.5 times as long as wide. The sagittal suture is straight along the anterior third of its length, becoming increasingly sinuous posteriad. The frontonasal suture is broadly U-shaped (Fig. 8B) with anterolateral corners retracted, and bearing a dorsal nasal facet. Anterolaterally and posterolaterally the frontal joins the prefrontal and postfrontal respectively, so that it borders the orbit for only about one quarter of its length (the second quarter from the rear). The prefrontal facet incises the dorsal surface of the frontal obliquely (Fig. $8A_1$) at the level of the second quarter of the frontal from the front. The facet protrudes slightly laterally from the main body of the frontal. It is convex in transverse section and longitudinally ridged, which suggests a rather rigid junction permitting no mobility in the transverse plane. The postfrontal facet incises the posterior quarter of the lateral frontal margin, but is usually little exposed in dorsal view. Between the prefrontal and postfrontal, the orbital margin of the frontal is slightly concave. The ventral surface of each frontal bears a strong, laterally concave sub-olfactory process (Fig. $8A_2$). The longitudinal concavity of the olfactory canal deepens at both ends. The posterolateral part of each frontal is slightly dorsally concave (Fig. 7B). It bears posterior and medial parietal facets facing ventrally (Fig. 8C), and a ventrolateral postfrontal facet (Fig. $8A_2$, D). However, the medial border of the process also bears a dorsal facet (Fig. 7B), and was probably overlapped by a thin superficial sheet of the parietal. The posterior border of the combined frontals is U-shaped.

The total length of frontals varies between roughly 15 and 22 mm. The posterior width is 100–118% of the anterior width. This variability affects the shape of the lateral border, which varies from almost straight to concave. Some larger specimens do not fit into the variability range of the majority form. They are relatively shorter and stouter (in ZPAL RV/96 posterior width attains ca. 155% of the anterior one), while the postfrontal facet invades the dorsal surface of the frontal. The large type is much less numerous in the assemblage. Whether it is a variant of the majority form or belongs to another animal cannot be resolved at the present time. The frontals of the majority variant are usually longer and more slender than those of *Euparkeria* (Ewer 1965), but the topography of the bones in the frontal region, including the suture structure, is exactly the same.

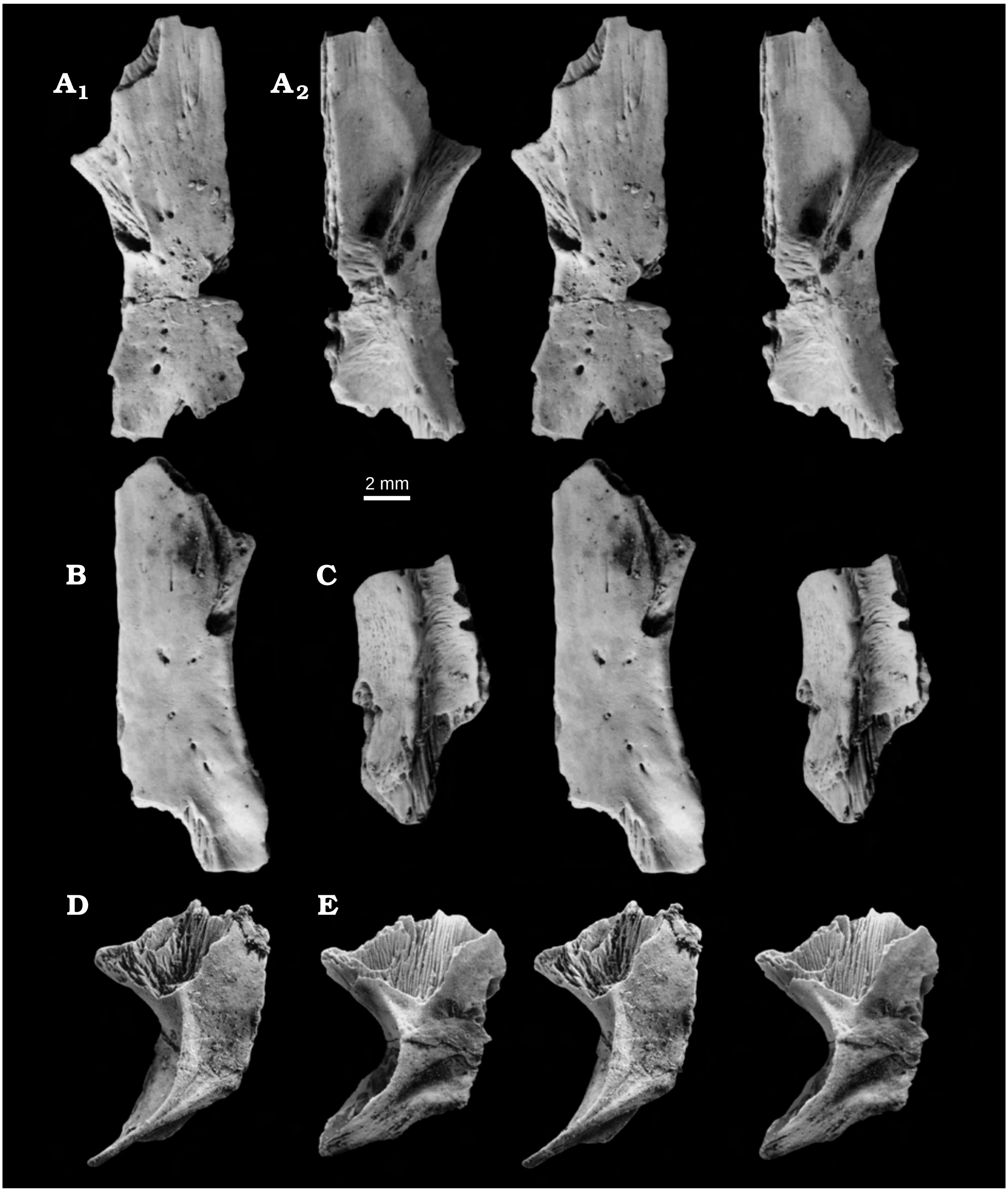

Fig. 7. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A**. Left frontal ZPAL RV/91, in dorsal (A_1) and ventral (A_2) views. **B**. Right frontal ZPAL RV/1370, in dorsal view. **C**. Posterior fragment of the right frontal ZPAL RV/250, in ventral view. **D**. Left parietal ZPAL RV/293, in dorsal view. **E**. Left parietal ZPAL RV/285, in dorsal view. SEM stereo-pairs.

Parietal. — The parietals (Figs 7D, E, 8B) are paired and there is no trace of a parietal foramen. By comparison with the frontal, the parietal is short (roughly about half the frontal length in sagittal axis). As a whole, the sagittal suture is interdigitating. The anterior half of the suture surface bears V-shaped ridges and differs from the posterior one, which is vertically ridged. The posterior part becomes thinner and more susceptible to damage. When the anterior parts are articulated, the posterior parts leave a long incision between them, which combined with the suture morphology is suggestive of the presence of an interparietal. This

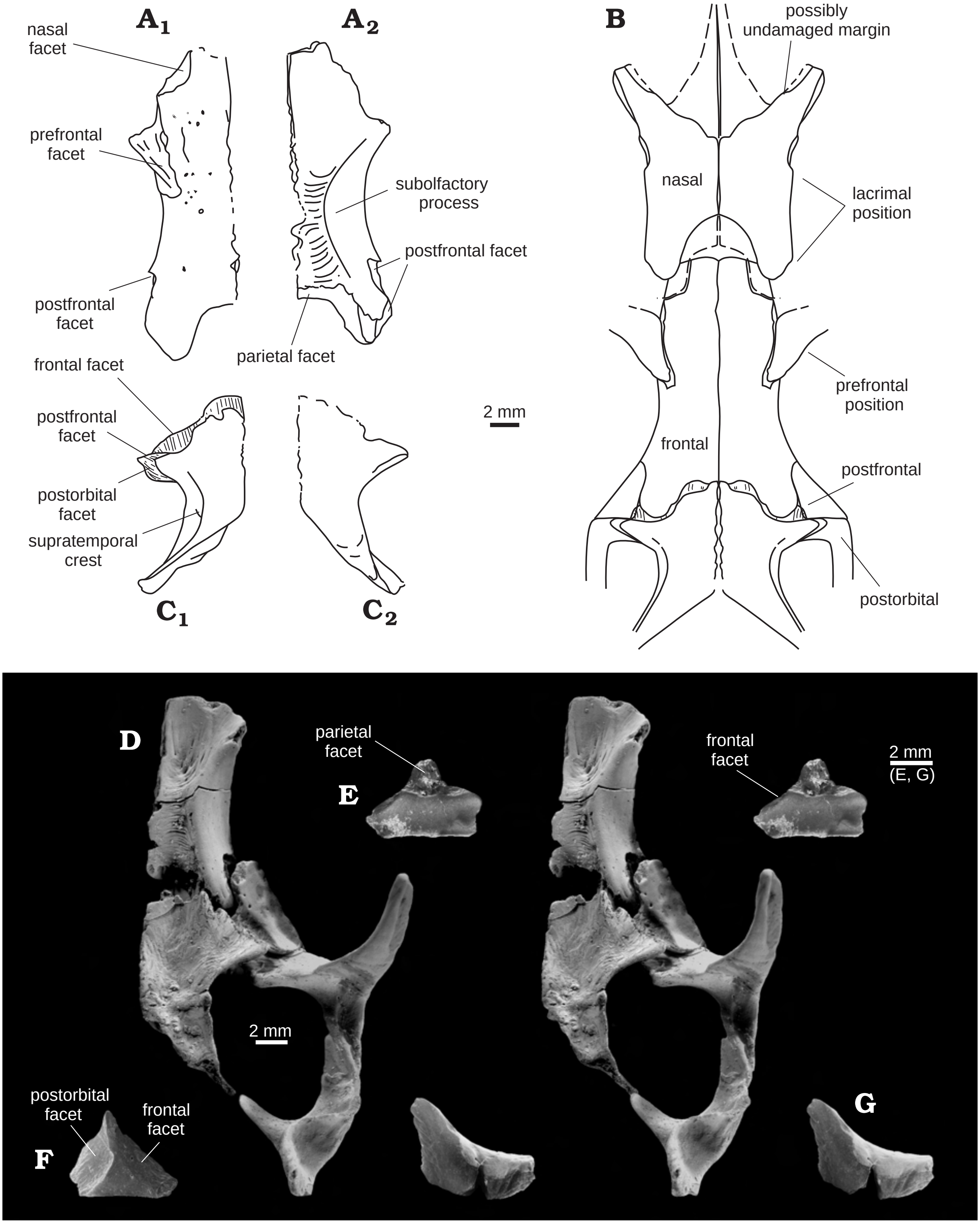

Fig. 8. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A**. Right frontal, in dorsal (A_1) and ventral (A_2) views. **B**. Skull roof, in dorsal view. **C**. Right parietal, in dorsal (C_1) and ventral (C_2) views. **D**. Combined left side skull roof bones of different individuals, in ventral view: frontal ZPAL RV/259, ZPAL RV/291 parietal, ZPAL RV/547 postfrontal, postorbital ZPAL RV/315, and squamosal ZPAL RV/134. **E**. Right postfrontal ZPAL RV/544, in ventral view. **F**. Right postfrontal ZPAL RV/543, in dorsal view. **G**. Left prefrontal ZPAL RV/66, in lateral view. A–C, reconstructions; E–G, SEM micrographs; D, E, G, stereo-pairs.

would be consistent with the structure of this region in the other basal archosauriforms (Ewer 1965, Gower 2003), but is not supported by actual preservation of the interparietal. The anterior part of the parietal bears a strong facetted flange that is wavy in transverse section (Fig. 7D, E). It accommodated the frontal medially, and the postfrontal and postorbital laterally (Fig. 8B$_1$, D). The central part is convex and swollen dorsally, and protrudes anteriad to fit the overlapping frontal. Laterally a longitudinal groove receives the rear of the descending crest of the frontal. The facet is longitudinally split to prevent lateral dislocation. The lateral wing of the parietal is oriented anterolaterally, and accommodates the combined postorbital-postfrontal. Its dorsal surface is convex. The ventral surface, correspondingly concave and roughened, may have received the dorsal part of the laterosphenoid. The lateral margin of the parietal bears an oblique surface for the origin of the temporal muscles. It faces dorsolaterally, is overhung by the supratemporal crest, and continues onto the lateral surface of the squamosal process.

In length, the squamosal processes probably exceeded that of the parietal body (see reconstruction Fig. 8D), but they are usually incomplete distally. Their posteromedial surfaces (sites of neck muscle attachment) are triangular, concave in transverse section, and are overhung by crests. They taper medially. The parietal and supraoccipital must have been connected by connective tissue. The ventral surface of the parietal has three concavities (Fig. 8D) matching the convexities of the dorsal surface: anteromedial, anterolateral (possibly receiving the laterosphenoid, see above), and posterior (extending approximately half the length of the squamosal process). In the distal half, the ventral surface of the process is more or less flattened, and probably fitted the end of the paroccipital process. A slit-like posttemporal fenestra perhaps separated the proximal parts.

The parietals are fairly uniform in overall shape, while differing in size (from about 8 to 13 mm in sagittal length). The supratemporal crests vary in strength.

Prefrontal. — The prefrontal forms a roughly semilunar conch (Fig. 8G) tapering both posteriorly and anteroventrally in the life position, and having a strongly concave ventromedial surface. The flat triangular and superficially ornamented dorsal wall of the bone (oriented to the left in Fig. 8G) overlaps the ridged prefrontal facet of the frontal (Figs 7A$_1$, 8A$_1$), and contributes to the skull table. Externally, the suture between the two bones is finely sinuous and extends along a parasagittal plane. Anteriorly the prefrontal becomes thinner and is rarely preserved intact, so that both its anterior extent and its contact with the lacrimal are poorly known. An elongated step-like surface preserved at the anterior border of ZPAL RV/66 (Fig. 8G, right lower angle of the specimen as oriented in the figure) is a fragment of the lacrimal facet.

Postfrontal. — The postfrontal is a small roughly triangular bone (Fig. 8E, F) that is wedged in between the parietal, frontal and postorbital (Fig. 8B, D). Its dorsal surface is a regular smooth triangle, the orbital border forming the longest side. Two ridged surfaces extend along the anterior and posterior sides of the triangle to contact the frontal and postorbital respectively. Both face mainly dorsally. The frontal facet is narrower and extends slightly onto the ventral side of the bone. The postorbital facet is larger and is not evident in ventral aspect. Between the two facets, there is a tiny triangular articular surface that is concave and ridged. This faces ventrally and slightly medially and contributes to the postorbital-postfrontal complex that overlaps the dorsal surface of the parietal. The orbital border of the postfrontal forms a smooth wall that is elongate in the parasagittal plane, but is only slightly concave longitudinally. In life position it faces ventrally and only slightly laterally.

Postorbital. — The postorbital is a triradiate bone (Fig. 9A–C). The axes of the posterior and ventral processes extend approximately at right angles to each other, but the processes themselves are connected by a more or less extensive blade of bone. This is laterally flat and medially concave. The posterior process fits into a groove on the squamosal to produce the upper temporal arcade. The medial process ascends slightly anteromedially (at ca. 130° to the ventral process). Its stout tip bears an ovoid concave parietal facet facing ventromedially, and this combines with the adjacent surface of the postfrontal to overlap the parietal (Fig. 8D). More anterior and lateral in position is an elongated postfrontal facet. The elongated, tapering ventral process is bent anteriorly at about half its length. It is sub-triangular in transverse section with its lateral surface flat. The anterior surface contributes to the curved posterior orbital border. It faces directly anteriad and is separated from the posterior surface by a sharp crest. The posterior surface is concave in transverse section and faces posteromedially. The slit-like jugal facet extends onto this surface along the distal half of the lateral border.

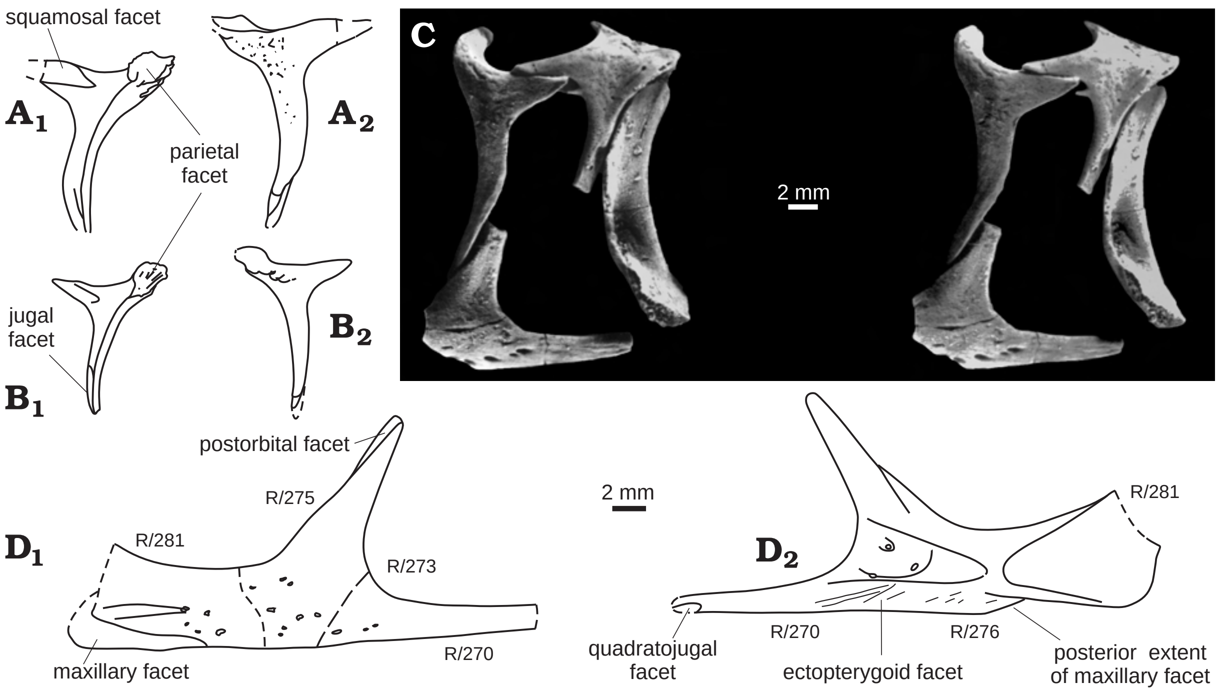

Fig. 9. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A**, **B**. Right postorbitals, two ontogenetic stages: ZPAL RV/318 (**A**) and ZPAL RV/319 (**B**). **C**. Left posterior skull fragment combined from different individual bones: jugal fragment ZPAL RV/273, postorbital ZPAL RV/319, squamosal ZPAL RV/871, and quadrate ZPAL RV/872. **D**. Reconstruction of the left jugal, mostly on the basis of the specimens illustrated in Fig. 11 (shortened catalogue numbers around). Medial (A_1, B_1, D_2) and lateral (A_2, B_2, C, D_1) views. C, SEM stereo-pair.

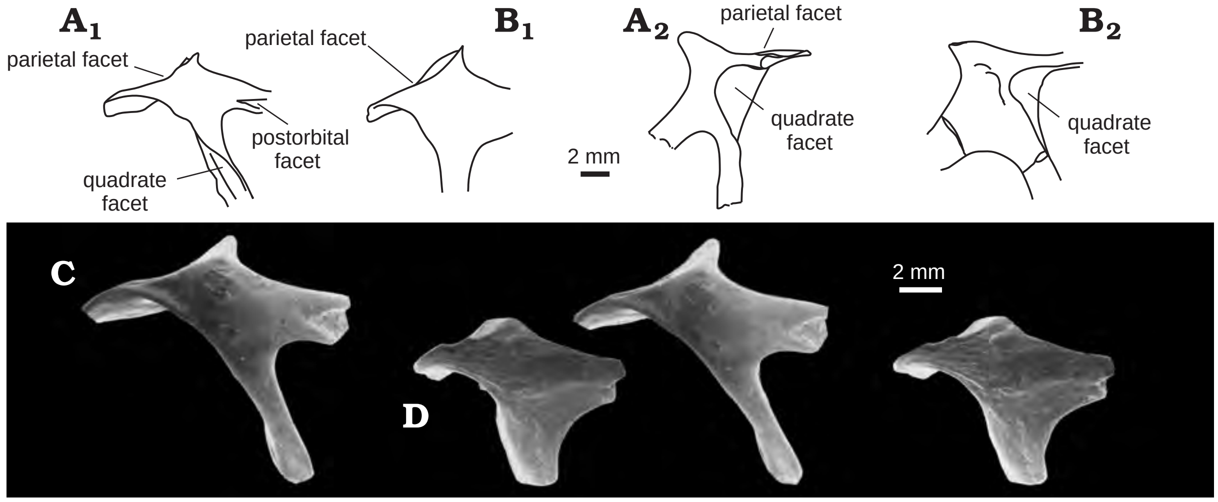

Fig. 10. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. Right squamosals: ZPAL RV/398 (**A**), ZPAL RV/399 (**B**), and ZPAL RV/27 (**D**). **C**. Left squamosal ZPAL RV/27. Lateral (A_1, B_1, C, D) and ventromedial (A_2, B_2) views. C, D, SEM stereo-pairs.

There is some variability in the postorbitals, in size, thickness, angulation between the anterior and posterior processes, and transverse section of the processes (more or less flattened laterally). However, the interesting parameters are difficult to measure accurately due to imperfect preservation.

Squamosal. — The squamosal is a quadriradiate bone that consists of a bulky rhomboid body with processes extending from each of its corners (Figs 9C, 10). The anterior process is stouter in lateral aspect than the posterior one, and bears a deep triangular socket on its lateral surface to receive the postorbital. The posterior one is twisted medially to overhang the quadrate, which makes its lateral wall more slender and posteriorly tapering. Both processes extend in line with the diagonal of the main body. This diagonal was oriented approximately horizontally as is the resulting supratemporal arcade. The posterior and medial processes contribute to an elongate rough parietal facet which generally faces posteromediad, but becomes more dorsal in orientation on the medial process. Ventrally, the squamosal extends into a long, slender process. Its lateral surface is flat and tapers to a point. A deep concavity between the posterior and ventral process received the quadrate head, while the lateral quadrate flange lay against the posterior wall of the ventral process.

There is variation in the size and proportions of the body of the squamosal, its shape and curvature, and in the angle between the postorbital and quadratojugal processes, but this cannot be quantified, partly because of differences in preservation. There seem to be two morphotypes, but they grade into one another. The smaller morphotype (width of the quadratojugal process: 1.0–2.1 mm, n = 7) is rhomboid in shape and the length of the body greatly exceeds its width (Fig. 10A_1, C). The quadratojugal process extends anteroventrad at an angle much less than 90° to the postorbital processes. The larger morphotype (Fig. 10B_1, D) (width of the quadratojugal process: 2–3.5 mm n = 7) is squarer in outline, with a quadratojugal process that is relatively stouter and flatter, as well as almost vertical in orientation, but this may be just a matter of size and individual age.

As illustrated by Ewer (1965, fig. 2), the anterior and ventral processes of the squamosal in *Euparkeria* enclose an angle of about 90°. In contrast, the same angle in *Sarmatosuchus* is 115° (Gower and Sennikov 1997, p. 63, fig. 3C).

Quadrate. — The quadrate (Fig. 11) has a pillar-like body arched in the parasagittal plane and posteriorly concave. The proximal head is simply a small rounded termination of the central pillar. The medial wing is triangular with its apex situated in the upper one third of the bone, and the base extending down to the lower one third of the pillar. The less extensive lateral wing is triangular with its apex more dorsally positioned, at about one quarter the quadrate height from the top. It is separated from the lower extremity of the bone by a deep notch that contributes to the quadratojugal foramen (Fig. 11A_1). The wings extend from the body in anteromedial and anterolateral directions, the anterior surface of the bone thus enclosing a widely open V-shaped concavity in transverse section. The lower part of the anterior face, depressed for the articulation with the pterygoid, is separated from the upper part by an oblique crest (pterygoid crest on Fig. 11A_1, B_2) extending ventrolaterad along the lower margin of the medial wing toward the quadratojugal articulation. This crest marks an abrupt change in orientation of the anterior surface of the bone. At the distal end of the pillar, there is a heavy medial condyle for the mandibular articulation (Fig. 11A_1). The lateral condyle protrudes laterad from the shaft. It is less developed than the medial one and is separated from the latter by a shallow smooth concavity. Both extend onto the anterior face of the bone, suggesting a posteroventral inclination of the bone in life (Fig. 11A_3, A_4). Given an approximately horizontal life position of the mandibular articulation, the upper concavity of the shaft faced anteriad and the lower one anteroventrad (Fig. 11A_3, A_4). The lower border of the medial wing should have been sub-horizontal in life position. The ventrolateral margin of the bone bears a narrow oval facet for the quadratojugal (Fig. 11A_1, C), while a row of tubercles, perhaps for ligaments, parallels this surface on the posterior face of the bone.

The height of the quadrate varies from 11 to 24 mm with a modal value of about 16 mm. One of the largest specimens is ZPAL RV/37. Allowing for differences in size, the quadrate of *Osmolskina czatkowiensis* is very similar to that of *Sarmatosuchus otschevi* (Gower and Sennikov 1997, p. 63, fig. 5).

Quadratojugal. — The quadratojugal (Fig. 12F) consists of two limbs enclosing an angle of ca. 40°, and contributing to a sub-triangular posteriorly rounded body. The body is medially concave to fit the ventrolateral extremity of the quadrate, exactly as in *Euparkeria* (Ewer 1965). The horizontal limb is a simple bar tapering anteriorly to fit the quadratojugal facet on the medial side of the jugal. The vertical limb is complicated by the addition of a medial lamina (or ridge). It closes the quadratojugal foramen laterally, and it is twisted just above it.

Jugal. — The jugal is a triradiate bone (Figs 9D, 12A–D). The middle part, including the postorbital process (Fig. 12C), is usually the best preserved, whereas the anterior and posterior rami are generally broken off. A number of anterior fragments may readily be combined with the middle parts, but only three specimens have been preserved with the base of the posterior ramus that demonstrates the existence of the lower temporal arcade (Fig. 9C).

The main part of bone is straight and sub-horizontal, but ascends anteriad to overlap the maxilla along an oblique line (Fig. 6D). The lateral surface is convex with a smooth sub-orbital part facing slightly dorso-

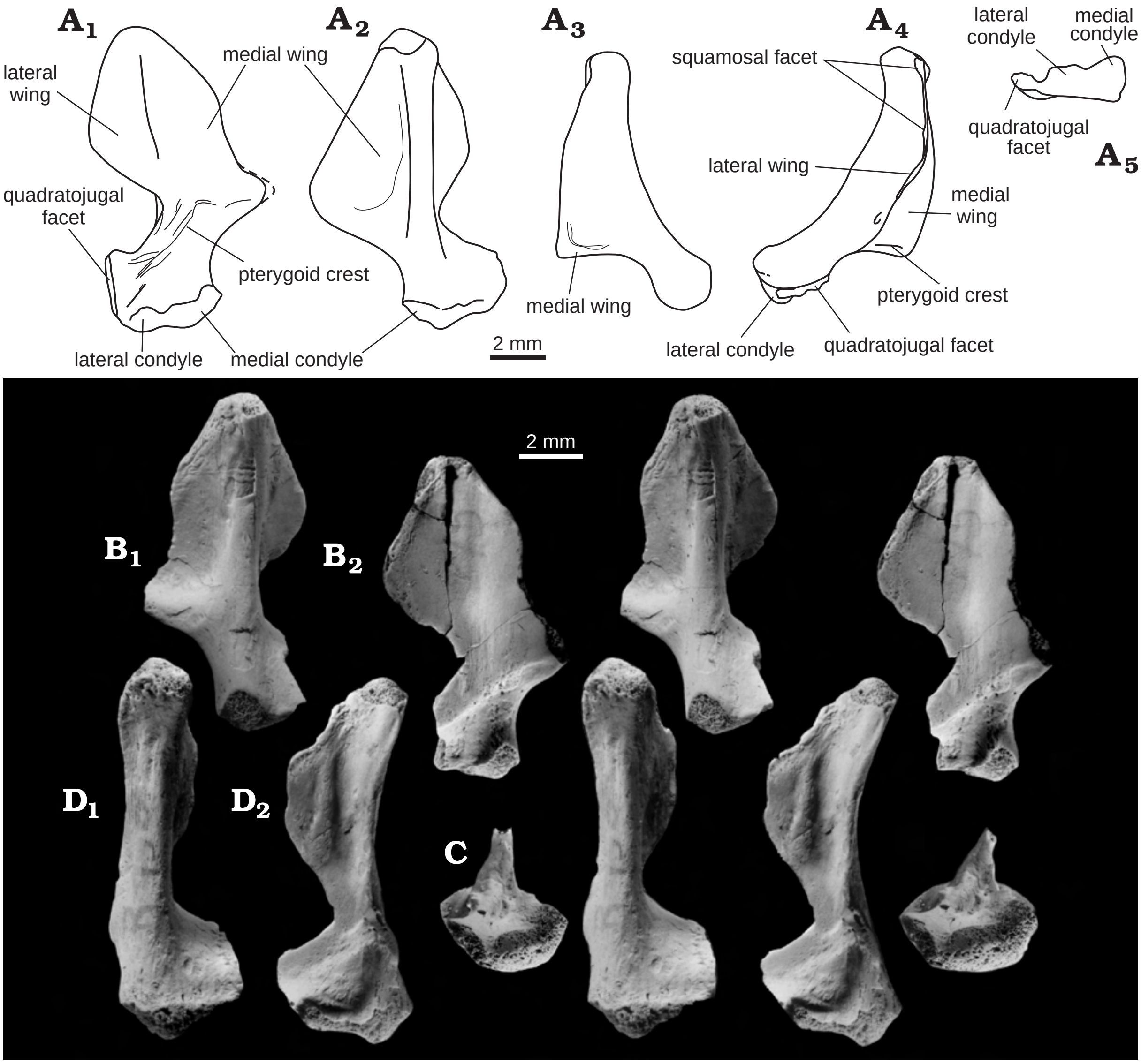

Fig. 11. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A**. Right quadrate reconstructed on the basis of the specimens illustrated below, in anterior (A_1), posterior (A_2), medial (A_3), lateral (A_4), and distal (A_5) views. **B**. Right quadrate ZPAL RV/38, in posterior (B_1) and anterior (B_2) views. **C**. Right quadrate ZPAL RV/39, in distal view. **D**. Right quadrate ZPAL RV/39, in posterior (D_1) and anteromedial (D_2) views. B–D, SEM stereo-pairs.

laterally and a strongly pitted ventral part facing ventrolaterally (Fig. 12A). The maxillary facet is complex. The main part of the facet is elongate and faces laterally but is set off from the main lateral surface of the bone (Fig. 12A). It must have been received into the furrow-like posteromedial surface of the maxilla (Fig. 6D). The posterior border of the main maxillary facet is always damaged. The same is true of the anterior extremity of the jugal, and hence the contact with the prefrontal and lacrimal remains unknown. The posterior process (Figs 9D, 12D, E) is long and narrow. As preserved, it makes up 58% of the reconstructed length of the bone. The quadratojugal facet is a long V-shaped incision in the ventromedial surface of the distal end (Fig. 12E). The postorbital process forms a triangle with a large base, and an apex directed posterodorsally with the slope of its axis at about 52° to 65° to the long axis of the bone.

The postorbital facet is a slit-like furrow extending on the anterior margin of the process, and, more dorsally, onto its medial side (Figs 12C, D). Medially, the quadratojugal and postorbital processes are separated from each other by a deep concavity extending sub-horizontally below the base of the postorbital process, and bordered ventrally by what is probably the ectopterygoid facet. However, the nature of the jugal-ectopterygoid contact is far from clear. Further anteriorly, a sub-triangular concavity, open anteriorly (Figs 9D_2, 12B), corresponds to the region overlying the maxilla. The concavity is bordered ventrally by a crest that

Fig. 12. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. Jugal fragments. **A**. Central portion with maxillary facet (left upper angle), and the base of a postorbital process ZPAL RV/274. **B**. Central portion with bases of both postorbital and quadratojugal processes ZPAL RV/277. **C**. Postorbital process with fragment of the main body ZPAL RV/275. **D**. Quadratojugal and postorbital processes ZPAL RV/273. **E**. Posterior part of jugal ZPAL RV/270 combined with quadratojugal ZPAL RV/394. **F**. Quadratojugal ZPAL RV/53. Lateral view (A, C_2, D, F) and medial view (B, C_1, E). Left bones, SEM stereo-pairs.

probably contacted the anterior flange of the ectopterygoid, overlying the maxilla medial to the jugal. A ventral incision separates the maxillary facet from the posterior part of the jugal (Fig. 12A).

As a rule, the anterior ramus is convex laterally in transverse section. Directly anterior to the postorbital process, and posterior to this process, the jugal wall is concave. Some specimens differ in having an evenly convex lateral surface with no concavities in the vicinity of the postorbital process. They are otherwise quite similar to the main type and are provisionally considered as variants. However, some very flat specimens (ZPAL RV/ 279 and 280), with a more vertical postorbital process (angle 72–78°), may belong to another animal.

PALATAL COMPLEX

Palatine. — As reconstructed on the basis of specimens ZPAL RV/33 and 34 (Figs 13A, B, 14A, B), the palatine is an elongated plate roughly rectangular in outline and approximately twice as long as wide (Fig. 13D). A V-shaped notch in its anterolateral end marks the posterior limit of the choana. The exact length and morphology of the anteromedial process are unknown, as are the posterior extent and outline of the bone and

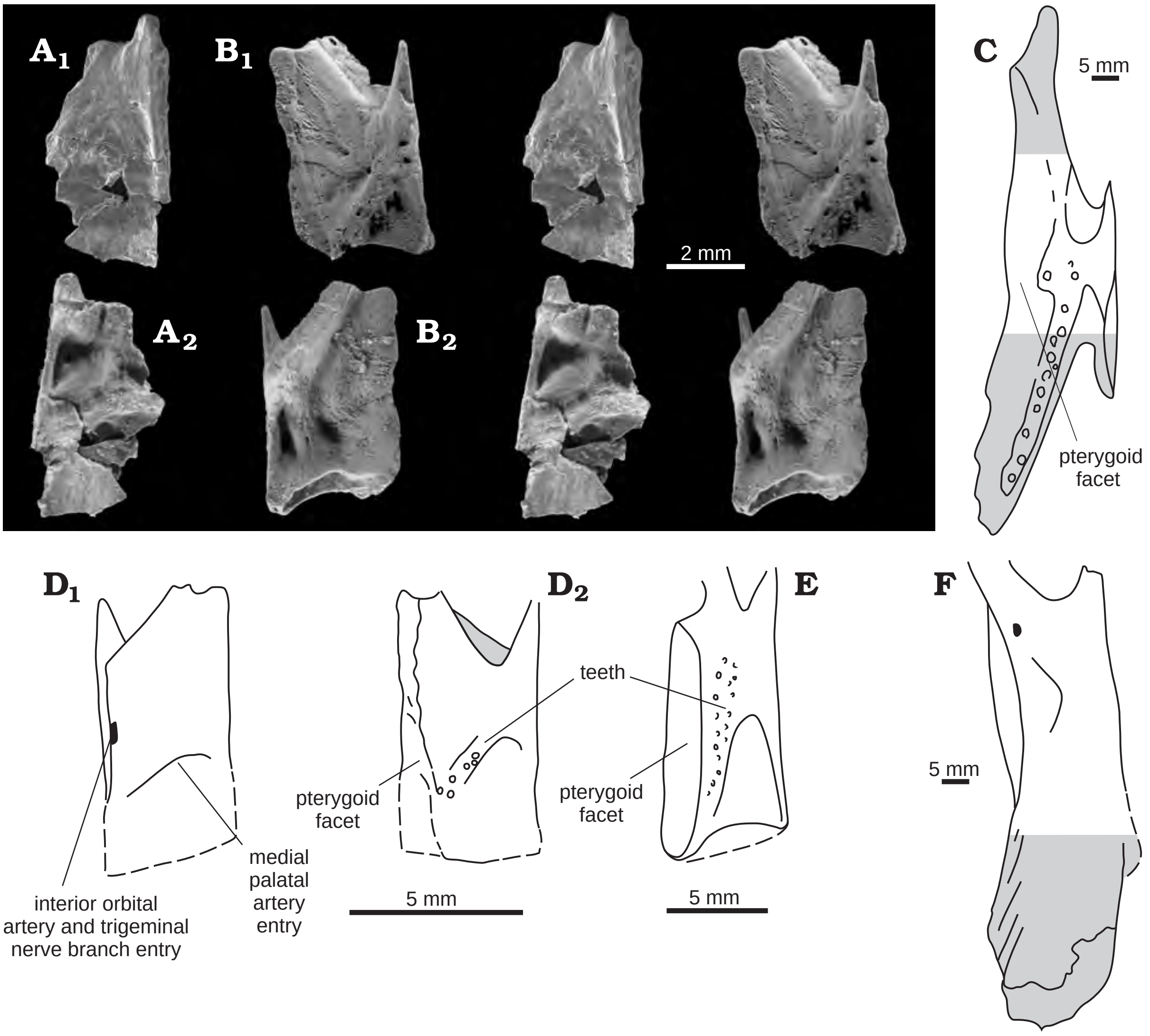

Fig. 13. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A**. Left palatine fragment ZPAL RV/34. **B**. Left palatine fragment ZPAL RV/33. **C**–**F**. Partial reconstructions of left palatines. **C**. *Sarmatosuchus otschevi* (after Gower and Sennikov 1997). **D.** *Osmolskina czatkowicensis*. **E**. *Euparkeria capensis* (after Ewer 1965, fig. 27). **F**. *Batrachotomus kupferzellensis* (after Gower 1999, fig. 14). All but A_2, B_2, D_1 in ventral view. Shaded areas show the missing parts. A, B, SEM stereo-pairs.

the shape of the sub-orbital fossa. As a whole the dorsal surface is concave because of the upward curvature of both the choanal border and the medial one, but the main portion is flat. A sharp arcuate, posteriorly concave crest borders a sub-transverse slit giving entry perhaps to branches of the medial palatal artery. Another foramen or foramina, situated at the lateral border of the bone, probably served for the entry of a passage used by the inferior orbital artery and a palatine branch of the trigeminal nerve (Fig. 13D_1). The general position of this passage in the palatine should correspond with that of the posterior opening of the superior alveolar canal of the maxilla (the posterior alveolar foramen of Oelrich 1956; see also Evans 1980, figs 21–25) which determines the mutual position of the bones. The maxillary facet is double and extends from the tip of the anterolateral process of the bone backwards (Fig. 14A, B). Ventrally, an elongated, ridged surface extends along the entire length of the bone. Close to the posterior border of the choana, this surface passes dorsally into a triangular facet along the medial border of the upturned flange of the palatine. The two parts enclose a longitudinal furrow that more or less matches the palatine facet of the maxilla (Fig. 14D). This places the palatine in position within the palate (Fig. 1A).

The ventral surface of the bone is bordered medially by a narrow pterygoid surface tapering forwards and extending medially in its posterior part. An oblique crest extends posteromedially almost in line with the lat-

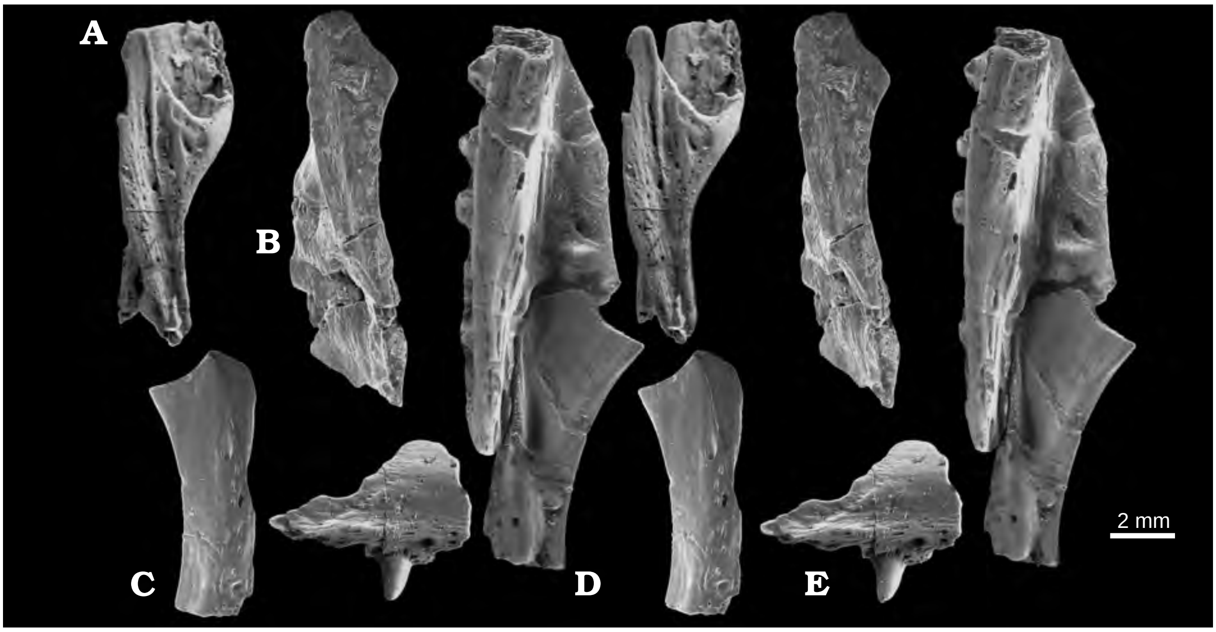

Fig. 14. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. Left palatines in lateral view exposing maxillary facet (anterior to the top): ZPAL RV/34 (**A**) and ZPAL RV/33 (**B**). **C**. Jugal fragment ZPAL RV/281, in lateral view. **D**. Posterior fragment of maxilla ZPAL RV/484 combined with the anterior part of the jugal ZPAL RV/281, in medial view. **E**. Posterior fragment of maxilla ZPAL RV/1371. SEM stereo-pairs.

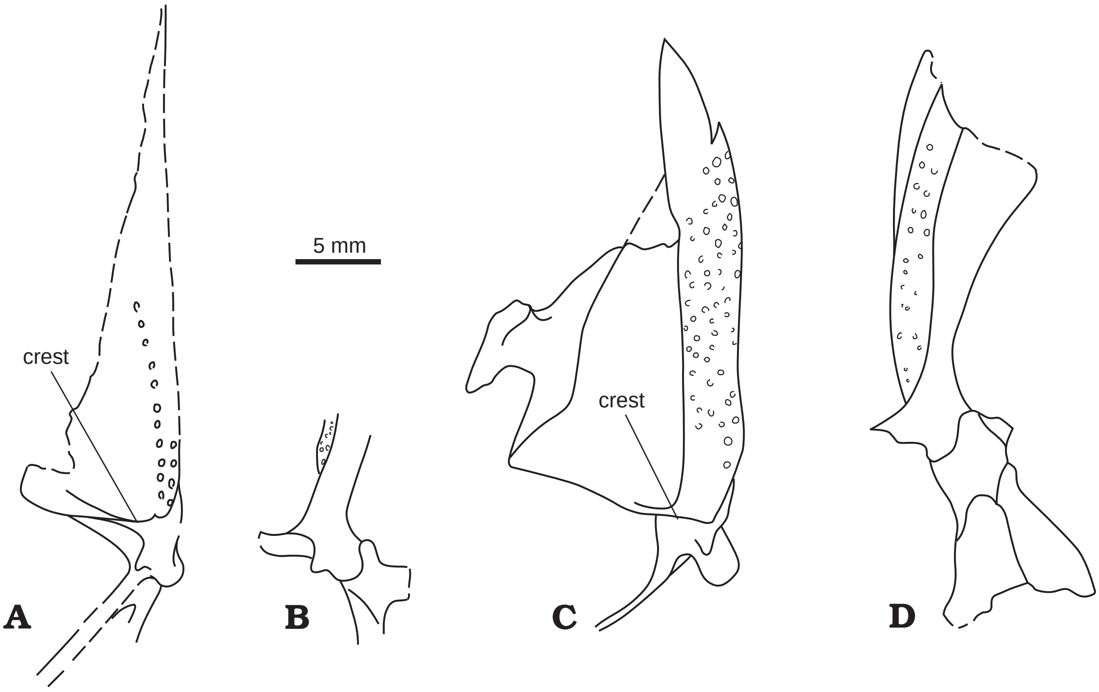

Fig. 15. Reconstructions of right pterygoids. **A**, **B**. *Osmolskina czatkowciensis*. **C**, **D**. *Euparkeria capensis* (a drawing after Ewer's 1965, fig. 26; stereo-photographs). Ventral (A, C) and medial (B, D) views.

eral border of the choanal notch. The crest bears traces of a tooth row that was probably continuous with that of the pterygoid. A triangular section of palatine blade, posterolateral to this crest, ascends obliquely toward the maxillary border.

The attribution of this type of palatine to *Osmolskina* is based primarily on its having a size that best fits the largest and most numerous bones of the assemblage. The possibility of procolophonid provenance has been considered, but seems unlikely because of its elongated and rectangular outline, with the choanal notch occupy-

Fig. 16. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A**–**C**. Central portions of left pterygoids. **A**. ZPAL RV/74. **B**. ZPAL RV/72. **C**. Basipterygoid facet and base of the quadrate process ZPAL RV/73. **D**. Right pterygoid combined with ectopterygoid ZPAL RV/604. **E**. Lateral part of the left ptergoid wing with ectopterygoid facet ZPAL RV/605. **F**. Left ectopterygoid ZPAL RV/465. **G**. Right ectopterygoid ZPAL RV/408. Ventral (A_1, B, D, G), medial (A_2), ventromedial (C), and dorsal (F) views. All but B, D, E SEM micrographs; all stereo-pairs.

ing a short margin. This differs from the short, sub-rhomboid palatine of procolophonians that bears articular facets on all margins, with the choanal notch situated in one corner (Carroll and Lindsay 1985, fig. 6E). As preserved the bone corresponds to the middle portion of the palates in *Sarmatosuchus otschevi* (Fig. 13C; Gower and Sennikov 1997, fig. 4B), *Batrachotomus kupferzellensis* (Fig. 13F; Gower 1999, fig. 14), and *Euparkeria capensis* (Fig. 13E; Ewer 1965, fig. 1), while corresponding to the latter species in detail (Fig. 13C–E).

Pterygoid. — The pterygoid consists of two wings, palatal and quadrate, united by a short neck. In dorsal aspect, the main part of the palatal wing is fan-shaped and convex in transverse section. However, towards the medial side, the convexity passes into a radially oriented furrow that, in turn, is bordered by the prominent dorsomedial border. The posterior angle of the palatal wing, between the fairly deep medial wall and the thick laterally directed posterior border, is ca. 80°. The ventral surface of the palatal wing is separated from the neck by a sharp crest (Figs 15A, 16B), and similar crest occurs in *Euparkeria capensis* (Fig. 15C). The lateral part of the palatal wing is ventrally concave and funnel-shaped. Sharply delimited on both sides, the dentigerous zone is flat, and bears about 4 longitudinal rows of small teeth. The anterior part of the pterygoid is never preserved, and was reconstructed (Fig. 15A) on the basis of the space left by the palatines and maxillae. The lateral extreme is a fairly stout, laterally thickened sub-quadrangular blade bearing a flat incision for the ectopterygoid (Fig. 16D, E). The ectopterygoid facet is never complete in existing material.

The pterygoid neck has a ventromedially protruding hooked process (Fig. 16A, C) which contributes to the basipterygoid articulation. Situated on the posterior face of this process, the articular surface is sub-perpendicular to the plane of the palatal wing. It continues onto the medial surface of the ventral twig of the quadrate process (Fig. 16A, C). A tuber for insertion of the pterygoideus muscle (Schumacher 1973) or for ligament attachment is situated about the middle of the neck. Its size is variable, and the apex is directed laterally. At the very base of the quadrate ramus is a bone blade that is flat both ventrally and dorsally. Distally, it divides into two processes and extends obliquely posterolaterally.

Ectopterygoid. — The ectopterygoid is a strongly curved bone with a relatively small hook-shaped lateral head and a body that extends strongly to a sub-triangular medial conch. The latter is dorsally convex (Fig. 16F) and ventrally concave (Fig. 16G). The concave surface is probably continuous with the concavity of the ventral surface of the pterygoid, and it is bordered by a V-shaped crest that opens medially. The pterygoid facets it bears are obscure, and contact must be reconstructed on the basis of the facet on the lateral margin of the pterygoid (Fig. 16D). The lateral head (turned down in Fig. 16F, G) bears an articular facet here interpreted as the jugal facet, but the nature of its contact with neighbouring bones is conjectural.

BRAINCASE

The braincase is represented by all constituent elements, with the exception of a laterosphenoid, the presence of which is conjectural. The braincase material is disarticulated except for the parabasisphenoid, which is a fully integrated element, and the exoccipitals that are almost always fused with the opisthotic (*e.g.*, ZPAL RV/115, 422). A few specimens also have the supraoccipital or prootic, or both (ZPAL RV/419), fused with the opisthotic, but in existing material, the *Osmolskina* exoccipitals are never fused with the basioccipital. The base of the cranial cavity is, as a rule, covered by unfinished bone, except for the ossified basal grooves for the metotic foramen, and occasionally the abducens grooves (ZPAL RV/424), as well as the articular facets for neighbouring bones in a few larger specimens.

Basioccipital. — The basioccipital (Fig. 17A, B) is a thick bone that is cordate in shape, with the apex forming the majority of the occipital condyle. It contacts the basisphenoid by means of two sub-circular surfaces facing anteriad and separated from each other by a notch (Fig. 17A_3, B_2). More laterally, an ovoid surface probably received the tip of the ventral ramus of the opisthotic that fitted between the basioccipital and the posterolateral parabasisphenoid wing. The surface is situated on the anterolateral face of each basal tuber. The exoccipital facets are symmetrical, flattened, and posterolaterally inclined. They almost touch one another in the midline, but do not completely exclude the basioccipital from the foramen magnum. Anteriorly, the exoccipital facets diverge, and the basioccipital contributes a narrow zone to the braincase floor. However, the contribution of the basioccipital to the braincase floor may have decreased in ontogeny with progressing co-ossification of the bones. An elongated furrow of finished bone, corresponding to the base of the embryonic metotic fissure (nerves IX and X), lies anterior to the exoccipital facets, and posterolateral to the opisthotic facet of both sides. The apices of the basal tubera are situated at about the anterior one third of the basioccipital length. Medially they meet the crests that border the V-shaped ventral concavity of the braincase floor posteriorly.

Supraoccipital. — The supraoccipital (Fig. 18) is a hexagonal plate that is thickened ventrally on both sides. The thickened parts bear oblique articular facets, for the prootic anterolaterally and for the opisthotic posterolaterally. The former is pierced by the entrance of the anterior semicircular canal, the latter by that of the posterior canal. The canals converge medially as more or less open furrows, and are sometimes separated from each other by a transverse septum (Fig. 18C_1). Their eventual fusion into a crus communis must have occurred below the ossified part. Between the lateral otic facets, the ventral surface of the supraoccipital provides a concave, fully ossified ceiling to the brain cavity. Its posterior border is laterally incised by surfaces for the exoccipitals. Between them, the border of the supraoccipital contributes to the foramen magnum. On the ventral surface of the bone, medial to the semicircular canal regions, the anterior margin bears symmetrical triangular incisions (Fig. 18A_1, C_1). The incisions display a surface of finished bone and extend laterally to the cavities continuous with the space for the dural venous sinus draining the prootic (see below) or for the endolymphatic ducts. The cavities most probably had their exits on the dorsal surface of the bone (Fig. 25B, C).

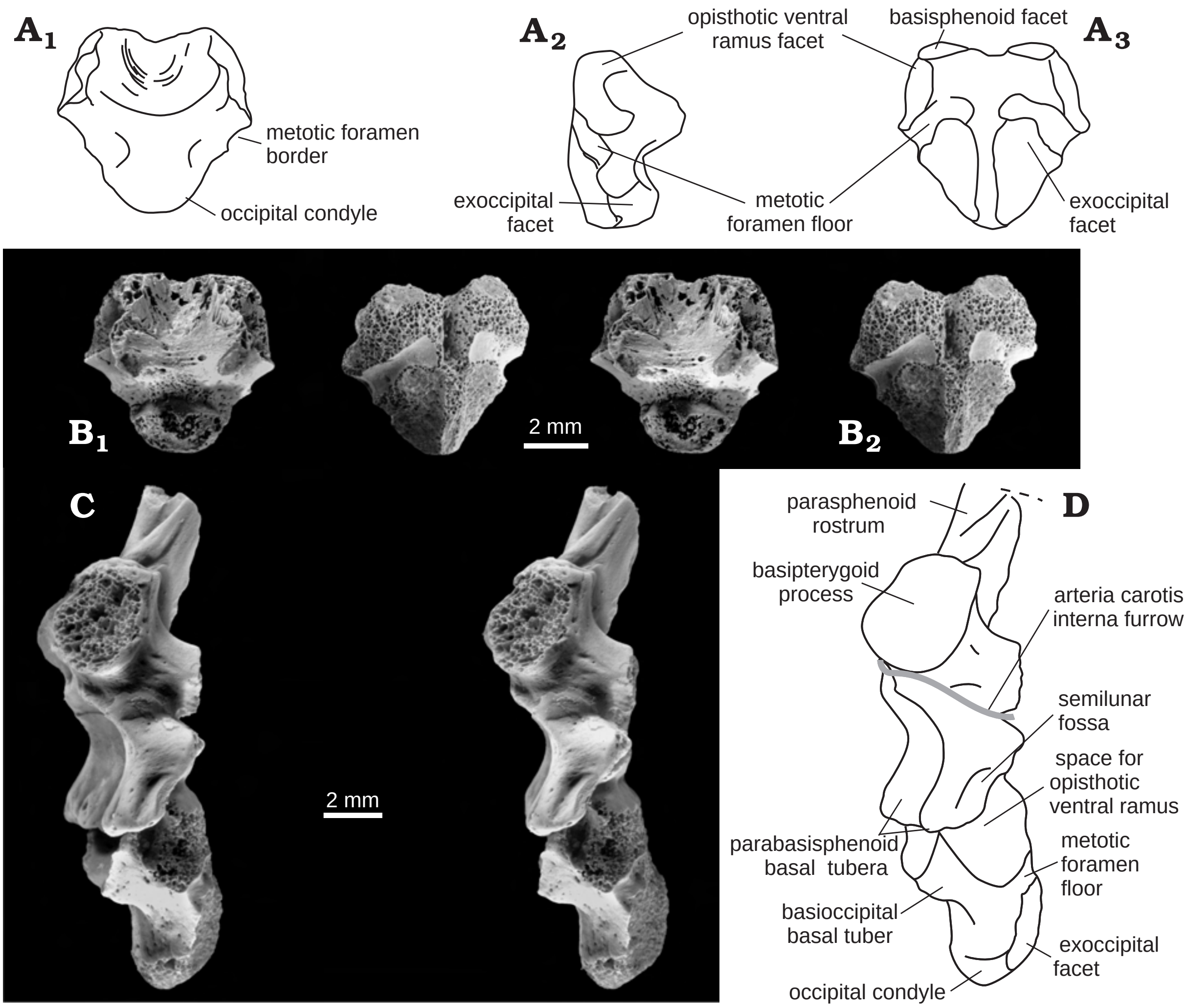

Fig. 17. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A**, **B**. Basioccipital ZPAL RV/114, in ventral (A_1, B_1), lateral (A_2), and dorsal (A_3, B_2) views. **C**, **D**. Parabasisphenoid with basioccipital ZPAL RV/413 combined from two specimens, in left lateral view. B, SEM micrographs; B, C, stereo-pairs.

The supraoccipital displays a fairly consistent structure, but the stage of ossification and the level of co-ossification with neighbouring bones vary with respect to the details of the posterior margin. The triangular surfaces for the exoccipitals are more or less widely spaced (Fig. 18B, D), sometimes separated by an acute roof above the foramen magnum incised in the sagittal axis, in some others the exoccipital facets are close together and blend to produce a small finger-shaped process (Fig. 18B). The specimens do not differ from one another in other aspects.

Exoccipital. — The exoccipitals (Fig. 19) are hour-glass shaped bones with enlarged upper and lower ends contacting the opisthotic, supraoccipital, and basioccipital respectively. The exoccipitals diverge dorsally and contribute to the lateral borders of the foramen magnum (Fig. 25), but do not usually make contact above it. Two hypoglossal foramina pierce the exoccipital pillar. The exits lie on the lateral side, with the larger one postero-dorsal to the smaller one, which almost touches the suture with the basioccipital. Two acute sub-vertical crests border the posterior foramen from both anterior and posterior sides (Fig. 24A). The anterior crest forms the posterior border of the metotic fissure while the opisthotic ventral ramus makes up the anterior wall of the fissure, and the basioccipital the furrow-like floor. The sutures between the exoccipital and the basioccipital close later in ontogeny than those between the exoccipital and the opisthotic, the latter two frequently being preserved as a single element (Fig. 25).

Opisthotic. — The opisthotic (Fig. 19) is a pyramidal bone that makes up the main body of the paroccipital process. The tip is bilaterally flattened and distally bears a dorsal ridge for the parietal contact. In

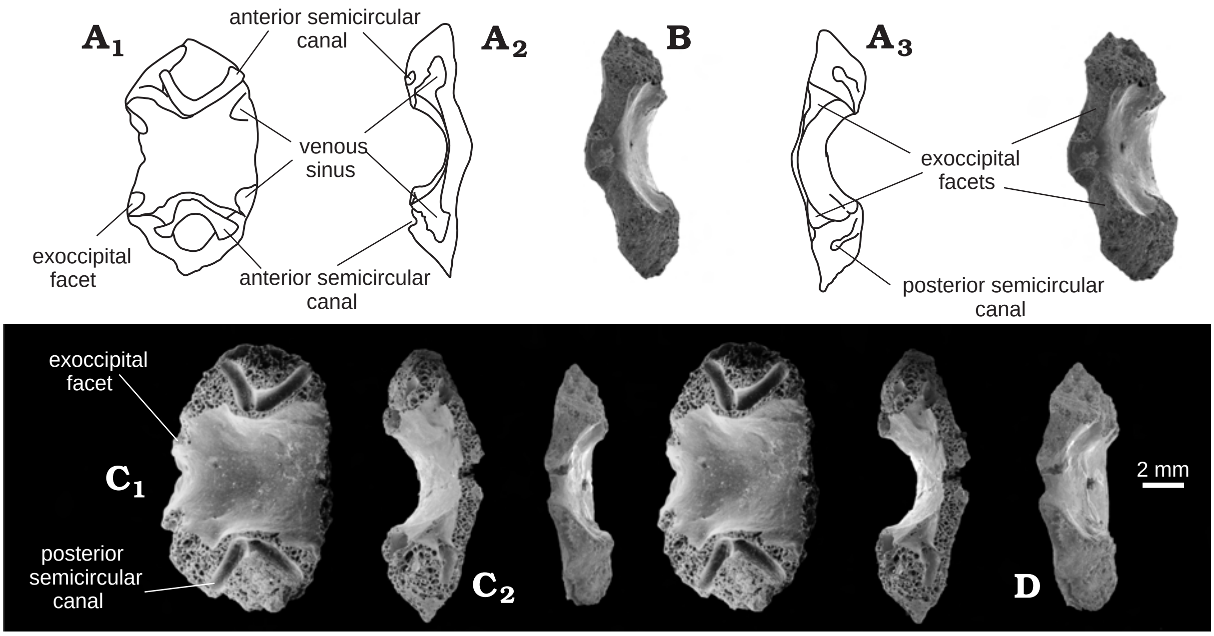

Fig.18. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. Supraoccipital: ZPAL RV/125 (**A**, **C**), ZPAL RV/420 (**B**), and ZPAL RV/417 (**D**). Ventral (A_1, C_1), anterior (A_2, C_2), and posterior (A_3, B) views. B–D, SEM stereo-pairs.

life, the paroccipital processes of both sides extend posteriad enclosing an angle of about 55° (Fig. 25B). The ventral surface bears three longitudinal crests (Fig. 19B_1). The blunt medial crest is continuous with the posterior wall of the exoccipital. Topographically, it roughly corresponds to the tuberal crest *sensu* Säve-Söderbergh (1947, see also Oelrich 1956) but is medial instead of lateral to the hypoglossal foramina. The lateral crest extends half way along the paroccipital process and is continuous with the main line of the prootic crest. Intermediate in position, the third, most acute, crest extends along the posterior side of the ventral ramus of the opisthotic. It roughly corresponds to the interfenestral crest of lizards (Oelrich 1956) in that it separates the region of fenestra ovalis from that corresponding to the embryonic metotic fissure. In *Osmolskina*, the metotic fissure is largely open, and no separate compensatory window is formed exactly as in the case of *Euparkeria* (Gower and Weber 1998). The "interfenestral crest" borders a stapedial fossa, which leads to the fenestra ovalis, widely open in *Osmolskina*.

The ventral ramus of the opisthotic has a twofold structure (Fig. 19A). It is composed of two elongated processes, the posterior one is fused along its anterior margin with a second process protruding from the ventral border of the posterior vestibular recess. The suture between the two parts remains visible in all specimens having the ventral ramus preserved. It produces a blunt ridge cutting the stapedial grove sub-perpendicular to its axis. The ridge produces a semicircle partly surrounding the fenestra ovalis. Anterior to it is a pit, possibly for the ligament supporting the stapes. The anterior margin of the ventral ramus is pierced proximally by a tiny canal extending posteriad (Fig. 19A). On the other side of the process it opens into the dorsal part of the metotic foramen, possibly carrying the glossopharyngeal nerve (IX), or a part of it.

The heavy proximal end of the opisthotic (Fig. 19A) bears articular facets for neighbouring bones: exoccipital, supraoccipital, and prootic, as well as for the basioccipital and possibly for the parabasisphenoid which it contacts by means of its ventral ramus. The contact between the opisthotic and exoccipital is subhorizontal, the latter extending ventromedially. Dorsolateral to it, and facing antero-medially, is the supraoccipital facet. This is slightly convex, and pierced by the circular opening of the posterior semicircular canal that penetrates the posterolateral margin of the supraoccipital after having left the opisthotic (Fig. 19A). The prootic facet cuts obliquely across the proximal end of the opisthotic. This surface is overlapped laterally by the posterior process of the prootic and is pierced by the horizontal semicircular canal. Below this, the opisthotic contains a large ventral cavity for the posteroventral part of the vestibule, with the exit of the horizontal semicircular canal and a posterior ampullary recess (Fig. 23A) into which the posterior semicircular canal opens. The lagenar recess must have been located medial to the ventral ramus Fig. 23A).

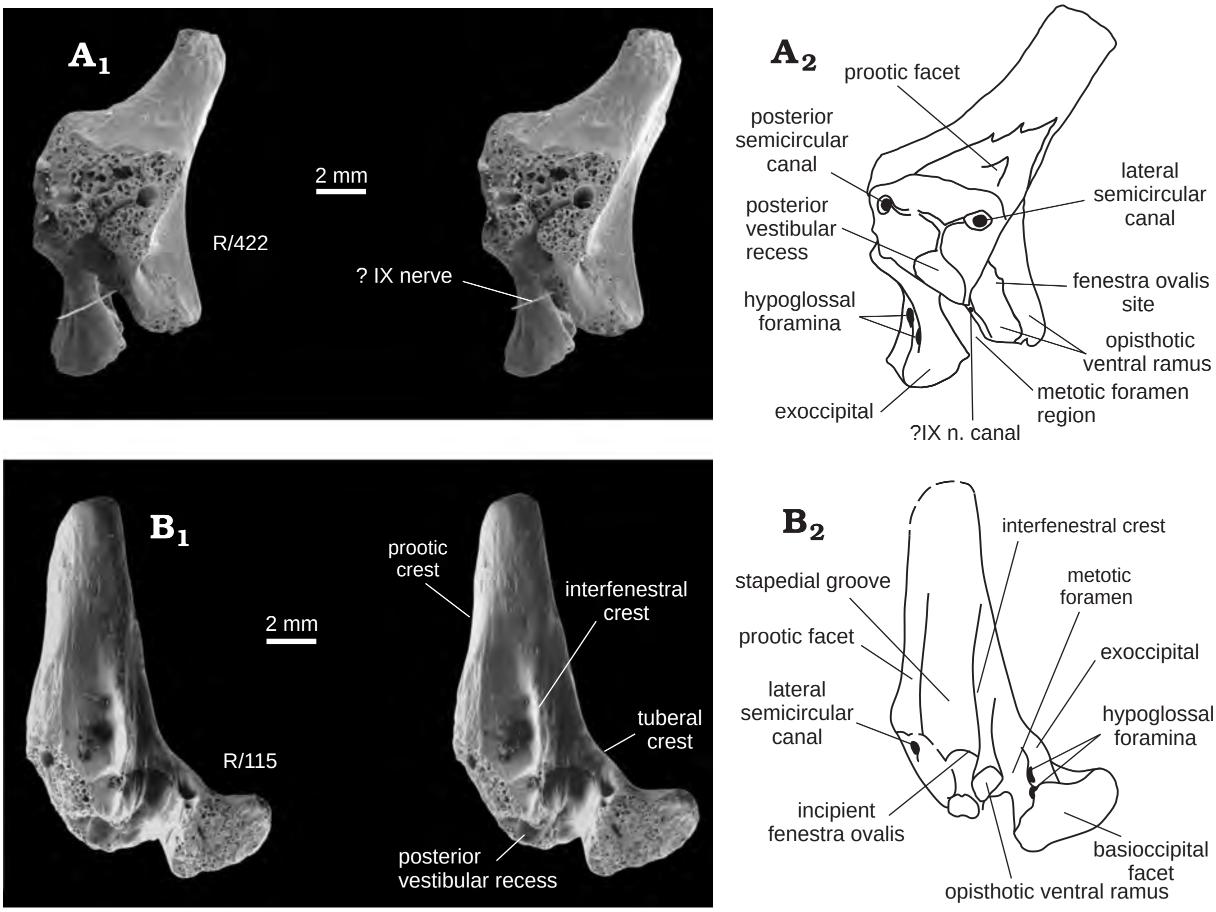

Fig. 19. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A**. Left opisthotic + exoccipital ZPAL RV/422, in antero-lateral view. White line in A shows the possible course of the IXth nerve canal. **B**. Left opisthotic + exoccipital ZPAL RV/115, in ventral view. A_1, B_1, SEM stereo-pairs. Shortened catalogue numbers indicate the specimens on which the reconstruction is based.

Parabasisphenoid. — Some specimens from Czatkowice 1 (*e.g*., ZPAL RV/412) display a clear division of the parabasisphenoid (Fig. 20C_2) into a spongy endochondral, probably basisphenoid part, and a thin sheet of finished dermal bone, probably corresponding to the parasphenoid. The parasphenoid rostrum is roughly U-shaped in transverse section. It bears a blunt sagittal crest ventrally and a longitudinal dorsal furrow. Although the exact life position is unknown, an oblique, anterodorsal orientation of the parasphenoid rostrum (Fig. 17C) is suggested by that of the neighbouring bones. As a whole, the parabasisphenoid is a triangular bone with the apex extended into an elongated parasphenoid rostrum and the body divided dorsally into anterior and posterior parts by clinoid processes united by a transverse crest (crista sellaris). The parasphenoid sheet extends posteriad over the ventral surface of the basisphenoid to produce large posterolateral flanges that cover the basisphenoid–basioccipital contact from below (Fig. 21C_1). They protrude well beyond the basisphenoid. Their tips have been referred to as parabasisphenoid basal tubera (Gower and Weber 1998), but in *Osmolskina* they seem to be produced by the parasphenoid. The flanges are separated from each other by a roughly V-shaped incision, the margin of which is very thin and usually badly damaged. It is therefore difficult to say how large the parasphenoid overlap was on the surface of the basioccipital. A pitted surface on the ventral aspect of the basioccipital (Fig. 17B_1) suggests that the parasphenoid retained a posteromedial flange similar to that of *Prolacerta*. There is however no evidence of a transverse thickening homologous to that in erythrosuchids (Parrish 1992, fig. 4) and described as an intertuberal plate by Gower and Sennikov (1996).

The braincase floor of *Osmolskina* is organised on two levels, the floor of the braincase cavity being situated significantly higher than the parasphenoid rostrum and more or less parallel to the latter. Between them the basisphenoid body is essentially vertically aligned. The anteriorly directed surface is occupied by the hypophysial fossa below and the dorsum sellae above it. The crista sellaris separates the dorsum sellae from

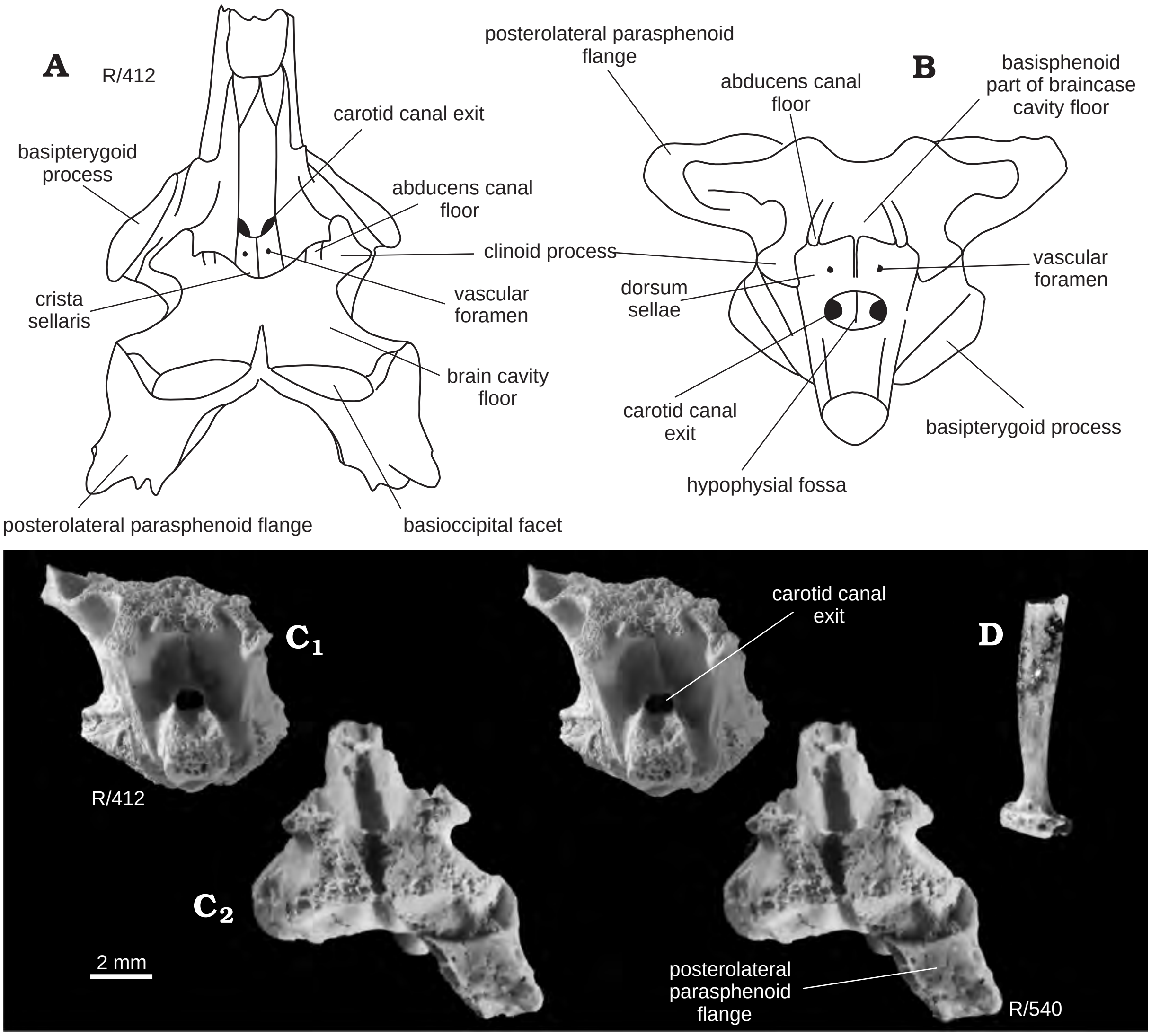

Fig. 20. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A**, **B**. Parabasisphenoid reconstruction based on specimen ZPAL RV/412, in dorsal (**A**) and anterior (**B**) views. **C**. Parabasisphenoid ZPAL RV /412, in anterior (C_1) and dorsal (C_2) views. **D**. Stapes ZPAL RV/59. C_1, C_2, stereo-pairs. Shortened catalogue numbers indicate the specimens on which the reconstruction is based.

the basisphenoid part of the braincase floor. Some specimens (Fig. 20A, C) preserve paired furrows of finished bone that cut through the crista sellaris and represent the floor of the abducens canals, the roof being made by the anterior inferior prootic processes. The hypophysial fossa is a small concavity continuous with the dorsal furrow of the rostrum (Fig. 20B, C_1). It is pierced by paired foramina for the cerebral branches of the carotid artery, but some additional vascular foramina produced by superficial bone bridges may also appear. A sagittal crest divides the dorsum sellae into bilateral concavities for eyeball muscles (*m. retractor bulbi* and *m. bursalis*) and the venous system (Säve-Söderbergh 1946). It is bordered on each side by an acute lateral crest, and is pierced by tiny vascular foramina. The dorsal surface of the basisphenoid is essentially X-shaped. The clinoid processes diverge anteriad. They are separated from the posterolateral parts of the basisphenoid by deep bilateral incisions. Each incision corresponds to the lateral depression of Gower and Weber (1998), and is a sub-vertical furrow on the lateral face of the parabasisphenoid destined for the palatal branch of the facial nerve that descended from the prootic. The internal carotid artery probably also used this passage to reach the entrance foramen on the ventral side of the parabasisphenoid between the basipterygoid processes.

Posteriorly, the basisphenoid bears paired ovoid surfaces for basioccipital contact. These are covered by a thin layer of finished bone. Lateral to them, small surfaces, one on each side, might have received the

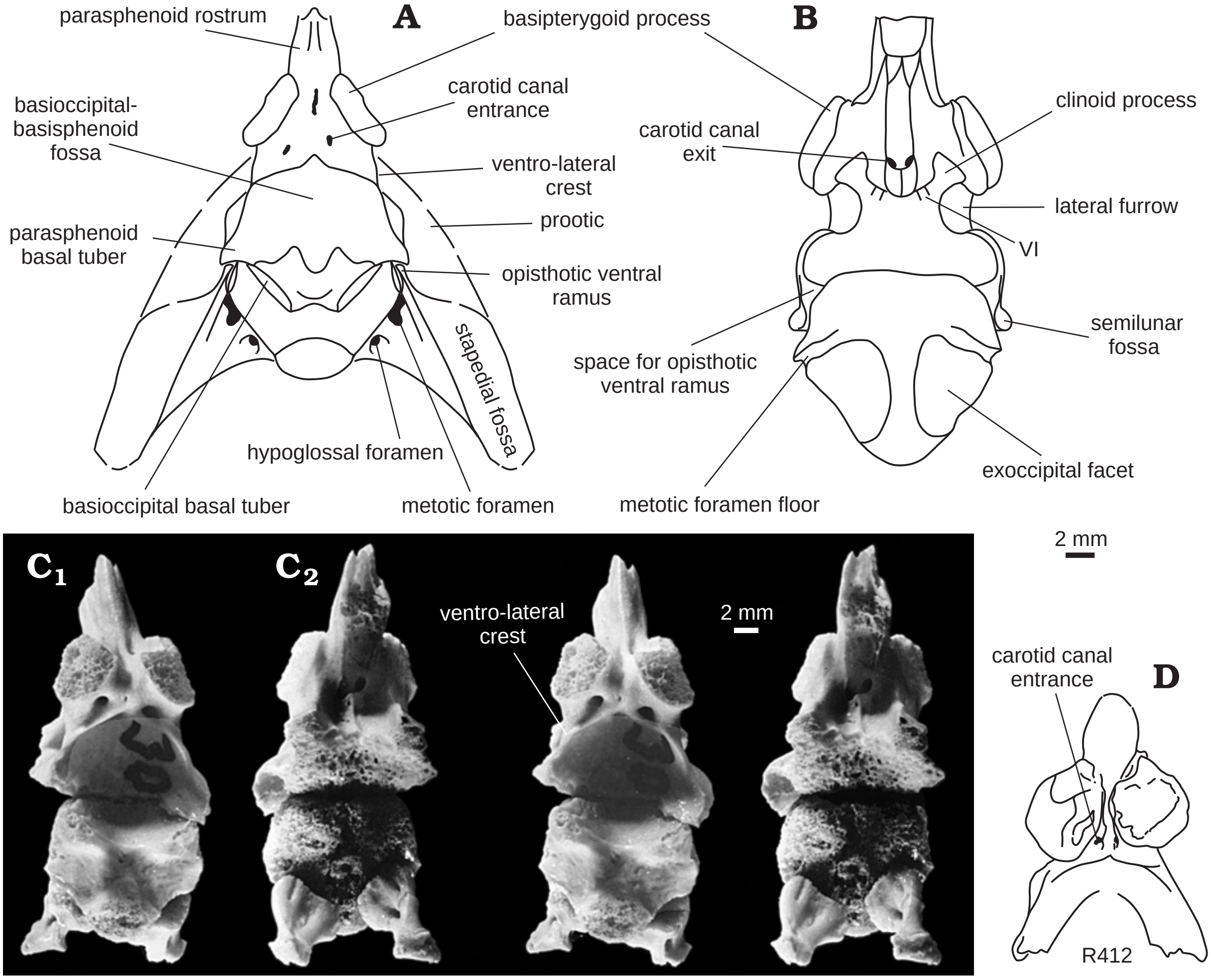

Fig. 21 *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A**. Braincase reconstruction, in ventral view. **B**. Reconstruction of parabasisphenoid combined with basioccipital, in dorsal view. **C**. Partial braincase ZPAL RV/413 combined from different individuals, in ventral (C_1) and dorsal (C_2) views. **D**. Parabasisphenoid ZPAL RV/412, in ventral view. C, stereo-pairs.

opisthotic ventral rami. The surfaces are bordered ventrally by well-ossified parasphenoid laminae extending posterolaterad (parasphenoid flanges), and facing dorsally.

The lateral wall of the parabasisphenoid (Fig. 24A) turns anteroventrally into the neck of the basipterygoid process. The dorsal border of the lateral wall extends between the clinoid process and the apex of the posterolateral parasphenoid flange, its posterior corner bearing a semilunar fossa (Fig. 24A) facing laterally. The anterior border of the wall is the lateral crest of the dorsum sellae, whereas the posterior one is the ventrolateral crest. Posterior to the basipterygoid process, the lateral wall of the parabasisphenoid bears a sub-vertical furrow (Figs 17C, D, 24A) for the palatine branch of the facial nerve and the internal carotid artery. At the contact with the prootic, the furrow is deep, and is bordered anteriorly by a distinct prootic crest (Fig. 24A). Both furrow and crest fade out ventrally. The nerve and artery must have wound around the posterior angle of the basipterygoid stalk, with the artery then dividing into two parts. As recognized by earlier authors (Evans 1986; Gower and Sennikov 1998), the cerebral part entered the foramen on the ventral side of the braincase (Fig. 21A), while the anterior, palatal branch, along with the palatine branch of the facial nerve, could have followed the sub-horizontal furrow on the ventral side of the parasphenoid rostrum (the palatine branch is lost in adult crocodiles; personal communication from the referee D. Gower).

Ventrally, the braincase is excavated by a deep fossa (Fig. 21C_1), referred to as basioccipital-basisphenoid fossa by Gower and Sennikov (1996). The fossa extends posteriorly to the apices of the parasphenoid flanges and is bordered laterally by the acute ventrolateral crests which fuse with each other posterior to the basipterygoid processes.

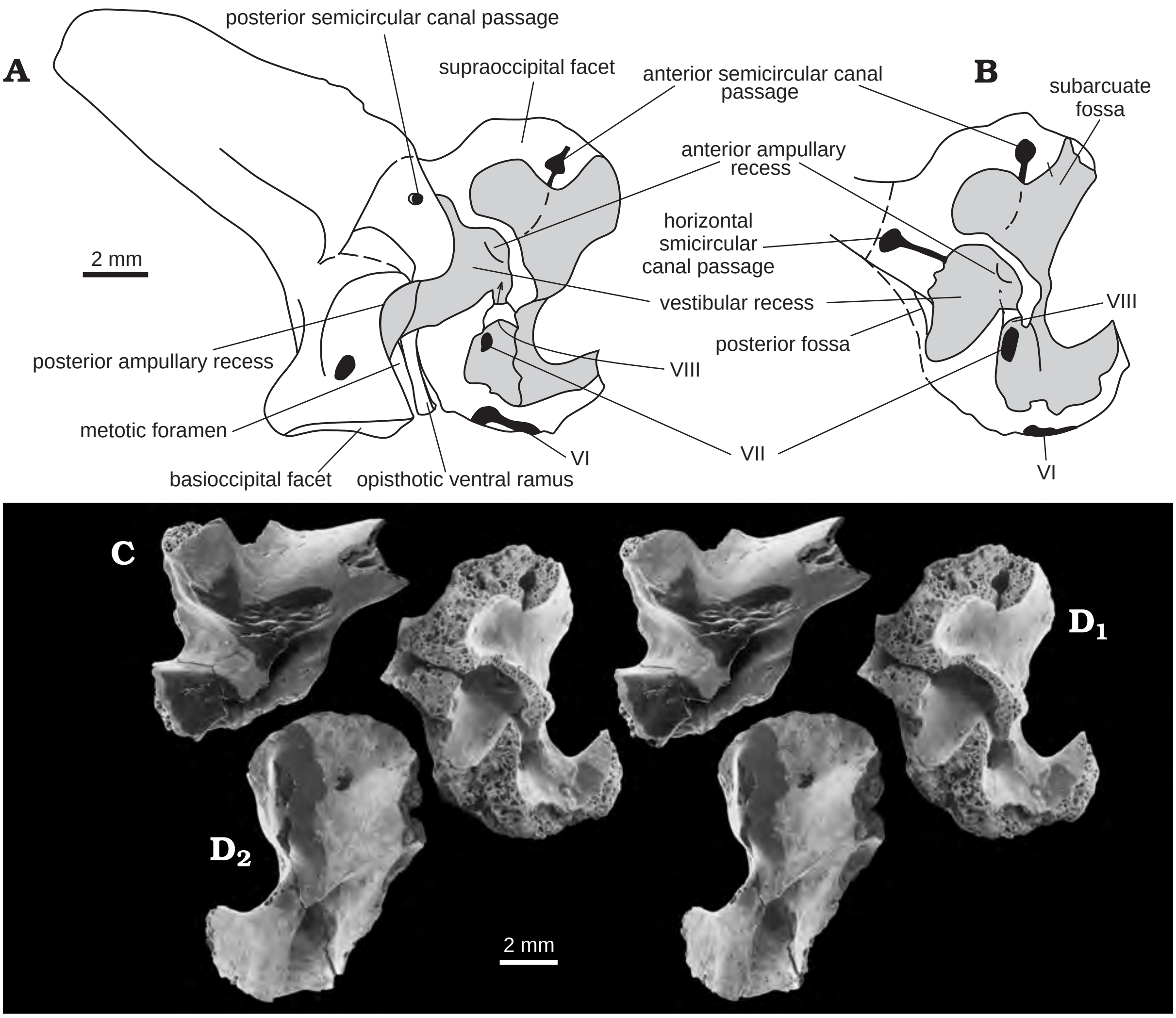

Fig. 22. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A**. Reconstruction of the opisthotic and exoccipital combined with the prootic, in medial view. **B**, **D**. Prootic ZPAL RV/124, in medial (B, D_1) and lateral (D_2) views. **C**. Prootic ZPAL RV/123, in lateral view. C, D, SEM stereo-pairs.

The basipterygoid processes are thick rounded bodies on short stout stalks that are mainly directed ventrally. An articular surface of finished bone is preserved in only a few specimens (*e.g.*, ZPAL RV/412), but usually the whole distal part is damaged. The mutual relations of the basipterygoid processes show some variability. This variability also affects the position of the carotid foramina, but, as a rule, they are situated on the ventral surface of the parabasisphenoid, posterior to the basipterygoid stalks and in front of the arched crest produced by fused anterior sections of the ventrolateral crests.

Prootic. — The prootic (Fig. 22) encloses the main part of the osseous labyrinth of the inner ear. Its lateral surface is dominated by elongated swellings corresponding to the anterior and lateral semicircular canals and ampullae (Figs 22, 23A, B). The position of the lateral canal determines the orientation of the long axis of the bone and this appears to be sub-vertical (Fig. 22A, B, D). Posteriorly, the main part of the prootic extends into a triangular process that overlaps the opisthotic, and is usually broken off. Anteriorly, the otic region is separated from the anterior inferior process by an open U-shaped trigeminal notch. The notch is partially divided by a protruding part of its margin into two parts (Fig. 24A), the upper part for the exit of the medial cerebral vein, and the lower part, the trigeminal notch proper, for the trigeminal nerve. On the lateral side of the bone (Fig. 22C, D), the trigeminal notch extends into a large sub-horizontal furrow under the prominence corresponding to the anterior ampullar recess. The furrow fades out posteriad where it is crossed by a sub-vertical anterior section of the prootic crest. The extension of the crest onto the opisthotic borders the stapedial fossa and forms the lat-

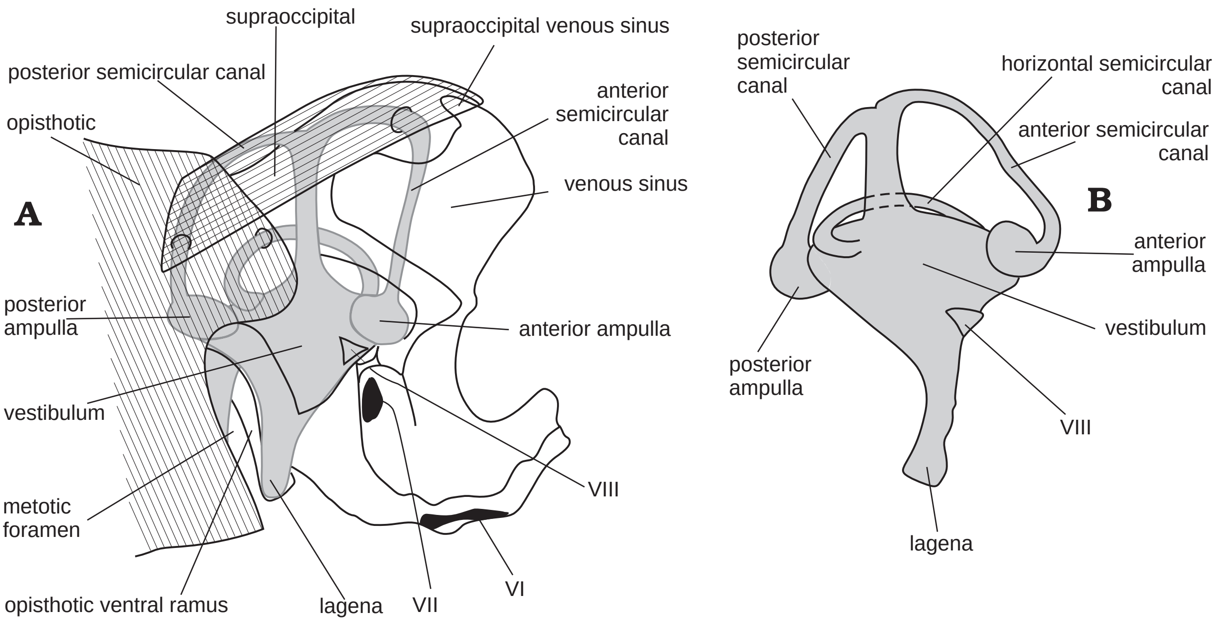

Fig. 23. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A**. Reconstruction of a labyrinth based on the bones illustrated in Fig. 22B, D_1. **B**. Labyrinth in *Alligator mississipiensis* (according to Wever 1978, fig. 24-15). Not to scale.

eral wall of the tympanic cavity. Anteriorly, it provided attachment for the aponeurosis of origin of the protractor pterygoideus muscle (Oelrich 1956). A single large circular foramen for the facial nerve (VII) is situated in a deep concavity posterior to the prootic crest (Fig. 22A) and is overhung by the crest. The groove for the palatine branch of the facial nerve, and for the carotid artery, extends anteroventrally from the facial foramen region. It passes from the prootic onto the basisphenoid, thus determining their mutual contact. The second furrow, for both the hyomandibular branch of the facial nerve and the carotid artery fades out posteriad. There is no distinct partition of the furrow into nervous and vascular parts.

The lateral surface of the anterior inferior process is flat, and bordered dorsally by a faint blunt horizontal crest (possibly for the protractor pterygoidei muscle: Oelrich 1956; Gower and Sennikov 1996; Gower 2002), and bordered posteriorly by the prootic crest. The anterior end of the process bears a slightly concave, anteroventrally directed facet of finished bone (ZPAL RV/532), the only possible trace of the laterosphenoid (if present). The abducens nerve presumably passed through the basisphenoid-prootic suture leaving shallow furrows in both elements (Fig. 20A, B, C_1). The canals certainly cut through the crista sellaris to open directly above the dorsum sellae. The ventral border of the anterior inferior process bears an elongated ventromedially facing facet for the clinoid process of the basisphenoid, but this is usually poorly preserved. When oriented, the prootics converge slightly anteroventrad. As preserved, they do not meet each other in the midline, but the lack of contact is probably only a matter of preservation or of poor ossification in immature animals.

In medial aspect (Fig. 22A, B, D_1), the prootic is excavated by a complicated system of concavities separated from each other by blunt ridges of unfinished bone that were probably extended by connective tissue in life. The supraoccipital and opisthotic facets contribute to the posterodorsal borders of the cavities. They face medially and bear a circular opening for the anterior semicircular canal near the anterior end, and a trace of the lateral canal along the posterior opisthotic process. The largest and most posterior of the cavities enclosed the lower lateral part of the vestibule. The lateral semicircular canal begins with the anterior ampullary recess in the deepest, most dorsal part of the concavity, and extends into the posterior process. It has its circular exit at the end of this process where it penetrates the lateral face of the opisthotic. The anterior semicircular canal extends directly dorsad to exit through the supraoccipital facet. Towards the posteroventral margin of the bone, the vestibular concavity has a funnel-shaped ventral prolongation that continues into the opisthotic (Fig. 22A) and includes the posterior ampullary recess with the entrance of the posterior semicircular canal. The funnel-shaped space (Fig. 22B, D_1, vestibular recess) must have housed the ventralmost part of the labyrinth that passed into the lagena (Fig. 23A, B; Wever 1978). There is no crest to separate the lagena from the main vestibular part. In contrast, a crest has been described in at least some archosaurs (Gower 2002; crista

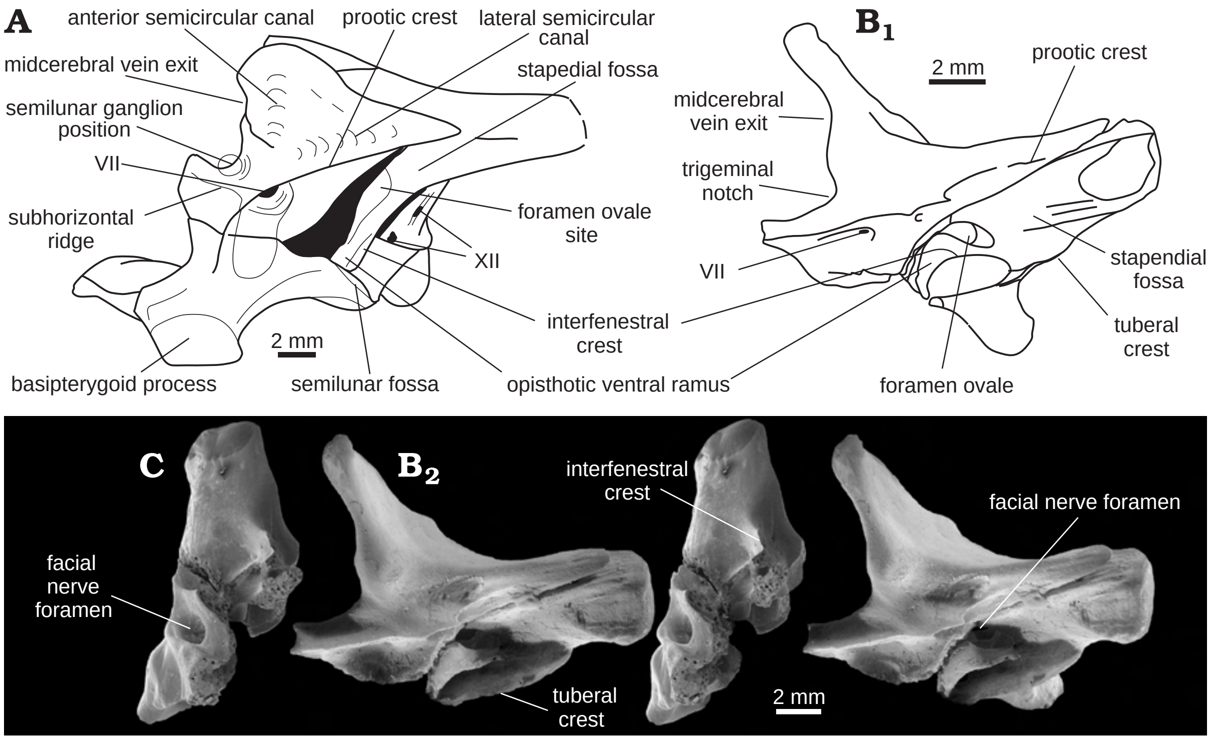

Fig. 24. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A**. Reconstruction of the braincase, in lateral view. **B**. *Varanus griseus* braincase, Recent, in lateral view. **C**. Opisthotic associated with fragmentary prootic ZPAL RV/540, in ventral view. B$_2$, C, stereo-pairs.

vestibuli). The lagena must have lain ventrally within the unossified part of the braincase wall. Ventral to the base of the posterior process, and posterior to the vestibular concavity, there is a triangular shelf (posterior fossa; Fig. 22B, D$_1$; see also ZPAL RV/532) facing posteromedially. It contributes a small anterolateral part to the stapedial groove.

Dorsal to the vestibular recess and separated from it by a ridge, and medial to the anterior semicircular canal, there is a shallow concavity corresponding to the subarcuate fossa (Fig. 22B). This is more or less circular in outline but opens into a wide funnel-shaped mouth anteriorly. It probably housed a cerebellar flocculus (concerned with the maintainance of equilibrium), and a dural venous sinus as in *Youngina capensis* and *Prolacerta broomi* according to the interpretation by Evans (1986, 1987). The venous sinus could have extended into a lateral cavity in the anterior border of the supraoccipital (Fig. 18A$_1$, A$_2$, C$_2$). The furrow perforated by the facial nerve (VII) forms a third anteroventral concavity in the medial face of the prootic. Anteriorly, this concavity opens towards the trigeminal notch. Posterodorsally a furrow, possibly for the vestibulocochlear nerve (VIII), leads into the vestibular cavity and is medially closed by a narrow bridge of bone.

Laterosphenoid. — As yet, the laterosphenoid has not been recognized in *Osmolskina*, and evidence for its presence is inconclusive. Regions of possible contact can be suggested on the basis of Clark's *et al* (1993, fig. 2) description of *Proterosuchus fergusi* in which the laterosphenoid articulates with the alar process (dorsal wing) of the prootic and with the tip of the anterior inferior process of the same bone (thus enclosing the trigeminal foramen). Dorsally, it meets the skull roof, articulating with a facet/recess on the under surface of the parietal wing (medial to the postfrontal articulation) as well as with the descending crest of the frontal. In *Osmolskina*, the dorsal wing of the prootic shows a small descending extension to the supraoccipital facet (Fig. 22) while the tip of the anterior inferior process, sometimes bears a small surface of finished bone that may be for the laterosphenoid. It should be stressed, however, that the trigeminal notch is much more open than it is in *Proterosuchus fergusi*. On the other hand, the underside of the lateral wing of the parietal bears a rugose surface, immediately medial to the postfrontal facet that matches the position of the laterosphenoid attachment surface in *Proterosuchus* (Clark *et al.* 1993, fig. 2).

In extant crocodiles, the laterosphenoid ossifies early in embryogenesis (Iordansky 1973, p. 252, fig. 13), and was probably ossified in *Osmolskina* despite the possible immaturity of the preserved bones.

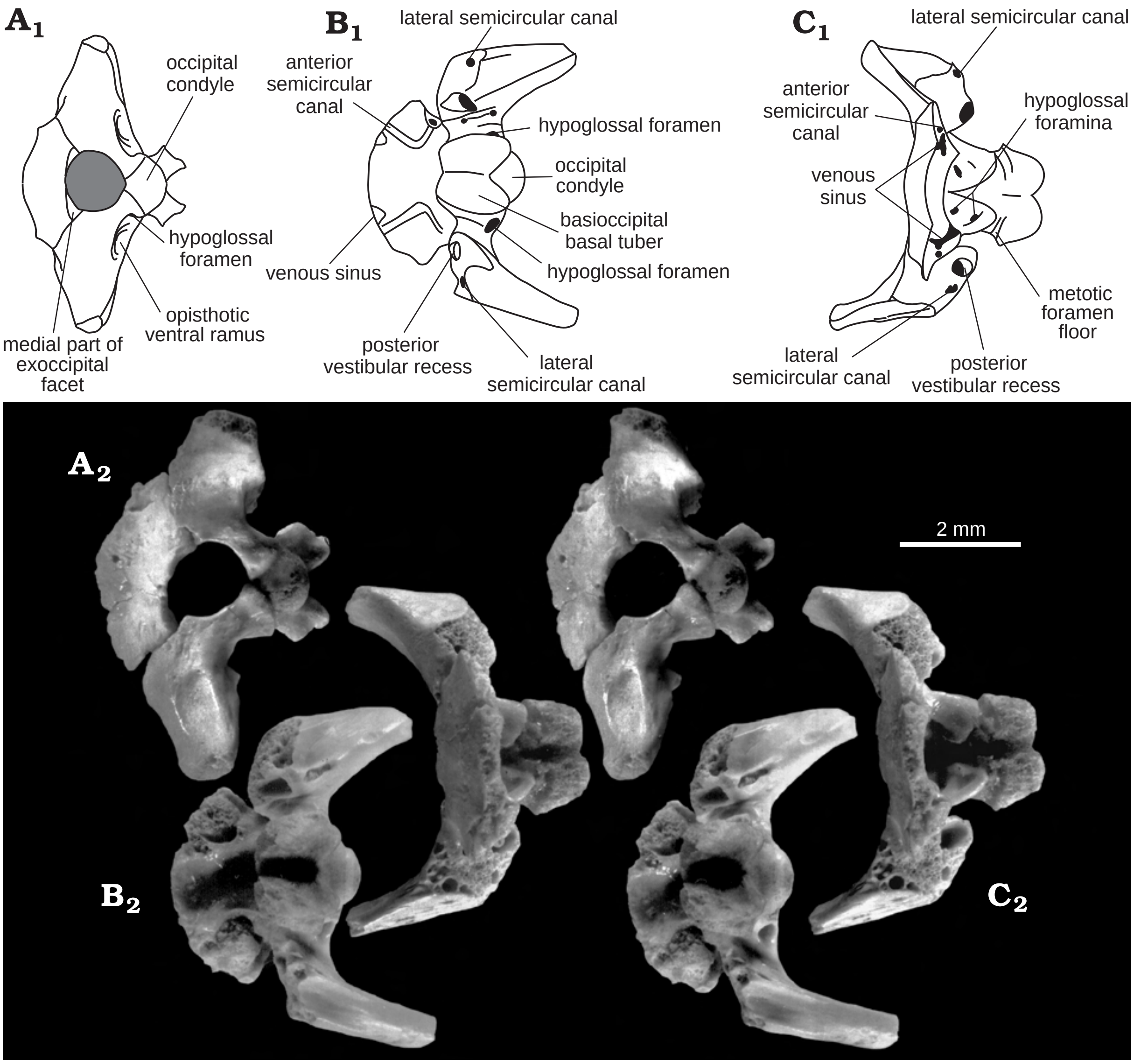

Fig. 25. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. Posterior part of the braincase ZPAL RV/424 combined from different individuals, in occipital (A), ventral (B), and anterior (C) views. A_2, B_2, C_2, stereo-pairs.

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Dentary. — As reconstructed, the dentary (Fig. 26A) is approximately six times longer than deep, slightly deeper at the posterior end. The posterior margin is always damaged, and shows neither facets for the posterior mandibular bones, nor the anterior border of the mandibular fenestra. The lateral face is convex in transverse section, uneven and permeated by nutrient foramina that are distributed mainly along the dorsal margin of the bone and in the mental region. As a rule, one of the foramina, situated at the level of the second tooth position, is much larger than the others. Some of the posterior foramina extend posteriad into furrows. Lingually, the Meckelian fossa is long and low, expanding slightly in the vertical plane towards the rear. It bears three foramina that probably carried the inferior alveolar nerve and its branches. The posteriormost foramen is situated slightly behind the mid-length of the bone and may have allowed the alveolar nerve to pass from the Meckelian fossa into the inferior alveolar canal. The Meckelian fossa is bordered by two ridges, both bearing faint traces of the splenial. The sub-dental ridge is sub-equal in depth to the fossa, and is deeper than the sub-Meckelian ridge. Anteroventrally, at about the fifth tooth position (Fig. 26C, D), it is obliquely cut by the splenial facet. The shape and anterior limit of the splenial (Fig. 26B) has been reconstructed from

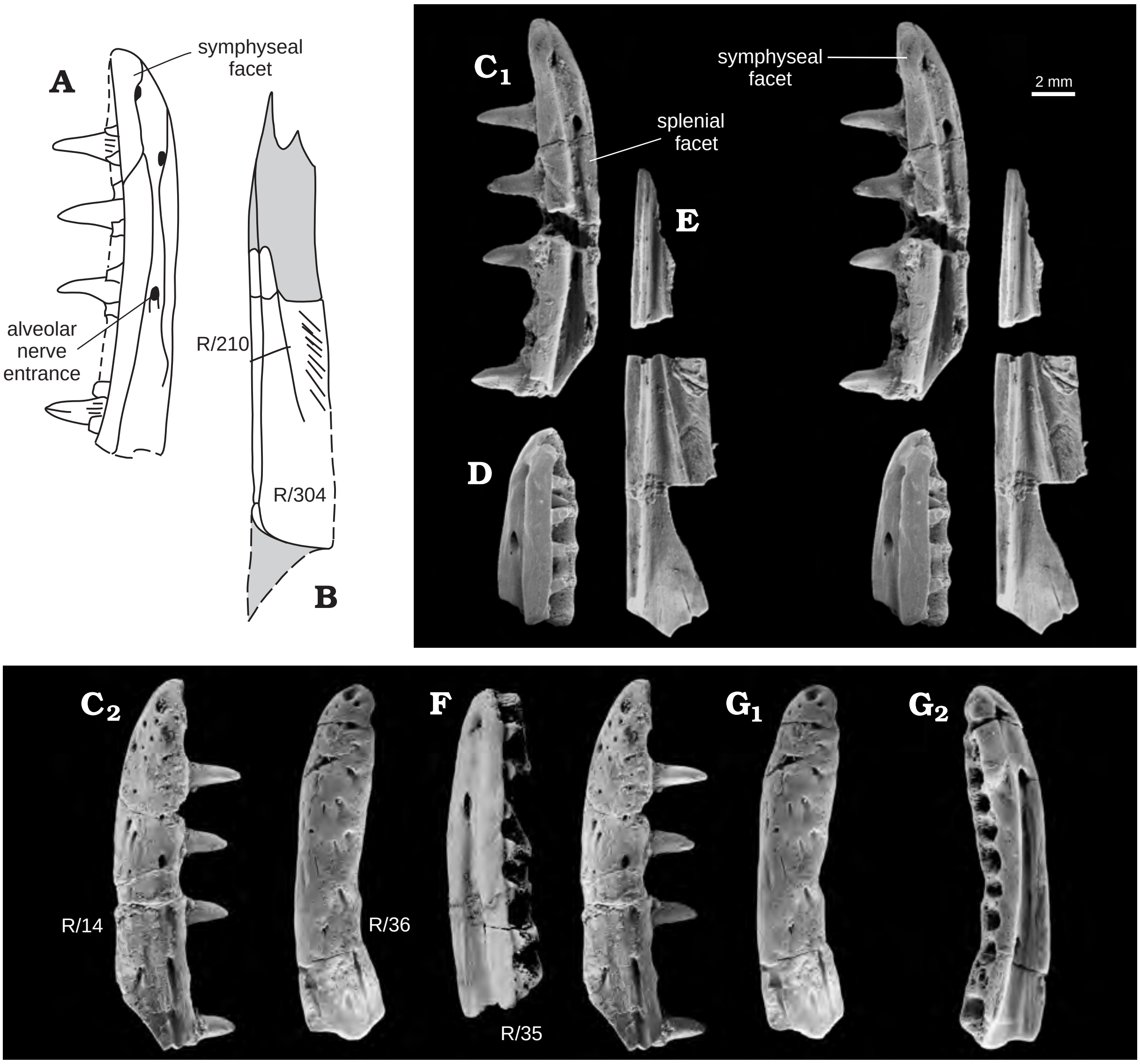

Fig. 26. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A**. Dentary reconstruction. **B**. Right splenial reconstruction based on ZPAL RV/210 and 304. **C**. Left dentary ZPAL RV/14. **D**. Anterior part of right dentary ZPAL RV/562. **E**. Right splenial ZPAL RV/304 (below) and ZPAL RV/210 (above). **F**. Right dentary ZPAL RV/35. **G**. Left dentary ZPAL RV/36. Lingual (A, B, C_1, D, E, F, G_2) and labial (C_2, G_1) views. C–G_2, SEM micrographs; all but F and G_2 stereo-pairs. Shortened catalogue numbers indicate the specimens on which the reconstruction is base.

these traces. The symphyseal surface is barely delimited, but seems to extend posteriorly to the fourth alveolus. The alveolar border is subdivided by interdental septa into alveoli that are usually preserved empty. Interdental plates border the lingual side of each alveolus at the front and rear (Fig. 30D, E). When the teeth are preserved they are fastened by spongy bone of attachment. The longest preserved specimen, ZPAL RV/36 (Fig. 26G_2), bears 12.5 alveoli. There is variation in the robusticity of the dentaries and in the corresponding shape of their anterior ends (Fig. 26C_2, F). This is considered to represent individual and ontogenetic variation.

Surangular. — The surangular is represented by numerous fragments (Fig. 27A, D, E), of which the most complete are from the posterior region. The bone usually breaks into pieces, particularly in its very fragile anteroventral portion. No part of the anteroventral border is ever preserved, and the presence of the mandibular fenestra may only be deduced from the dorsal border of the angular (see below). The outline of the fenestra (Fig. 1F, G) is conjectural, but the lateral wall of the surangular is quite deep at its contact with the dentary, suggesting a fairly low position for the inferred fenestra.

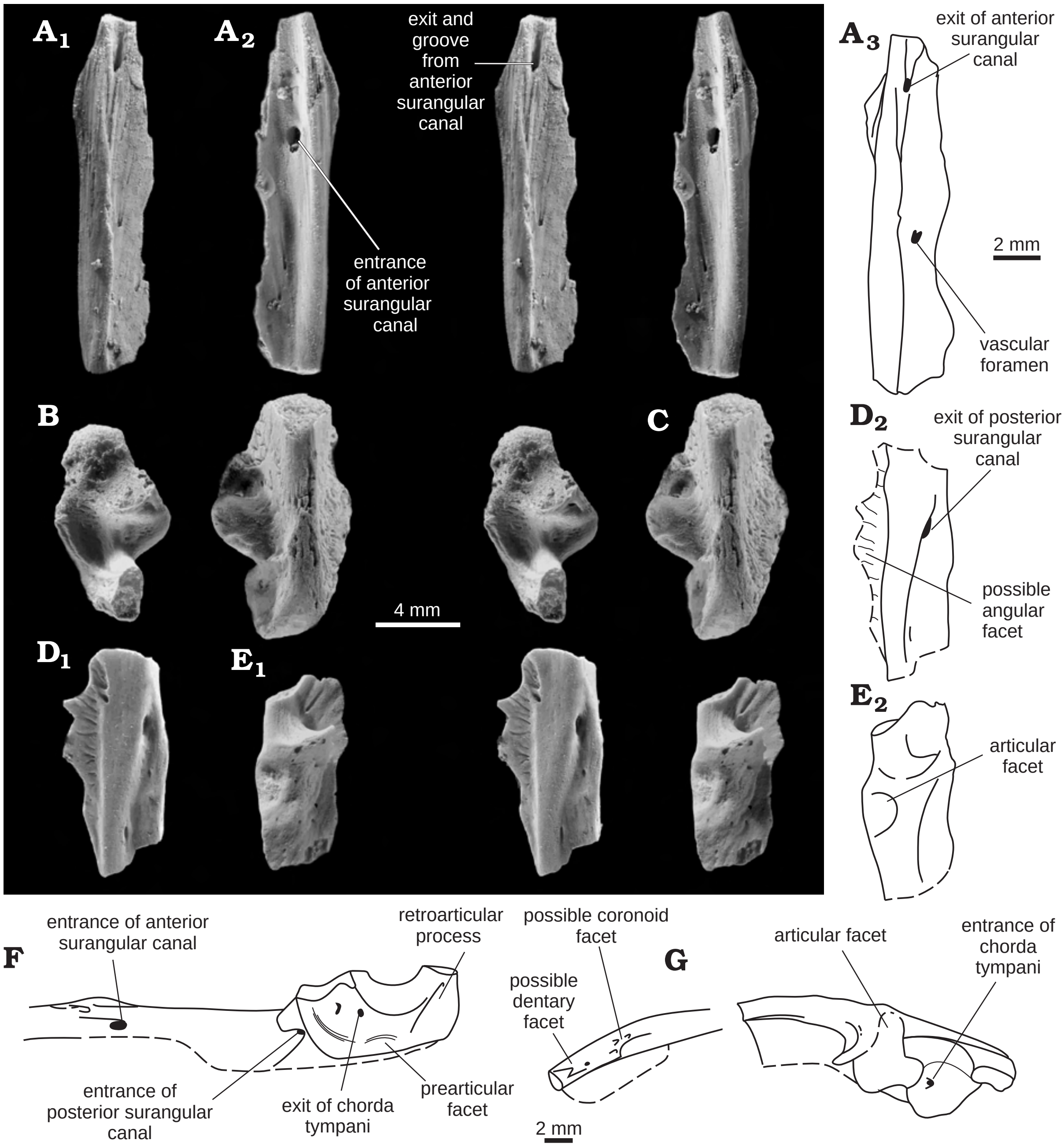

Fig. 27. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A**. Anterior fragment of right surangular ZPAL RV/551, in dorso-lateral (A_1, A_3)) and medial (A_2) views. **B**. Left articular ZPAL RV/549, in dorsal view. **C**. Left articular ZPAL RV/321, in ventral view. **D**. Posterior end of the left surangular ZPAL RV/550, in ventral view. **E**. Posterior end of the left surangular ZPAL RV/548, in dorsal view. **F**, **G**. Reconstruction of the surangular and articular, in medial (**F**), and dorsal (**G**) views. A_1, A_2, B, C, D_1, E_1, SEM stereo-pairs.

The bone is a flat elongated plate that is laterally convex along the longitudinal axis. It is overhung, both laterally and medially, by a thick dorsal ridge. In the posterior portion of the bone, the dorsal ridge produces a hook-like medial projection that forms an anterior buttress for articulation with the articular bone. This part is pierced by two foramina (Fig. 27D–F) probably corresponding to the entrance (the medial one) and the exit (the lateral one) of the posterior surangular canal (Oelrich 1956). Posterior to the hook-like projection, the surangular extends into a long pyramidal process, its ventrolateral wall (Fig. 29A_1) tapering posteriad. The longitudinal convexity of the dorsomedial wall of the pyramid (Fig. 27E) matches the concavity of the ventrolateral face of the articular (Fig. 27C). The third wall of the pyramid (Fig. 29A_3) is an elongated triangular continuation of the thick dorsal ridge of the anterior portion.

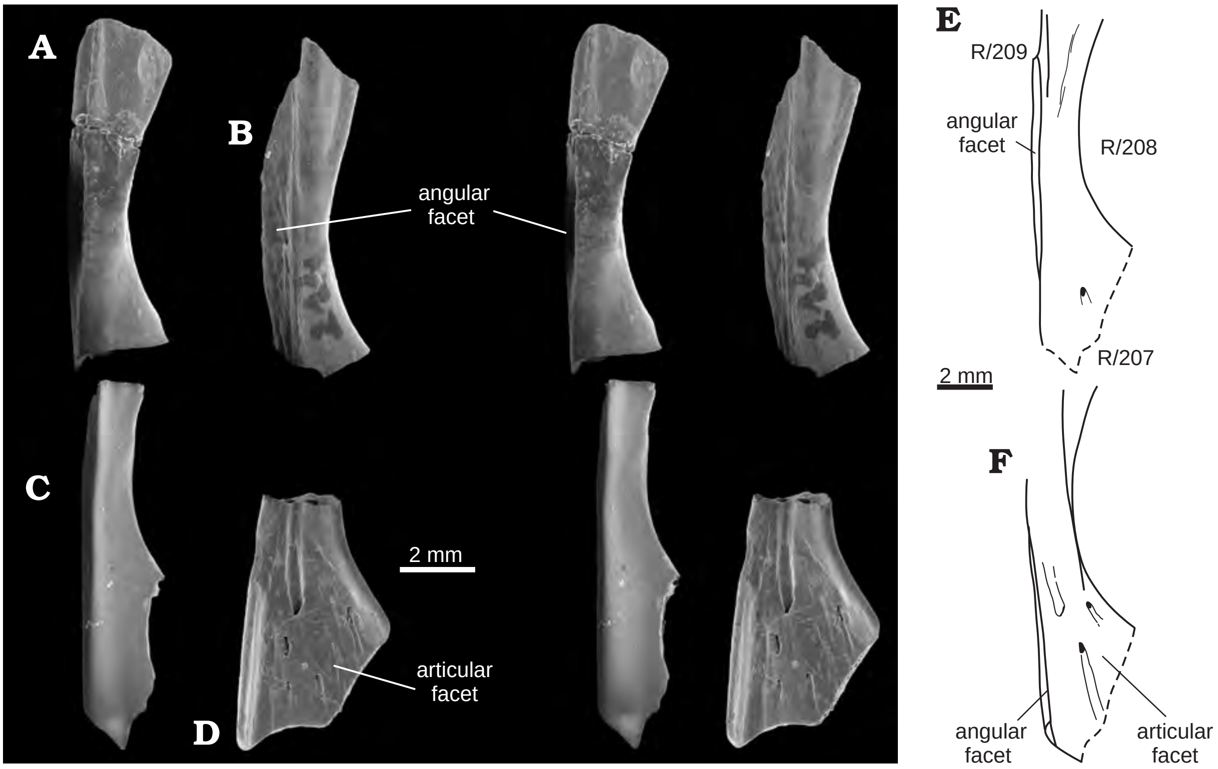

Fig. 28. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. Prearticular: ZPAL RV/208 (**A**), ZPAL RV/214 (**B**), ZPAL RV/ 209 (**C**), and ZPAL RV/207 (**D**). **A**–**C**. Right bones, in medial view. **D**. Right bones, in lateral view. **E**, **F**. Reconstructions of the bone, in medial (E) and lateral (F) views. A–D, SEM stereo-pairs. Shortened catalogue numbers indicate the specimens on which the reconstruction is base.

Anterior to the hook-like projection, the dorsal ridge is bordered by two crests, a lateral one that overhangs the lateral face of the bone (Fig. 27A$_1$), and a medial one (Fig. 27A$_2$) that passes gently into the concave dorsomedial surface of the mandibular fossa. The lateral crest probably corresponds to the structure described as an external flange of the surangular. This marks the origin of the lamina lateralis of the tendon supporting pterygoideus posterior muscle in extant crocodiles (Busbey 1989) and birds (Lakjer 1926). Clark *et al.* (1993) considered it to be characteristic of basal archosauriforms.

The anterior end of the dorsal ridge is produced into a small dorsal tuber, in front of which is a ridged surface (Fig. 27A$_2$) for possible articulation with the coronoid, although it might be, partly or entirely, a trace of the attachment of the mandibular adductor tendon. More anterior and slightly medial to this surface is the dentary facet. This part of surangular is pierced by foramina for branches of the mandibular artery and the mandibular division of the trigeminal nerve entering the mandibular fossa. This probably corresponds to the anterior surangular foramen (Oelrich 1956). The medial surface of the surangular (Fig. 27A$_1$, F) is a possible entrance, the lateral a possible exit (Fig. 27A$_1$, A$_3$) for the anterior surangular canal. The main plate of the surangular forms the lateral wall of the mandibular fossa and the posterodorsal border of a probable lateral mandibular fenestra. Where preserved, the lateral surface of the posteromedial border of the surangular bears an obliquely ridged facet for the overlapping angular (Fig. 27D$_1$, D$_2$).

Splenial (Fig. 26B, E). — The best-preserved splenials (PAL RV/210, 211, and 304) are too large to match the preserved dentaries, and are assigned only tentatively. This bone may be reconstructed from facets on the medial surface of the dentary (Fig. 26C$_1$) and angular (Fig. 29E). Based on the best-preserved specimen (ZPAL RV/210), the splenial was an elongate sub-triangular bone contacting the dentary ridges bordering the Meckelian fossa (see above). It must have extended to at least the fourth tooth position, its anterior border descending obliquely to a point between the third and second tooth position, before turning down around the level of the middle inferior alveolar nerve foramen, to the level of the second tooth position. Medially, the splenial is flat, except for the ventral border that curves towards the dentary. The lateral (internal) surface is correspondingly concave ventrally. Its lower border is overhung in a step-like manner by a hori-

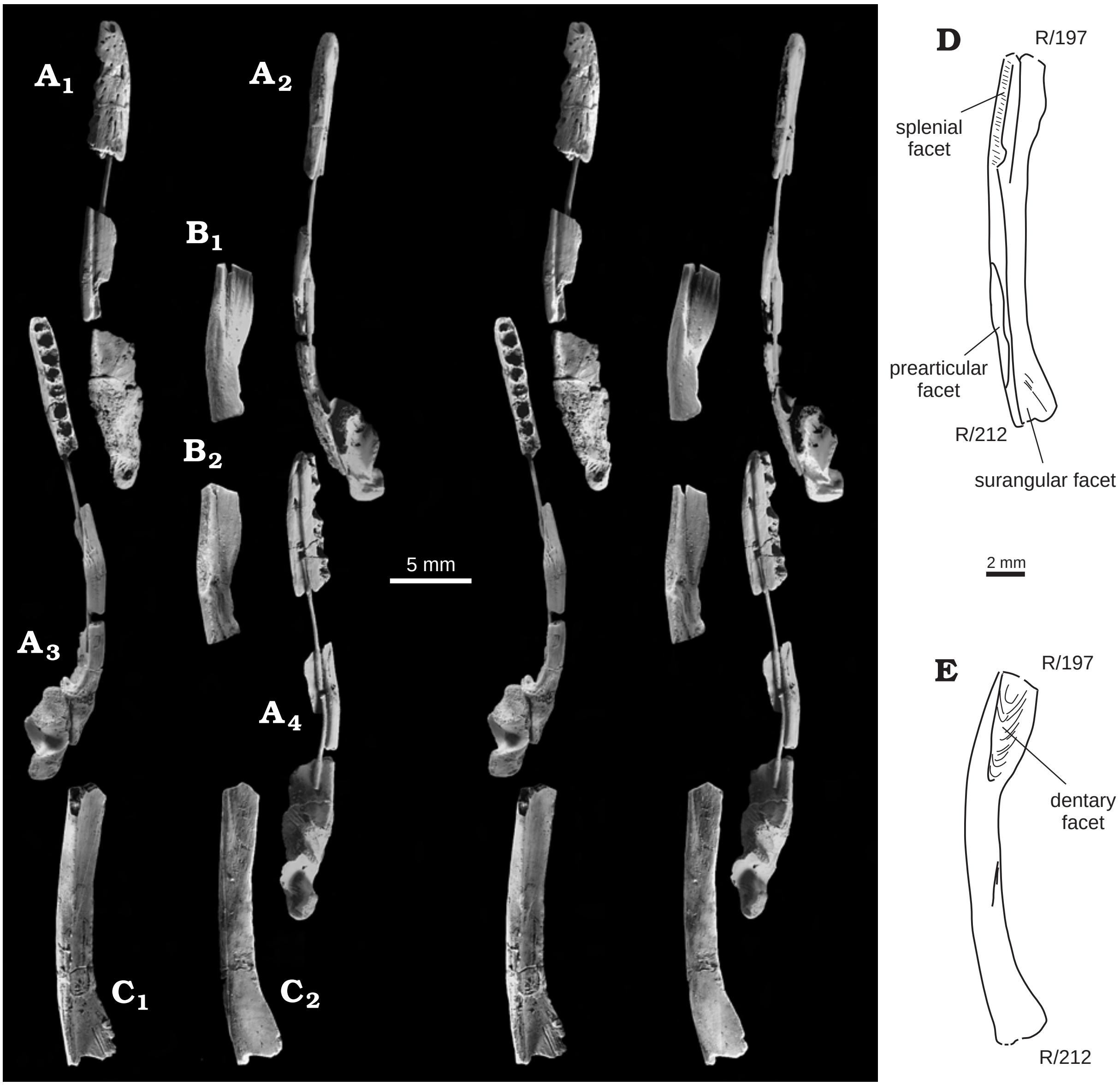

Fig. 29. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A**. Right mandible ZPAL RV/ 35+35a combined from different individuals, in lateral (A$_1$), ventral (A$_2$), dorsal (A$_3$), and medial (A$_4$) views. **B**. Anterior portion of right angular ZPAL RV/197, in lateral (B$_1$) and medial (B$_2$) views. **C**. Posterior portion of angular ZPAL RV/212, in lateral (C$_1$) and medial (C$_2$) views. **D**, **E**. Reconstructions of right angular, in medial (D) and lateral (E) views. A–C, SEM stereo-pairs. Shortened catalogue numbers indicate the specimens on which the reconstruction is based.

zontal shelf that must have met the dorsomedial surface of the dentary sub-meckelian ridge (see above), whereas the ventral margin of the splenial contacted the medial surface of the ridge. The lateral (intramandibular) concavity of the splenial is subdivided by a longitudinal anteroventral crest.

Articular (Figs 27B, C, F, G, 29A). — In the Czatkowice material, the articular is never co-ossified with the surangular. This may be a genuine character or a reflection of immaturity. The articular is a fairly massive, ventrally crested, and dorsally tripartite bone. The anteriormost part of the dorsal face is occupied by articular cotyles for the quadrate condyles, and is divided posteriorly by a prominence (Fig. 27B). It is covered by unfinished and usually damaged bone, but was probably completed by a laterally protruding part. The central and posterior parts of the articular contribute to the retroarticular process. The central part displays a saddle-shaped dorsal surface divided into two concavities by a sagittal crest. The posterior part is a heavy, laterally compressed process (Fig. 27B) referred to as a “hooked ascending process” in *Batrachotomus kupferzellensis* (Gower 1999). It was probably for the attachment of the depressor mandibulae muscle tendon, as in extant crocodiles. When the surangular is oriented in a possible life position, the hooked ascending process of the articular is inclined medially. This inclination is similar to that in *Batrachotomus* (Gower 1999), but differs from that of crocodiles. The ventrolateral aspect of the articular bears a concavity (Fig. 27C) matching the convexity of the posterior process of the surangular to which it is applied (Fig. 27E). The medial surface is overhung by a protruding semi-circular shelf, and is pierced by a foramen (Fig. 27B, C, G). A similarly located foramen in extant crocodiles is an entrance into a blind pneumatic space (foramen aerum Iordansky 1973). In *Osmolskina*, the foramen leads to a canal that opens on the dorsomedial surface of the articular, exactly as it does in numerous rauisuchians and is similarly interpreted as a chorda tympani canal (Gower 1999). The structure of the retroarticular process is closely comparable to that of an extant crocodile, but is shorter and broader. It is longer than in *Batrachotomus* (Gower 1999).

Prearticular. — As reconstructed (Fig. 28E, F) from fragmentary remains (ZPAL RV/207–209, 213–215), the prearticular consists of an elongated body joining two sub-triangular ends. Ventrally, the bone angles laterally along a straight ridge to form a horizontal step-like shelf extending toward the angular. The dorsal border of the bone is arcuate. It bordered the medial entrance to the mandibular fossa. The posterior end probably had a wide contact with the articular, and the anterior end ascended slightly towards the splenial and coronoid, but the structure of these contacts is unknown. The internal surface of the bone that walls the mandibular fossa medially is slightly concave in transverse section, and is richly permeated by neurovascular canals.

Angular. — This element is usually preserved in pieces (Fig. 29B–E). The longest specimen (ZPAL RV/212) demonstrates that the posterior end of the angular is slightly larger than the rest, and was covered by traces of radiating blood vessels on its inner, concave surface. The dorsal part of this surface probably overlapped the ventromedial margin of the surangular (Fig. 27D_2), but the surface does not reach far anteriorly. The more anterior dorsal border of the angular bears no trace of facets for the surangular and, thus, probably bordered the mandibular fenestra.

Along the ventral border of the bone there is an elongated surface that should have matched the one on the prearticular shelf, but the match is not perfect. Specimen ZPAL RV/197 is an anterior fragment of a right bone (Fig. 29B). A long triangular lateral facet (Fig. 29E), open dorsally but ending ventrally in a deep sub-horizontal furrow, probably received a posterior process of the dentary that is not preserved in the material, whereas an elongated ventral step in the medial surface probably met the splenial (Figs. 29D, 36E–G). The position of the angular in relation to the other mandible bones, and particularly to the surangular, is far from clear.

Coronoid. — The coronoid has not been identified and the only information on this bone is a possible trace of this bone (Fig. 27G) at the anterior end of the dorsal ridge of the surangular (see above). Its position is reconstructed (Fig. 1G) on the basis of crocodile structure.

DENTITION

General remarks. — *Osmolskina* is well represented by jaw elements and many isolated teeth, but no specimen has a complete dentition preserved. This causes some difficulty in determining regional variation (see below). Those jaw fragments retaining teeth, firmly held by bone of attachment, are mostly large and perhaps closer to maturity. The teeth are typically worn, lack surface features, and may represent an adult morphology somewhat different from that of the majority of isolated teeth in the deposit.

Basic tooth morphology. — In describing a typical tooth, we are focusing on isolated, unankylosed, and therefore immature examples from the mid-part of the tooth series. A typical tooth of this type (*e.g.*, Fig. 30B) has a root and crown of roughly equal proportions. The tooth is widest at the gingival boundary. The root tapers only slightly towards the tip, but the crown does so sharply. The surface of the root is generally marked by parallel longitudinal striae reflecting the development of periodontal connective tissue holding the tooth in place; the cross-section remains ovoid (long axis anteroposterior). The crown is labio-lingually compressed and has a posteriorly recurved tip (convex anterior margin, concave distal one). The surface of the crown is shiny and smooth except for keeled and serrated anterior and posterior edges. The posterior margin bears a row of around 25 denticles (independent of tooth size) along the entirety of its edge. The anterior margin usually bears denticles on only the apical half (although the row may be longer), but these denticles are borne on a distinct, lingually inflected keel that may continue further than the serrations themselves. A broad furrow separates this

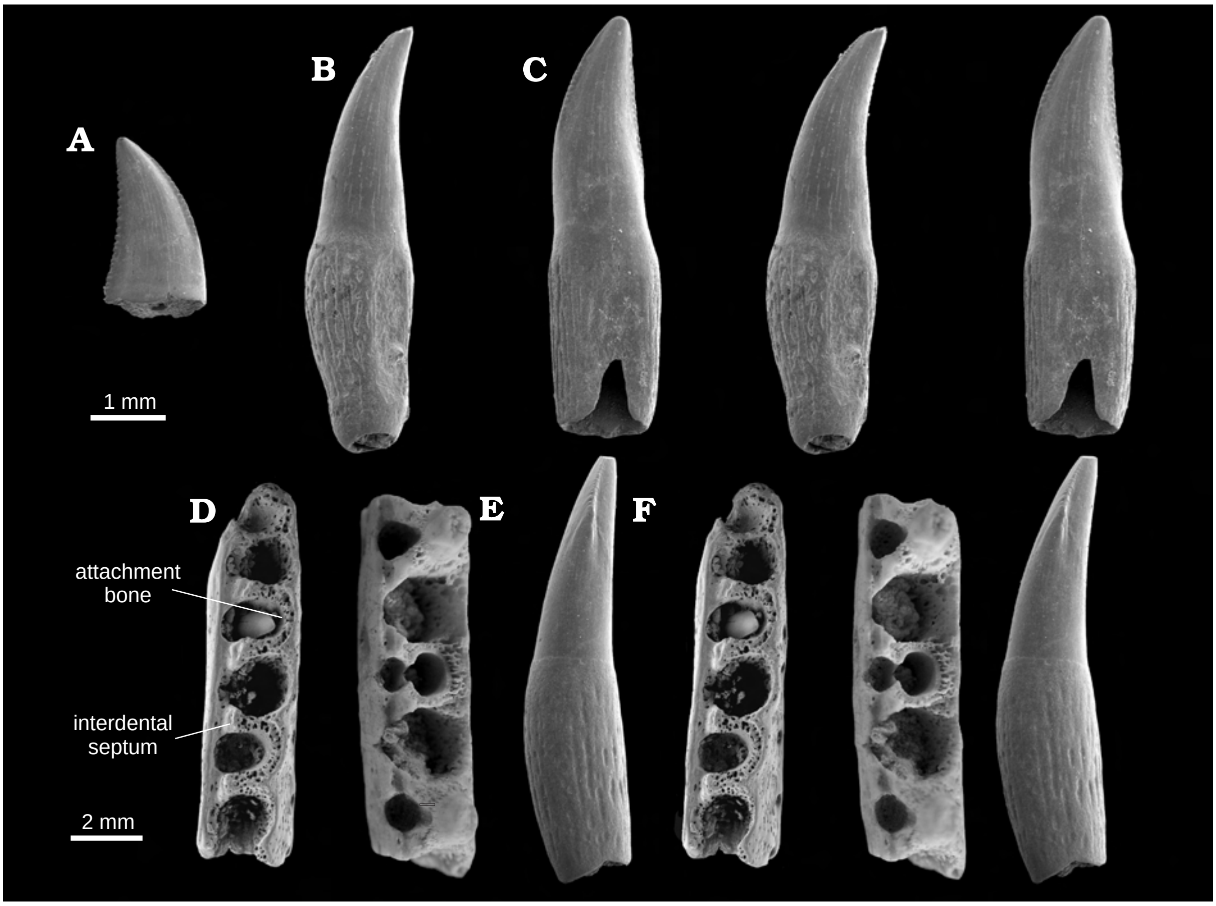

Fig. 30. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A**–**C**, **F**. Isolated teeth. **A**. Juvenile tooth crown ZPAL RV/565. **B**. ZPAL RV/564. **C**. ZPAL RV/566. **F**. ZPAL RV/567. **D**. Anterior part of right dentary ZPAL RV/562. **E**. Middle part of right maxilla ZPAL RV/563. Lingual (A–C, F) and occlusal (D, E) views. SEM micrographs; all but A stereo-pairs.

anterior keeled margin from the remainder of the tooth surface on the lingual side (the labial side of the tooth curves uniformly) (*e.g.*, Fig. 30F). The denticles themselves are close set with parallel, weakly grooved margins and square or slightly rounded apices. Together they form a sharp, serrated cutting edge.

Implantation and replacement. — The implantation is fully thecodont. In a typical mid-jaw tooth, the root and the crown are of roughly equal length. The alveolar margin of each tooth-bearing element is divided into a series of rounded alveoli by a combination of lingual interdental plates and interdental septa (a combination referred to as an interdental unit by Senter 2003) composed mainly of bone of attachment (Fig. 30D, E). The attachment bone forms a thin layer on the internal wall of the alveolus in juveniles or where the teeth are not yet fully implanted (Fig. 30D), but fills the alveolus and blends with the surface of the tooth itself where the teeth are mature (Fig. 30E). During replacement, the lingual side of the alveolar bone is eroded first then the attachment bone, and finally the root. Once the functional tooth is lost, the replacement tooth fills up a socket, but is only weakly attached. Only once the root is fully formed does bone of attachment become deposited around it. The high incidence, therefore, of isolated unerupted crowns (Fig. 30A), and complete but not yet fully attached, teeth, suggests that replacement was rapid. The rarity of fully attached teeth may suggest that much of the material is immature.

Two specimens (ZPAL RV/ 562 and 563) provide a good demonstration of the stages of implantation, attachment, and replacement. The juvenile jaw ZPAL RV/562 (Fig. 30D) contains no implanted teeth, but there is a single unerupted tooth crown in tooth position three. The alveoli have only a thin layer of attachment bone on the walls. The unerupted tooth crown is pristine and the anterior and posterior serrations are clearly visible. This is a labio-lingually compressed tooth of the type described above as typical. ZPAL RV/563 (Fig. 30E) is the central part of an older maxilla, preserving five tooth positions from the level of the anterior maxillary pillar backwards. It shows alternate tooth replacement. Positions one, three and five (as preserved) contain mature teeth (broken tooth bases), while positions two and four are empty and presumably held developing teeth. Again, the structure of the interdental septa (interdental plate and bone of attachment) is clearly visible. All three implanted teeth are firmly attached, but all are undergoing replacement from the lingual side, as shown by the cavities that notch both the alveolar margin of the maxilla and the alveolar attachment bone. The cavities must have contained very small loose replacement teeth now lost. Presumably once the mature teeth had finally been eroded, lost, and replaced, the developing teeth in positions two and four would have been firmly implanted.

Variation. — As far as can be judged from the jaw elements themselves, the teeth vary in size and, to some degree, morphology along the jaws, and show some differences between elements.

Each premaxilla contains four teeth housed in large rounded sockets (Fig. 2). The teeth are relatively longer and narrower than those on the dentary and maxilla, and are more rounded in cross-section. None of the teeth preserved in situ bears serrations, but some isolated teeth of otherwise similar morphology bear serrations on a sharp keel along the posterior margin only, the anterior margin of the tooth being rounded. In ZPAL RV/88 (Fig. 2B), only the most medial premaxillary tooth is preserved. It is fully rounded in cross-section with no trace of keels. In contrast, ZPAL RV/83 (Figs 2A, 3D) preserves the last premaxillary tooth, and, although broken, the cross-section shows a clear posterior keel and a slight anterior ridge.

Each maxilla bears an estimated 13 teeth. These vary in size with the largest teeth in positions four to eight, in the region of the nasal process and anterior pillar. This is reflected by an increased depth of the supra-alveolar ridge (Fig. 6C–E). Behind this point the teeth decrease in size, with the most posterior teeth being tiny denticles. On the limited evidence available, the most anterior maxillary teeth resemble those of the premaxilla in being rather more rounded in cross-section.

At least 13 teeth were present in the dentary which is never complete. Overall, the dentary teeth seem to have been slightly smaller than those on the maxilla. The dentary ZPAL RV/14 demonstrates that teeth in positions four to eleven were subequal in size. Judging by alveolar size and depth, the first two positions were held by relatively small teeth and this may reflect the slightly overhanging position of the premaxilla reconstructed for this animal.

DISCUSSION

As revised by Juul (1994), the diagnosis of archosauriforms (Gauthier *et al.*1988) has been reduced to two well supported synapomorphies, the possession of an antorbital fenestra and an ossified laterosphenoid (see also Clark *et al.* 1993), supplemented by a third, the possession of a mandibular fenestra (Parrish 1992; Juul 1994). Of these, only the antorbital fenestra has been confidently reconstructed in *Osmolskina*, while the presence of the laterosphenoid was deduced on the basis of the prootic and the skull roof morphology, and that of the mandibular fenestra was reconstructed from the outline of the angular margin. The presence of all the above synapomorphies would be expected in *Osmolskina*, because this genus presents a combination of many other archosauriform features such as the very small postfrontal (character 1 of Gauthier 1988, and of Benton and Clark 1988), the tall columnar quadrate (Romer 1956), and deep rooted (thecodont) teeth (characters 8 and 18 Gauthier *et al.* 1988) showing lateral compression and serrated margins (character 12 of Benton and Clark 1988, and character 7 of Gauthier *et al*. 1988 respectively), as well as characters relegated by Juul (1994) to some less inclusive groups.

The absence of teeth on the transverse flange of the pterygoid (character 21 of Gauthier *et al.* 1988) is consistent with a position crownward of proterosuchids, while the retention of toothed zones along the medial margin of the pterygoid and on the palatine (the vomer is not identified) tends to exclude *Osmolskina* from the crown-group. The presence of interdental plates tends to locate *Osmolskina* more crownwords than the erythrosuchids. They are perfectly developed also in *Euparkeria* (Senter 2003). According to Juul (1994), the interdental plates are characteristic of some basal archosaurs (rauisuchians, *Herrerasaurus*, *Ornithosuchus*), while being absent from non-archosauriform Archosauromorpha (rhynchosaurs and *Prolacerta*), proterosuchids (Cruickshank 1972, Gower and Sennikov 1997), and erythrosuchids (Parrish 1992, Gower 2003). However, the relationship between *Osmolskina* and the Erythrosuchidae is far from clear. *Osmolskina* differs in its much smaller size and lighter build as well as in having a ventral maxillary margin that is straight instead of convex. Some characters considered derived within the non-archosaurian archosauriforms (Juul 1994, p. 38), such as a fairly large antorbital fenestra with an antorbital fossa around it, and the absence of a parietal foramen cannot discriminate between the above taxa. The antorbital fossa does occur in erythrosuchids (Juul 1994, p. 6; Gower 2003), and both its size and the structure of its anterior border are similar in *Erythrosuchus* (Parrish 1992, fig. 6), *Osmolskina*, and *Euparkeria* (Ewer 1965, fig. 22). The parietal foramen is retained only in *Garjainia* (Parish 1992, p. 96).

The above discussion shows only that *Osmolskina* is a non-archosaur archosauriform situated more crownward than the proterosuchids in the phylogeny.

In the Appendix 2, *Osmolskina* has been added to the data matrix of braincase characters of Gower and Sennikov (1996), although this has been restricted to those characters and taxa relevant to the present case. The characters discussed below are numbered and scored according to Gower and Sennikov (1996) unless otherwise indicated.

Character 1. — Position of the entry foramina for the cerebral branches of the internal carotid artery: ventral or ventrolateral = 0, lateral =1 (according to Gower and Sennikov 1996)). Gower (2002) updated this character, and recognized three states: foramina posterior = 0; posterolateral = 1, and anterolateral = 2. Our scoring is different: foramina lateral to the ventrolateral crests = 0; directly ventral, anterior to the fused ventrolateral crests = 1; lateral to basipterygoid stalks = 2. *Osmolskina* is scored 1.

According to Gower (2002), the foramina on the posterior surface of the parabasisphenoid occur in non-crown-group archosaurs, *Proterosuchus*, *Garjainia*, and *Euparkeria*, so this state is probably equal to the ventral or ventro-lateral position of Gower and Sennikov (1996).

In our opinion, all the genera included in our matrix (Appendix 2) have the carotid foramina situated close to the ventral surface of the parabasisphenoid, and also posterior to the basipterygoid processes, and so qualifications such as just ventral or posterior are not informative enough. Our position is that there is a difference between *Proterosuchus* and *Euparkeria–Osmolskina* that should be expressed in scoring. The illustrations of braincases in *Prolacerta* and *Proterosuchus* (Gow 1975, figs 35A, 36C; Evans 1986) suggest they are similar in having the foramina located lateral to the ventrolateral crests of the parabasisphenoid, which is probably also true of *Fugusuchus* given the reconstruction of Gower and Sennikov (1996, fig. 4D). The anteriormost parts of the crests converge gradually over a long distance and at a small angle to each other, whereas in *Osmolskina* they turn abruptly mediad and fuse with each other. This change in the course of the ventrolateral crests associated, for simple geometrical reasons, with both a sub-vertical position of the basisphenoid (character 7), and a more vertical position of the basipterygoid processes (character 7a), both derived according to Gower and Sennikov (1996), is considered derived as well. If it is correct, the directly ventral position of the carotid foramina, anterior to the fused ventrolateral crests (we score 1 herein) should also be considered derived with respect to their primitive lateral position in proterosuchids, *Prolacerta*, and a prolacertiform grade animal from Czatkowice 1 (Borsuk-Białynicka and Evans 2009, fig. 8E_1). *Osmolskina* shares the position "directly ventral, and anterior to the fused ventrolateral crests" with *Euparkeria* (Gower and Weber 1998, fig. 4), *Dorosuchus* (Sennikov personal communication), *Garjainia* (Gower and Sennikov 1996, fig. 1), *Xilousuchus* (Gower and Sennikov 1996, fig. 5), and probably *Turfanosuchus* (Wu and Russell 2001, fig. 5). The directly ventral position of the foramina (1) in the rhynchosaurs (*Mesosuchus*, Dilkes1998; *Hyperodapedon*, Benton 1983, figs 10, 11), which are among the outgroups of archosauriforms, is probably homoplastic in view of the highly specialized skull.

The lateral position of the carotid foramina has been considered a synapomorphy of proterochampsids + crown-group archosaurs (Parrish 1993), or of the crown-group alone (Gower and Weber 1998). The Crurotarsi (at least *Postosuchus*, *Batrachotomus*, *Parasuchus*, and *Stagonolepis*) have these foramina in a lateral position (Chatterjee 1978; Gower and Sennikov 1996; Gower 2002), and the same is true of early ornithodirans (*Marasuchus*, Sereno and Arcucci 1994; prosauropods, Galton and Upchurch 2004; and basal Saurischia, Langer 2004). However, the Middle Triassic *Arizonasaurus babbitti* from the United States (Gower and Nesbitt 2006), and the Late Triassic dinosauriform, *Silesaurus opolensis*, from Poland (Dzik 2003) have the carotid foramina directly ventral.

Character 2. — Basisphenoid intertuberal plate: present = 0; absent = 1. *Osmolskina* is scored 1. The basisphenoid intertuberal plate is a transverse septum separating the parabasisphenoid from the basioccipital part of the ventral concavity. Parrish (1992) proposed that it was an autapomorphy of erythrosuchids. According to Gower and Sennikov (1996), it was shared not only by *Proterosuchus* and *Fugusuchus* but also by *Prolacerta*, and on this basis has been considered plesiomorphic of archosauriforms. In our opinion, this would suggest that what is labelled basisphenoid intertuberal plate might be homologous with the posterior margin of the parasphenoid, at least in some taxa.

According to Gow (1975, figs 35, 36), the parasphenoid of early diapsids was long and bridged the gap between the overlying basisphenoid and basioccipital. It has subsequently shortened, in parallel and at different rates, in different diapsid clades, although its posterolateral corners continued to contribute to the basal tubera, and the posteromedial part retained a horizontal flange protruding posteriad to overlap the basioccipital. This horizontal flange is variable in size and shape, and its presence is here considered as a primitive character state. It occurs in *Prolacerta* (Gow 1975, figs 35; Evans 1986, figs 4, 5) and in *Osmolskina*, (according to impressions left on the basioccipital surface Fig. 33B), and probably corresponds to the thickened border of the parasphenoid in *Proterosuchus* (Gow 1975, fig. 36). The erythrosuchid intertuberal plate unites the basal tubera of the parabasisphenoid, but extends clear of the posterior border of this bone (as demonstrated by *Garjainia* and *Xilousuchus*, Gower and Sennikov 1996, figs. 2, 5; and *Erythrosuchus*, Gower 1997, fig. 2). It does not seem to be homologous with the posteromedial parasphenoid flange of other archosauriforms and *Prolacerta*, but was probably added to it. If this interpretation is correct, its presence would be derived as originally stated by Parrish (1992). Its absence in *Prolacerta* and non-erythrosuchid archosauriforms, including both *Osmolskina* and *Euparkeria*, would be primitive (contra Gower and Sennikov 1996). However, this problem requires further study and this equivocal character is removed from the matrix (see Appendix 2).

Character 3. — Abducens canal position: between the basisphenoid and prootic = 0, within prootic only = 1. *Osmolskina* is scored 0. In early amniotes, as exemplified by *Captorhinus* and *Milleretta* (Evans 1986), the abducens canals are located within the basisphenoid. A canal situated within the prootic-basisphenoid suture is characteristic of the immediate outgroups of the Archosauriformes (*Prolacerta*, Evans 1986; *Hyperodapedon*, Benton 1983), as well as of *Proterosuchus* (Cruickshank 1972) and *Euparkeria* (Gower and Weber 1998). In some erythrosuchids, at least, the canal has shifted into the prootic (Gower and Sennikov 1996). However, in basal archosaurs it seems to remain within, or return to, the basisphenoid (*e.g.*, the phytosaurian *Parasuchus*, Chatterjee 1978; and the prosauropod *Thecodontosaurus*, Benton *et al.* 2000). If properly reconstructed (Figs 20A, 21B), *Osmolskina* shares the primitive archosauromorph condition, but the polarity of this character, and its developmental basis, remain unclear.

Character 5. — Ventral ramus of the opisthotic: prominent = 0; recessed = 1. *Osmolskina* is scored 0.

Character 6. — Ridge on the anterior inferior prootic process below the trigeminal notch: present = 0; absent = 1. *Osmolskina* is scored 0.

Character 7. — Basisphenoid orientation: horizontal = 0 , sub-vertical = 1. *Osmolskina* is scored 1.

Character 7a. — Basipterygoid processes directed laterally = 0, ventrolaterally =1. *Osmolskina* is scored 1. Based on the work of Gower and Sennikov (1996, description and fig. 4C, D) the braincase of *Fugusuchus* is primitive not only in having a horizontal basisphenoid, but also in having laterally directed basipterygoid processes and carotid foramina lying lateral to the ventrolateral crests (though ventrolateral with respect to the whole braincase). In contrast, erythrosuchids (*Erythrosuchus*, *Garjainia*, and *Xilousuchus*) display a high braincase with a very short, sub-vertically oriented parabasisphenoid (Gower 1997; Gower and Sennikov 1996). In *Xilousuchus* (Gower and Sennikov 1996, fig. 5), the processes are slightly more lateral, whereas in *Garjainia* (Gower and Sennikov 1996, fig. 1) and *Erythrosuchus* (Gower 1997, figs 2, 11) they are directed more ventrally. As a result, the carotid foramina are further apart in *Xilousuchus* and less so in the illustrated representatives of *Garjainia* and *Erythrosuchus*. *Euparkeria* has a sub-vertical parabasisphenoid (Ewer 1965, Gower and Weber 1998, p. 385). The basioccipital-basisphenoid fossa seems to be wedged slightly between the carotid foramina (Gower and Weber 1998, fig. 4) as it is in *Osmolskina*, and in both genera the foramina are located close to one another posteromedial to the basipterygoid processes on the ventral surface of the parabasisphenoid (Fig. 21A, E). The whole pattern seems to fall within the range of variability manifested by the erythrosuchids, which was probably the range of the non-archosaurian archosauriforms crownward of *Proterosuchus*. However, the braincase of *Sarmatosuchus otschevi* from the Anisian of Russia, considered to be a proterosuchid Gower and Sennikov 1997, is strikingly derived in having essentially vertical alignment, with a ventrolateral orientation of the basipterygoid processes as well as ventral orientation of the internal carotid foramina.

Clark *et al.* (1993) considered that the verticalization of the parabasisphenoid, which occurred during the early course of archosauriform evolution, resulted in an increase in the space available for the adductor muscles. According to these authors, this was an adaptation towards macropredaceous habits. A reorientation of the basipterygoid processes to a more vertical position, closer to each other, may have been a response to the same selective agent. As hypothesised above, the changes in the basisphenoid configuration influenced the position of the anteriormost parts of the ventrolateral crests so that they were pushed back and became confluent. They eventually fused across the midline to form a sharp border to the basisphenoid fossa. As the basipterygoid processes were pushed together towards the midline, the entry foramina for the cerebral branches of the internal carotid artery followed them onto the ventral side of the braincase, into the space anterior to the basioccipital-basisphenoid fossa. The internal carotid artery extends down the dorsomedial wall of the tympanic fossa in lizards at least (Oelrich 1956) or along the ventrolateral crests (Evans 1986; Gower 2002). Its cerebral branch would have passed from the lateral to the ventral face of the parabasisphenoid to reach the entry foramen. The ventral position of the foramina required that the artery wound ventrally around the posterior surface of the basipterygoid process. This probably accounts for the S-shaped path of the carotid artery (Gower and Weber 1998) associated with verticalization of the basisphenoid. The return of the foramina to the lateral side of the parabasisphenoid, which occurred in crown-group archosaurs, probably eliminated this convolution to make the path of the artery more direct.

Character 9. — Prootic midline contact on the endocranial floor: absent = 0; present = 1. *Osmolskina* is scored 1.

The lack of a midline contact of the prootics on the endocranial floor might be correlated with an exposure of the basisphenoid in the midline (character 10), but according to Gower and Sennikov (1996), this is not always the case. Apart from *Parasuchus* (Chatterjee 1978), *Osmolskina* probably has the prootic contact (limited to the crista sellaris region) and, at the same time, the midline exposure of the basisphenoid in the braincase floor.

Character 10. — Basisphenoid midline exposure on endocranial cavity floor: present = 0; absent = 1 *Osmolskina* is scored 0.

Character 11. — Semilunar depression: present = 0; absent = 1 *Osmolskina* is scored 0.

Further character states preserved in *Osmolskina* (Appendix 2) and scored “0” on the basis of Gower and Sennikov (1996) are as follows:

Character 16. — Number of hypoglossal foramina: two = 0; one = 1. *Osmolskina* is scored 0. The character may be uninformative because it shows some variability *e.g.*, *Hyperodapedon* can have two or three foramina (Benton 1983) and the number supposedly changes with age in *Sphenodon* (SEE). If Gower and Sennikov’s (1996) scoring is correct, both *Euparkeria* and *Osmolskina* and some archosaurs (see Appendix 2) show the primitive state, whereas the condition in erythrosuchids and *Fugusuchus* which have only a single foramen is derived.

Character 17. — Ventral contact of the exoccipitals in the sagittal plane: absence = 0; presence = 1. *Osmolskina* is scored 1. This character appears to be quantitative and gradual rather than qualitative. In both *Osmolskina* (Figs 17, 25) and *Euparkeria* (Ewer 1965, p. 391; Gower and Weber 1998, fig. 4) the basioccipital is almost excluded from the border of the foramen magnum. The state in these taxa is far from primitive and close to the derived condition, and so is scored as such (Appendices 1 and 2).

Character 25. — Fusion of opisthotic with exoccipital: absent = 0; present = 1. *Osmolskina* is scored 1. The elements are suturally distinct in *Prolacerta* (Evans 1986), but the condition is variable in rhynchosaurs Benton 1983, p. 632). In *Osmolskina* the exoccipital is consistently tightly fused with the opisthotic, even in smaller (probably younger) individuals, in contrast to the condition in a prolacertiform-grade reptile (Borsuk-Białynicka and Evans 2009) represented in the Czatkowice 1 assemblage.

Character 26. — Medial wall of the vestibule (character 7 of Gower 2002): unossified = 0; ossified = 1. *Osmolskina* is scored 0. This character discriminates, more or less, between non-crown group archosauriforms and archosaurs, although some archosaurs (phytosaurs) display the primitive state, and the character should be scored on adult individuals as it is age dependent.

Character 30. — Supraoccipital contribution to the foramen magnum: no contribution = 0; supraoccipital contributes to foramen magnum = 1. This character may be subject to ontogenetic variation, as is character 17, because fusion involves enlargement of bones. In *Osmolskina* the exoccipital facets are variably spaced on the supraoccipital margin (Fig. 18). In *Euparkeria capensis* the exoccipital facets are separated as shown by Ewer 1965, fig. 2b). *Prolacerta* is polymorphic in this respect (Evans 1986).

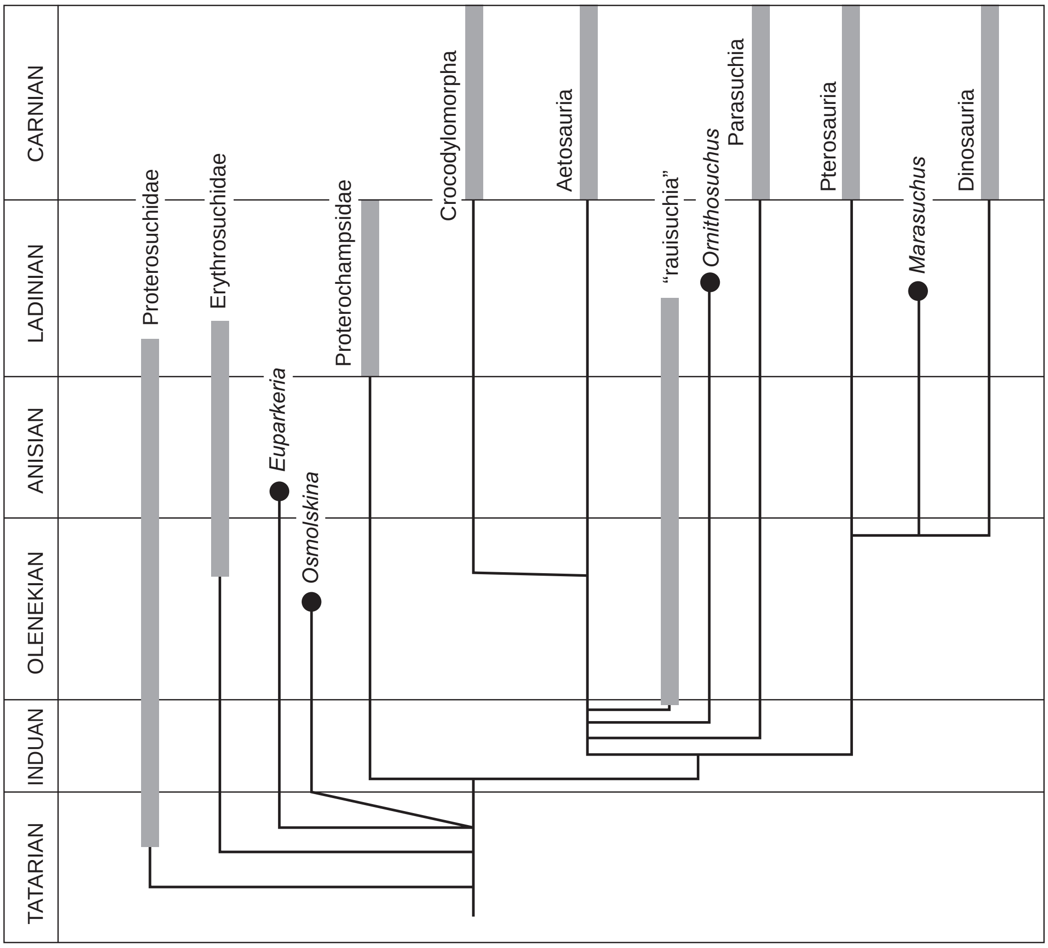

Fig. 31. Pattern of early archosauriform evolution based on Gower and Wilkinson's (1996, fig. 4) cladogram plotted against biochronology mainly after Gower and Sennikov (2000). Position of Aetosauria modified according to Gower and Walker (2002).

The following non-braincase characters might be of some phylogenetic value. They are added to those of Gower and Sennikov (1996), and are numbered consecutively here.

Character 33. — Snout position: snout not downturned = 0; snout downturned due to internal geometry of the premaxilla = 1; snout downturned due to angulation of premaxilla-maxilla contact = 2. *Osmolskina* is scored 1. The downturned appearance of the snout was originally considered as a proterosuchid character (Charig and Sues 1976), but occurs in some other archosauriforms and is not always homologous. Two factors may contribute to this character: the internal geometry of the premaxilla, with the ventrolateral border descending anteroventrally so that its anterior end lies below the horizontal palatal process, as in *Proterosuchus* Cruickshank (1972) and *Sarmatosuchus* (Gower and Sennikov 1997, p. 62), and the oblique orientation of the premaxilla resulting from its joint with the maxilla. The downturned snout we reconstruct for *Osmolskina* results from the second factor (Fig. 3B, C_2), and this is also the case for some other stem-group archosauriforms and early archosaurs, as exemplified by *Erythrosuchus* (Gower 2003) and *Riojasuchus* (Parrish 1993, fig. 4A) respectively. It may suggest a degree of kinetism at this joint. In *Osmolskina* a small additional antorbital foramen may have opened within the premaxilla-maxilla suture (Figs 1B, 3B) as a by-product of this loose contact.

Character 34. — Ventral pterygoid crest on the posterior border of the palatal wing of the pterygoid: absent = 0, present = 1. *Osmolskina* is scored 1 (Fig. 15A). In *Euparkeria* (Ewer 1965, fig. 1b), *Sarmatosuchus* (Gower and Sennikov 1997, fig. 4A), *Gracilisuchus* (Romer 1972b, fig. 3), and seemingly *Proterosuchus* (Cruickshank 1972, fig. 3), the palatal wings of the pterygoids are also bordered posteriorly by a distinct, anteriorly concave, crest but this is not the case in *Prolacerta* (Gow 1975, fig. 17, see also Borsuk-Białynicka and Evans 2009). The crest is a potential synapomorphy of the Archosauriformes, but requires further comparative studies.

Summing up the results of the above discussion, *Osmolskina* is identical to *Euparkeria* in all 12 characters that can be scored (Appendix 2). Given this correspondence, a phylogenetic analysis of *Osmolskina* seems redundant at the present time as this genus would take exactly the same position in the archosauriform phylogeny, crownward of proterosuchids and close to the crown group (Fig. 31), as does *Euparkeria* (Gower and Wilkinson 1996). Several of their character states (characters 3, 5, 6, 10, 16) suggest a position stem-ward of erythrosuchids, from which *Osmolskina* and *Euparkeria* also differ in overall skeleton and vertebrae proportions. This position is firmly supported by three of 13 braincase character states (1, 7. 7a). They are mostly those of the braincase verticality complex discussed above. The unique combination of primitive and derived character states of the whole skeleton (Appendices 1 and 2; Borsuk-Białynicka and Sennikov 2009) shared by *Osmolskina* and *Euparkeria*, as well as a general similarity of the body form, leads us, with reservation, to accord them family status within Euparkeriidae Huene, 1920 although as yet no unique shared derived character states have been identified to support the monophyly of Euparkeriidae Huene 1920 (Charig and Sues 1976).

Osmolskina (Borsuk-Białynicka and Evans 2003) is differentiated from *Euparkeria* at a generic level based mainly on skull proportions. *Osmolskina* has the preorbital part of the skull less elongated than *Euparkeria*, a difference that is best expressed in maxilla proportion, the maximum length to depth being 5:1 and 7:1 respectively, but the maxillary tooth count is estimated as 13 in both genera. According to our reconstruction, the premaxilla is downturned in *Osmolskina*, and it is probably separated from the maxilla by an additional antorbital foramen. Its body is shallower (maximum length to depth 10:3) than in *Euparkeria* (10:4), and its posterolateral process slopes at an angle of about 50° in contrast to the near vertical orientation in *Euparkeria*. Orbit shape also differs. In *Osmolskina*, the ventral border of the orbit is smoothly concave due to the widely divergent processes of the jugal, whereas the same region is more angular in *Euparkeria*. Finally, unlike the mandible of *Euparkeria*, that of *Osmolskina* does not increase in depth posteriorly. We acknowledge that many of these differences could be artifacts of reconstruction. However, in the absence of articulated material, these reconstructions represent the best approximation of the real state.

CONCLUSIONS

Osmolskina czatkowicensis is a non-archosaur archosauriform situated more crownward than the proterosuchids in the phylogeny of Archosauriformes (Fig. 31), in exactly the same position on the cladogram as is usually accorded to *Euparkeria capensis* (Gower and Wilkinson 1996).

Osmolskina and *Euparkeria* share a unique combination of primitive and derived archosauriform character states of the braincase (see above) and postcranium (Borsuk-Białynicka and Sennikov 2009). On this basis, they are tentatively placed as sister taxa within a monophyletic Euparkeriidae Huene, 1920, although no synapomorphy has been found to support the clade.

The differences between *Osmolskina* and *Euparkeria* are here regarded as generic. Among them, only one, the localization of the coracoid foramen (Borsuk-Białynicka and Sennikov 2009), is uncontentious. Some differences in skull morphology, and notably skull proportions, are dependent on the accuracy of the reconstructions. Nonetheless, given the geographical (Europe *versus* South Africa) and stratigraphical (earliest Late Olenekian *versus* Anisian) differences, although these do not represent valid criteria in themselves, it seems preferable to retain generic distinction pending the recovery of further material from other localities.

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APPENDIX 1

Character list based mainly on Gower and Sennikov (1996). Character numbering according to the same authors.

1. Cerebral branches of the internal carotid entrances: lateral to the ventrolateral crests = 0; directly ventral, anterior to the fused ventrolateral crest = 1; lateral to basipterygoid stalks = 2
3. Abducens canal: between the basisphenoid and prootic = 0; within prootic only = 1
5. Ventral ramus of the opisthotic: prominent = 0; recessed = 1
6. Ridge on lateral surface of anterior inferior prootic process below the trigeminal notch: present = 0; absent = 1
7. Basisphenoid: oriented horizontally = 0; or more vertically = 1

7a. Basipterygoid processes: directed laterally = 0; ventrolaterally = 1

9. Prootic midline contact on endocranial cavity floor: absent = 0; present = 1
10. Basisphenoid midline exposure on endocranial cavity floor: present = 0; absent = 1
11. Semilunar depression: present = 0; absent = 1
16. Number of hypoglossal foramina: two = 0; one = 1
17. Midline contact of the exoccipitals in braincase floor: absent = 0; present = 1
25. Fusion of opisthotic-exoccipital: absent = 0; present = 1
26. Medial wall of vestibulum: open = 0; ossified = 1

APPENDIX 2

Character state matrix for selected Archosauromorpha with *Osmolskina* included.

Character no	1	1	3	5	6	7	7a	9	10	11	16	17	25	26
Prolacerta	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hyperodapedon	1	0	0	0	0	0	0	0	0	1	0	1	1	0
Proterosuchus	0	0	0	0	0	0	0	?	?	0	?	?	?	0
Erythrosuchus	1	1	1	1	1	1	1	1	1	0	1	1	1	0
Euparkeria	1	1	0	0	0	1	1	1	?	0	0	1	1	0
Osmolskina	1	1	0	0	0	1	1	1	0	0	0	1	1	0
Dorosuchus	1	?	?	0	?	1	1	?	?	?	?	?	0	?
Turfanosuchus	1	?	?	0	?	1	1	?	?	1	0	?	1	?
Chanaresuchus	2	2	?	?	?	?	0	0	?	?	?	?	?	?
Parasuchia	2	2	0	1	1	?	1	1	0	1	0	1	?	0
Batrachotomus	2	2	?	0/1	0	1	1	1	1	1	1	1	1	1
Stagonolepis	2	2	?	0	1	1	?	?	?	1	0	?	?	1

Batrachotomus according to Gower (2002)
Dorosuchus according to Sennikov (1989, 1995)
Euparkeria according to Gower and Weber (1998)
Hyperodapedon after Benton (1983)
Proterochampsa according to Romer (1971)
Prolacerta according to Gow (1975, fig. 35)
Stagonolepis according to Gower and Walker (2002)
Turfanosuchus according to Wu and Russell (2001, p. 43, figs 3, 5)

ARCHOSAURIFORM POSTCRANIAL REMAINS FROM THE EARLY TRIASSIC KARST DEPOSITS OF SOUTHERN POLAND

MAGDALENA BORSUK-BIAŁYNICKA and ANDRIEJ G. SENNIKOV

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Postcranial bones of archosauriform reptiles from the Early Triassic karst deposits of southern Poland (Czatkowice 1 locality, Kraków Upland) have been assigned to two genera and species *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003 and *Collilongus rarus* gen. et sp. n. *Osmolskina* dominates the Czatkowice 1 fauna. Its postcranium is shown to be close to that of the Anisian South African *Euparkeria capensis*, the postcranial characters making an even stronger case than those of the skull. This similarity confirms the unity of the tetrapod fauna across Early Triassic Pangea.The exact relationships of *Collilongus*, based only on cervical vertebrae, remains unknown. The list of archosauriform synapomorphies, encompassing only skull characters according to current knowledge, is supplemented by one postcranial character: the sacral rib facet at least partly overlapping the medial wall of the acetabulum.

Key words: basal Archosauriformes, early Triassic, microvertebrates, Poland.

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INTRODUCTION

The main focus of this paper is a detailed description of the postcranial anatomy of a small euparkeriid reptile, *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, from the Early Triassic karst deposits of the Czatkowice 1 locality near Kraków, southern Poland (Paszkowski and Wieczorek 1982). Its skull bones have been described elsewhere (Borsuk-Białynicka and Evans 2009a).

Although reconstructed from disarticulated bones, this reptile significantly supplements the early fossil record of Archosauriformes. The term Archosauriformes (*sensu* Gauthier 1986 = Archosauria *sensu* Romer 1956), including Archosauria *sensu stricto* and some basal groups, is here preferred over the Archosauria *sensu lato* of many authors (*e.g.*, Juul 1994 and Gower and Wilkinson 1996). This terminological choice better corresponds, in our opinion, to the distinguished position of crown group archosaurs within the more inclusive clade.

Osmolskina czatkowicensis belongs to a diverse small vertebrate assemblage including three other diapsids, as well as procolophonids, amphibians (Borsuk-Białynicka *et al.* 1999) (among them a pre-frog salientian *Czatkobatrachus polonicus*; Evans and Borsuk-Białynicka 1998, 2009), and fish. This assemblage displays extensive similarities at a suprageneric level with Gondwanan Olenekian to Anisian faunas, a pattern that probably dates back to the Permian uniformity of tetrapod faunas across Pangea. However, the absence of therapsids from the Czatkowice 1 assemblage is noticeable. According to current knowledge (Shishkin and Ochev 1993; Lozovsky 1993), the north-south continuity of the Pangean tetrapod fauna was disturbed, then interrupted, at the Permo-Triassic boundary, by aridisation of the climate. This led to the development of a broad arid belt that extended across the majority of North and South America, central and northern Africa, and eastern Europe including the East European Platform and Cis-Urals, as well as Poland. A lack of therapsids is distinctive for the Olenekian faunas of this belt. Archosauriform remains are variously distributed over the belt. The North American Torrey and Wupatki Member of the Moenkopi Formation, correlated with the Late Olenekian (Morales 1993), have yielded no archosauriform body fossils at all but rich archosauriform ichno-fossils are present. Archosauriforms only appear in the Anisian Holbrook member of the Moenkopi Formation (the rauisuchid *Arizonasaurus* Nesbitt, 2005). Further to the East, the European Bundsandstein, the Middle and Upper part of which are roughly Olenekian in age, has yielded the long-spined *Ctenosauriscus* (Krebs 1969), dated as early Late Olenekian (Ebel *et al.* 1998), but probably related to *Arizonasaurus* (Nesbitt, 2003, 2005) and rather poorly known. In contrast, the Cis-Uralian Permian to Triassic tetrapod succession (Shishkin and Ochev 1993) has yielded a rich archosauriform assemblage, with a material assigned to proterosuchids, erythrosuchids, euparkeriids and rauisuchids (Sennikov 1995 and references therein). The absence of common archosaurian elements across Olenekian Euramerica, in contrast to the uniformity of its temnospondyl fauna, suggests (Shishkin and Ochev 1993) that terrestrial life was confined to isolated realms separated by aquatic barriers. The specific environment of the Czatkowice 1 karst region in the early Late Olenekian (Paszkowski 2009; Shishkin and Sulej 2009) is consistent with a certain degree of faunal endemism.

Osmolskina is the dominant archosauriform of the Czatkowice 1 assemblage. It is the second euparkeriid genus reported from the Laurasian part of Pangea, *Dorosuchus* Sennikov, 1989 from the Anisian of Russia, being the first one. Proterosuchids and erythrosuchids were apparently absent from Czatkowice 1, and rauisuchids have yet to be recognized with any certainity. Rauisuchids are a problematic group currently considered crurotarsians (Gower 2000; Gower and Nesbitt 2006), hence Archosauria *sensu stricto* (under the definition accepted herein), and are mainly middle through late Triassic in age. Their presence in the Olenekian, strongly suggested by Russian authors (Sennikov 1995 and references therein; Gower and Sennikov 2000), implies a still earlier split of the Archosauria. This is why the question of their presence in the earliest Late Olenekian (Shishkin and Sulej 2009) Czatkowice 1 assemblage is of great interest. While the archosauriform bones are readily distinguishable from the non-archosauriform ones, uncertainty as to the range of variability within *O. czatkowicensis* raises a problem of conspecifity of the Czatkowice 1 archosauriform material as a whole. Whether or not any archosauriforms other than euparkeriids (= "*Euparkeria* grade archosauriforms") occurred in the Early Triassic Czatkowice 1 assemblage is a question we address in the present paper.

All Supplements are on-line under the address http://www.palaeontologia.pan.pl/SOM/PP65-Borsuk-Białynicka and Sennikov.pdf

Institutional abbreviations. — GPIT, Institut und Museum für Geologie und Paläontologie der Universität Tübingen, Germany; PIMUZ, Paläontologisches Institut und Museum der Universität, Zürich, Switzerland; PIN RAS, Paleontological Institute Russian Academy of Sciences Moscow, Russia; SAM, South African Museum, Cape Town, Republic of South Africa; SMNS, Staatliche Museum für Naturkunde Stuttgart, Germany; ZPAL, Institute of Paleobiology Polish Academy of Sciences, Warsaw, Poland.

Acknowledgments. — Mariusz Paszkowski and Józef Wieczorek (Jagiellonian University) discovered the Czatkowice 1 breccia, and kindly offered it for study to Teresa Maryańska and the late Halszka Osmólska who transferred it to the senior author (MBB). MBB is indebted to following persons and institutions that allowed the study of archosauriform material in their collections: Rupert Wild at the Staatliche Museum für Naturkunde Stuttgart, Germany; Michael Maish at the Institut und Museum für Geologie und Paläontologie der Universität Tübingen, Germany, and Helmut Mayr at the Bayrische Staatssammlung für Paläontologie und Historische Geologie, München, Germany. Many thanks are due to Susan E. Evans for her continued help and critical comments during these studies, and to Caroline Northwood (La Trobe University, Victoria, Australia) who was the first to make some order in the postcranial archosaurian remains from Czatkowice 1. Thanks are also due to the following staff members of the Institute of Paleobiology, Polish Academy of Sciences in Warsaw: Ewa Hara for preparation of the material, Marian Dziewiński for photographs, Cyprian Kulicki for SEM micrographs, and Alexandra Hołda-Michalska for preparing computer illustrations. The research of the senior author was partly supported by the State Committee of Scientific Research, KBN grant No 6 PO4D 072 19. The junior author was supported by the Russian Foundation for Basic Research, project N.N. 05-05-65146, 08-05-00526, 07-05-00069, and by the Program 15 of the Presidium of the Russian Academy of Sciences "The Origin of the Biosphere and Evolution of the Geo-Biosystems", Subprogram II.

GEOLOGICAL SETTING

Czatkowice 1 was the largest of the karst forms developed in the Carboniferous Limestone quarry and including bone breccia. For the details of geological setting see Paszkowski and Wieczorek (1982), Paszkowski (2009), and Cook and Trueman (2009). The vertebrate assemblage extracted from the Czatkowice 1 breccia, includes both terrestrial and amphibious animals and some fish (Borsuk-Białynicka *et al.* 1999). Based on the *Parotosuchus* fauna (Shishkin and Sulej 2009), the most precise age dating for Czatkowice 1 breccia is an earliest Late Olenekian (corresponding to the lowermost Yarenskian stage). Probably, the material of Czatkowice 1 breccia was deposited in a freshwater pool, developed within a collapsed paleodoline (Paszkowski 2009) within an oasis, in an otherwise arid Central European Scythian environment (Ochev 1993; Shishkin and Ochev 1993). The Czatkowice 1 assemblage is distinguished by the small size of the component taxa, and this is consistent with the endemic character of a small oasis. Alternatively it could merely be a depositional artefact.

MATERIAL AND METHODS

The material comes from a single fissure exposure, referred to as Czatkowice 1 (Paszkowski and Wieczorek 1982; Paszkowski 2009). The bone breccia was prepared chemically in acetic acid. The material consists of about hundred more or less complete postcranial bones, and many hundreds of fragments. The bones are disarticulated, and mostly damaged or broken into pieces (some of which were glued back together). The relatively low level of abrasion suggests rather gentle transport over, at most, a short distance (Cook and Trueman 2009). Most of the material is stored in the Institute of Paleobiology, Polish Academy of Sciences, with some specimens in the Museum of the Earth, Polish Academy of Sciences.

General morphology, size and frequency, corresponding to those of skull bones (Borsuk-Białynicka and Evans 2009a) form the basis for identification of the postcranial bones of *Osmolskina* amongst the main bulk of the material. Three problems that appear are: a possible size overlap with the second, generally smaller, diapsid from the same material (Borsuk-Białynicka and Evans 2009b), questionable conspecifity of the archosauriform bones from Czatkowice 1, and poor discrimination between ontogenetic and taxonomic variability. The small number of adequately preserved specimens made any statistical test impossible to apply. Only a few measurements approximate variability ranges (Supplements 1 and 2).

Only mature vertebrae were eventually chosen for measurements, their maturity being determined on the basis of fusion of neurocentral sutures (Brochu 1996). The age criteria are less precise in the case of long bones. Their size variability is here considered in terms of continuous ontogenetic growth, but the poor preservation of the articular ends suggests a taphonomic bias towards the accumulation of immature specimens at least in this bone category.

The mesopodial bones present a very special problem. Among the numerous small bones of the Czatkowice 1 material, the proximal elements of the tarsus (astragalus and calcaneum) are specific enough to be recognized, and even assigned to particular taxa, but distal tarsals and carpals are extremely difficult to discriminate from one another and to assign with any confidence. The combination of different kinds of variability, such as hand and foot length disparity, and inter-podial and individual variation, makes the reconstruction of the extremities speculative. The known *Euparkeria* foot structure has been used as a reference. The phalanges are the best preserved and most abundant postcranial elements. As such, they represent the best material for statistical studies, but these are relegated to future comparative studies in the frame of the whole Czatkowice 1 assemblage.

The character list summarized by Juul (1994) and modified according to information available from the *Osmolskina* remains, incomplete as it is, has been used in the present paper (Appendix 4). As *Osmolskina* does not differ from *Euparkeria* in those characters for which it can be scored, its inclusion into the matrix does not change it in any way. Analysis of this matrix by cladistic computer programs is thus redundant. Simple statistical methods have been used for taxonomical problems.

The terminology used for the orientation of the long bones follows Gower (2003) in applying the terms: ventral for the flexor side, and dorsal for the extensor side.The terms lateral and medial will be used for the side views of the bones, corresponding to semierect position of appendages. Anterior and posterior are sometimes used to give more precision in the description of the details.

Some terms that refer to vertebral structure, such as posterior centrodiapophyseal crest and posterior centroparapophyseal crest, are from Wilson (1999).

The term “grade” used herein refers to the taxa that share the same combination of plesiomorphic and apomorphic characters but no synapomorphy unique for them.

SYSTEMATIC BACKGROUND

The Archosauria *sensu* Gauthier 1986 (= Avesuchia of Benton 1999) are restricted to the most recent common ancestor of Aves and Crocodilia and all its fossil and extant descendants. Several taxa once considered basal archosaurs belong to a more inclusive taxon, Archosauriformes (Gauthier 1986). One of the character states excluding taxa from the crown group is the lack of a posteriorly deflected calcaneum synapomorphic of Archosauria (Juul 1994, p. 38). Instead, they retain a plesiomorphic, virtually transverse orientation of the tarsus. Gower and Wilkinson (1996) found general agreement in the sequence of basal archosauriform groups recovered by consecutive cladistic analyses (Sereno and Arcucci 1990; Sereno 1991; Parrish 1993 and Juul 1994). According to all these authors, the Proterosuchidae is the outermost archosauriform taxon, the Erythrosuchidae are to be located one step more crownward, followed by the Early Anisian South African *Euparkeria* and the Middle to Late Triassic South American Proterochampsidae (Gower and Wilkinson 1996).

The genus *Euparkeria* was erected and first described by Broom (1913a, b), later by Haughton (1922), and then by Ewer (1965). Huene (1920) first used the family name Euparkeriidae to include *Euparkeria* and ?*Browniella* (*contra* to Huene’s *Broomiella*), a questionable genus subsequently synonymized with *Euparkeria* (Haughton 1922, Ewer 1965). Huene gave no family diagnosis and did not further comment on the new family, but it has been used to include several subsequent genera such as *Dorosuchus* (Sennikov 1989) from the Anisian of Russia, as well as *Turfanosuchus* (Young 1973), *Wangisuchus* (Young 1964), and *Halazhaisuchus* Wu (982), all from the Anisian of China. Two of these, *Turfanosuchus* and *Wangisuchus* have been shown to have a crocodilian-like ankle joint (Gower and Sennikov 2000), which excludes them from the Euparkeriidae. *Dorosuchus* (Sennikov 1995) is known from a braincase and isolated postcranial bones.

Among proterosuchid taxa recorded in the literature, only four genera are adequately preserved and described, with their attribution supported by phylogenetic analysis (Gower and Sennikov 1997). They are as follows: *Archosaurus*, the only Permian proterosuchid; the Early Olenekian South African *Proterosuchus* (Broili and Schroeder 1934; Cruickshank 1972); the Early Triassic *Fugusuchus* from China (Cheng 1980; Gower and Sennikov 1997); and the Anisian *Sarmatosuchus* from Russia (Sennikov 1994; Gower and Sennikov 1997). *Chasmatosuchus* Huene, 1940 and *Gamosaurus* Otschev, 1979, possible proterosuchian taxa from the Olenekian of Russia, were based only on vertebral material (Supplement 3), and their attribution remains problematic. *Vonhuenia* Sennikov, 1992, with its low braincase and an iliac blade that does not extend anteriad, might be a proterosuchid.

Erythrosuchids are adequately known from rich Russian, South African, and Chinese materials (*Garjainia*, *Erythrosuchus*, and *Shansisuchus* respectively). The affiliation of two additional Russian taxa, *Chalishevia* Otschev, 1980 and *Uralosaurus* Sennikov 1995, based on fragmentary material, is less certain.

The rauisuchids are another group represented in the Triassic of Russia, but mostly by vertebrae. Rauisuchid affinity has been demonstrated in three cases, those of *Vytshegdosuchus zheshartensis* Sennikov, 1988, *Tsylmosaurus jakovlevi* Sennikov, 1990, and *Scythosuchus* (Sennikov 1999), but attribution of other genera (*Dongusuchus*, *Energosuchus*, *Jaikosuchus*, *Jushatyria*, see Supplement 3) remains tentative (Gower and Sennikov 2000). Four of these genera, *Tsylmosuchus*, *Vytshegdosuchus*, *Jaikosuchus* (Sennikov 1995), and *Scythosuchus* (Sennikov 1999), come from the Olenekian, and the occurrence of *Tsylmosuchus* in the Early Olenekian demonstrates an unexpectedly early appearence of the archosauriform crown-group Archosauria.

SYSTEMATIC PALEONTOLOGY

Clade Archosauromorpha Huene, 1946

Clade Archosauriformes Gauthier, 1986

Family **Euparkeriidae** Huene, 1920

Provisional diagnosis. — Basal archosauriforms differing from crown-group Archosauria in the lateral orientation of the calcaneal tuber and the unossified medial wall of the otic capsule. They share a vertical orientation of the basisphenoid and the absence of an astragalocalcaneal canal with all archosauriforms except proterosuchids. They differ from erythrosuchids in the lighter construction of the skeleton, relatively smaller skull, and generally more elongate cervical vertebrae (centrum length/depth usually around 1.4–1.6 instead of 0.4–1.0 in erythrosuchids).

Remarks. — Among the numerous characters *Osmolskina* shares with *Euparkeria*, none can be shown to be synapomorphic at family level. However, a combination of primitive and derived archosauriform character states places the two genera in exactly the same position on the cladogram of Archosauriformes. This, in combination with a general similarity of body form, leads us, with reservation, to accord them family status within Euparkeriidae Huene, 1920. The differences between *Osmolskina* and *Euparkeria* are here regarded as generic. Among them, only one, the localization of the coracoid foramen, is uncontentious; the others are dependent on the accuracy of the reconstructions.

Generic composition. — *Euparkeria* Broom, 1913, *Osmolskina* Borsuk-Białynicka *et* Evans, 2003, most probably *Dorosuchus* Sennikov, 1989.

Occurrence. — Olenekian to Anisian of Pangea (localities in Europe and South Africa).

Genus ***Osmolskina*** Borsuk-Białynicka *et* Evans, 2003

Diagnosis. — As for the species.

Osmolskina czatkowicensis Borsuk-Białynicka *et* Evans, 2003

Holotype: The fragmentary maxilla ZPAL RV/77; Borsuk-Białynicka and Evans 2003, fig. 2A.

Type horizon: Early Late Olenekian.

Type locality: Czatkowice 1, southern Poland.

Material. — Numerous disarticulated postcranial bones (see Borsuk-Białynicka and Evans 2009a, for skull details). Catalogued postcranial specimens are: 63 measured vertebrae (Supplement 1); twelve scapulae: ZPAL RV/881–885, 902, 1161, 1261, 1282–1286; eight coracoids: ZPAL RV/890–891, 903, 1166–1169, 1311; eleven humeri ZPAL RV/1164, 1262–1263, 1266–1272, 1277; ten ilia: ZPAL RV/630, 678, 679, 911–913, 918, 919, 924, 925; four ischia: ZPAL RV/887–889, 892; five pubes: 905–907, 909, 910; fifteen femora: ZPAL RV/938–940, 1252, 1254, 1264, 1287–1302, 1304; 18 tibiae: ZPAL RV/1165, 1171, 1176, 1177, 1221, 1222, 1257–1260, 1265, 1303, 1306, 1317–1321, fragmentary radius ZPAL RV/1232 and ulnae ZPAL RV/1230 and 1279; fragmentary fibulae ZPAL RV/1182, 1225, 1247; numerous tarsal bones, of which the astragalus: ZPAL RV/811, a calcaneum ZPAL RV/810, and a fourth distal tarsal ZPAL RV/812 are catalogued and figured.

Measurements. — Appendix 1, Supplement 1.

Occurrences. — Type locality only.

Emended diagnosis. — An euparkeriid similar to *Euparkeria capensis*, but smaller, having a modal skull length of about 60 mm, modal femur and tibia length about 40 mm and 30 mm, respectively. *Osmolskina czatkowicensis* differs from *Euparkeria* in having a slightly overhanging premaxilla (but less so than in proterosuchids) that was weakly attached to the maxilla (with no peg and socket articulation developed), and was probably separated from it by a slit-like additional antorbital space; in having a subquadrangular nasal process of the maxilla, and in having a barely recessed antorbital fenestra. In *O. czatkowicensis* the preorbital part of the skull is less elongated than in *Euparkeria* which is best expressed in maxilla proportion, the maximum maxilla length to depth being 5:1 in *O. czatkowicensis* (7:1 in *E. capensis*). The estimated tooth count is 13 in both species. The premaxillary body is finer in *O. czatkowicensis* (maximum length to depth 10:3) than in *E. capensis* (10:4).The posterolateral process of the premaxilla slopes at an angle of about 50° in *O. czatkowicensis* while being almost vertical in *E. capensis*. In *O. czatkowicensis* the orbit is more rounded while tapering ventrally in *E. capensis.* The mandible of *O. czatkowicensis* does not increase in depth posteriorly unlike that of *Euparkeri*a. *O. czatkowicensis* differs from *Euparkeria* in the shorter humerus, more twisted femur (distal to proximal end angle in *Osmolskina* about 55°, in *Euparkeria* 32°), the extremely anterior position of the coracoid foramen or notch and less compressed teeth. Compared to *Dorosuchus* (femur about 90 mm, tibia about 70 mm in length, femur twist about 40°), *Osmolskina* is smaller and has a more twisted femur.

VERTEBRAL COLUMN

General features. — All regions of the vertebral column of *Osmolskina czatkowicensis* are represented in Czatkowice 1 material. The vertebral centra are holochordal and slightly amphicoelous, with slightly concave but not recessed lateral flanks. Neurocentral sutures are evident only in the smaller vertebrae. The dorsal surface of each centrum bears a deep pit, both longitudinal and transversal sections of the centrum being V-shaped. The vertebrae look rather short and tall, but the centrum length to posterior height ratio usually exceeds that of *Euparkeria capensis* (Appendices 1 and 2). It varies (Supplement 2) from 1.0–1.38 in the axis, increases to about 1.4–1.6 in postaxial cervicals, and decreases to 1.3–1.4 at the transition between the neck and thorax. It increases again to about 1.5–1.7 in dorsals, decreasing to about 1.56 in the first sacral centrum, and then to 1.38 in the second sacral and the short caudals of the tail base. The caudals get increasingly longer and slimmer down the tail. The parapophysis and diapophysis remain separate throughout most of the dorsal series. Intercentra were probably present within the cervical series, and probably absent in the dorsal series.

Atlas/axis complex. — The atlas consists of the intercentrum and paired neural arches (Fig. 1B, G). Isolated intercentra (*e.g.*, ZPAL RV/397 and 1149) are fairly frequent in the material. The largest and most frequent intercentrum type has been tentatively attributed to *Osmolskina* on the basis of size and neural arch fit. It is a transversally elongated, dorsally concave, beam of bone, with dorsally curved ends (Fig. 1B, C). The anterior surface bears a concave facet (Fig. 1B) for the occipital condyle, dorsolaterally flanked by two others facets for the neural arches (Fig. 1G). Much less concave is the posterior facet for the axis intercentrum which itself is unknown, as is the proatlas. The paired atlantal neural arches match the intercentrum (ventrally) and the paired, circular facets of the axis (posterodorsally) (Fig. 1G).

The axis (Figs 1A, 2A) is represented by seven specimens, all rather small. The centrum is short (Supplement 1), high, and triangular in transverse section owing to a prominent ventral crest with excavated flanks and a blunt edge. With the ventral crest aligned horizontally, and both the anterior and posterior faces of the centrum ori-

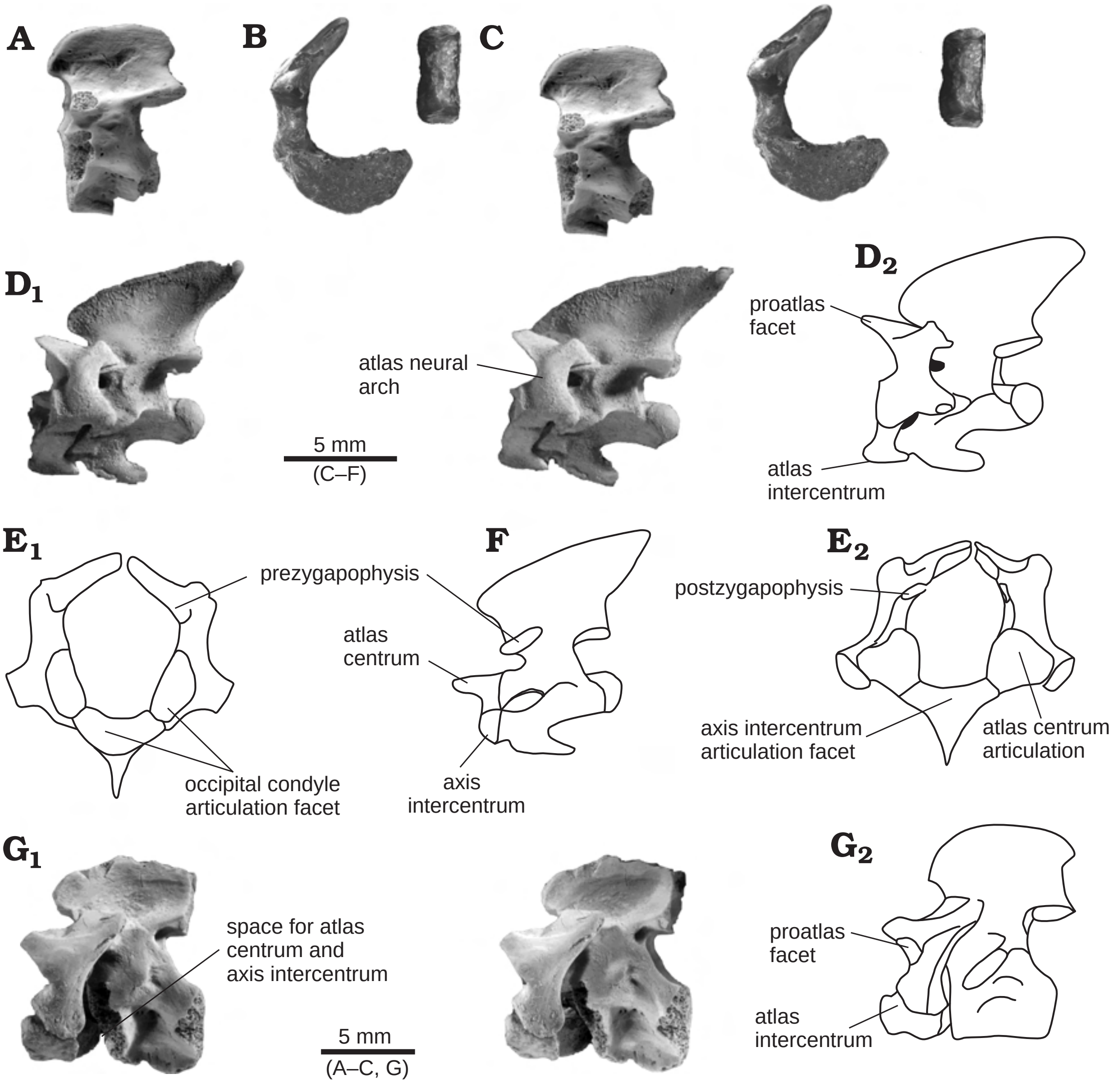

Fig. 1. **A**–**C**, **G**. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A**. Axis ZPAL RV/570, in left lateral view. **B**. Atlas intercentrum with right neural arch ZPAL RV/1149, in cranial view. **C**. Atlas intercentrum ZPAL RV/397, in ventral view. **G**. Axis ZPAL RV/672 combined with atlas neural arch and atlas intercentrum, in left lateral view. **D**–**F**. *Ctenosaura* sp. (Squamata), ZPAL RI/8, Recent. **D**. Atlas and axis in left lateral view. **E**. Atlas intercentrum and neural arches in cranial (E_1) and caudal (E_2) views. **F**. Axis with atlas centrum and axis intercentrum in left lateral view. A–D_1, G_1, SEM stereo-pairs.

ented vertically, the dorsal surface of the centrum slopes posteroventrally (Fig. 1A). The neural canal is slightly flattened bilaterally. The dorsal margin of the neural spine is longer than the neural arch, and it overhangs the postzygapophyses which themselves protrude posterior to the centrum. The dorsal margin of the spine curves downward so that its anterior and posterior apices are slightly hooked. The spine extends into two posteriorly concave crests on the postzygapophyses which delimit a triangular cleft for the interspinal ligaments and muscles. The prezygapophyses bear flat circular facets, one half-way up each neural arch, to receive the neural arches of the atlas. The axial centrum is unfinished anteriorly where it should contact the odontoid process (*i.e.*, atlas centrum). In *Osmolskina*, in contrast to crocodiles, the odontoid process remains free from the axis even when the neurocentral sutures close. Neither the atlas centrum nor the axis intercentrum have yet been identified.

The size and shape of the axial neural spine in *Osmolskina* are similar to those of *Euparkeria* (Ewer 1965, p. 402, fig. 7c), but the neural arch pedicels of *Osmolskina* are deeper (Fig. 3A, B), so that the neural arch as a whole is taller and the anterior zygapophyses are placed relatively more dorsally.

Postaxial presacral vertebrae. — The postaxial cervicals (Fig. 2C–F, H) display a steep posteroventral slope of the dorsal surface of the centrum as does the axis, so that the anterior and posterior faces of the

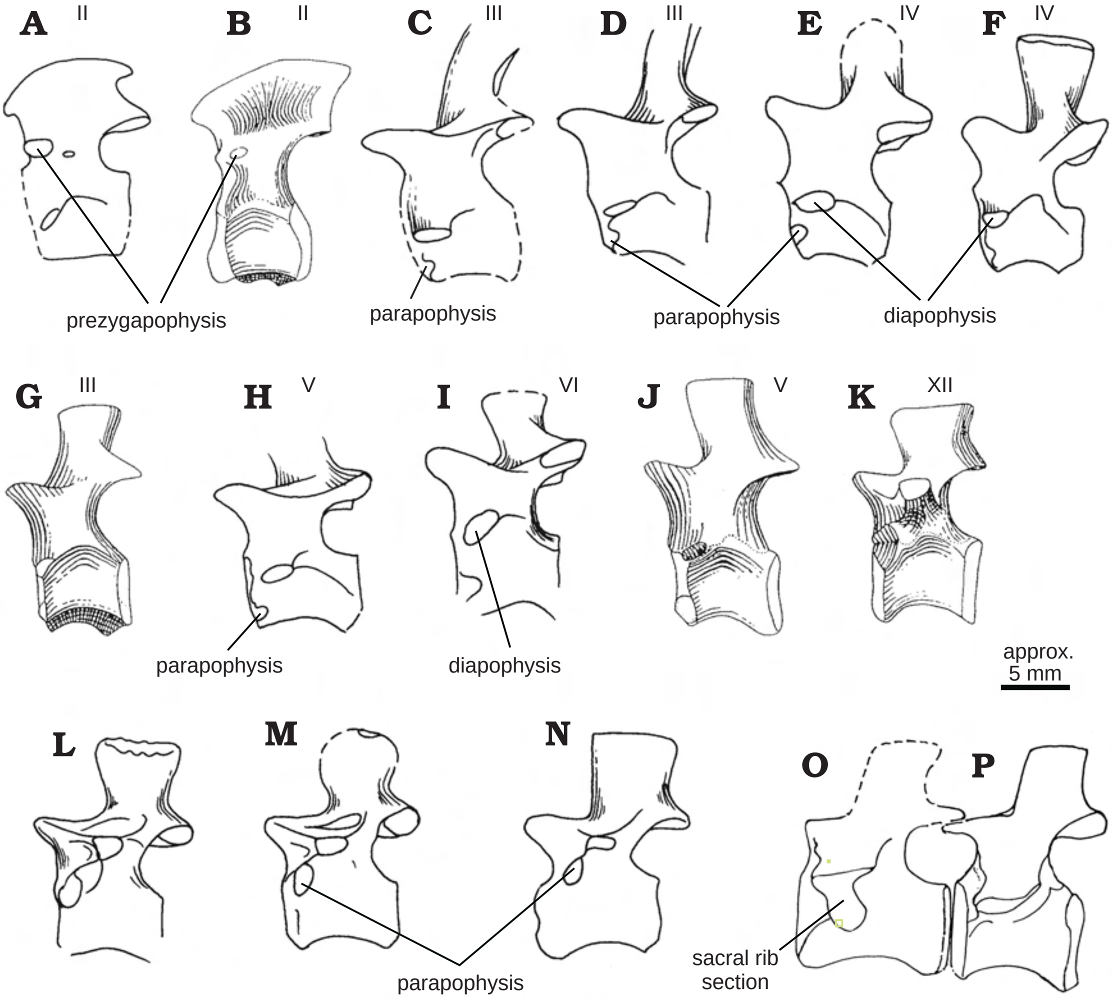

Fig. 2. **A**, **C**–**F**, **H**, **I**, **L**–**P**. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A**. Reconstruction of the axis on the basis of ZPAL RV/570 and 637. **C**, **D**. Two possible third cervicals: ZPAL RV/635 (**C**) and ZPAL RV/636 (**D**). **E**, **F**. Two possible fourth cervicals: ZPAL RV/577 (**E**) and ZPAL RV/571 (**F**). **H**. A possible fifth cervical ZPAL RV/573. **I**. A possible sixth cervical ZPAL RV/607. **L**–**N**. Three roughly consecutive dorsals: ZPAL RV/633 (**L**), ZPAL RV/632 (**M**), and ZPAL RV/575 (**N**). **O**. First sacral ZPAL RV/642. **P**. Second sacral ZPAL RV/640. **B**, **G**, **J**, **K**. *Euparkeria capensis* Broom, 1913 (after Ewer 1965). **B**. Axis. **G**. Third cervical. **J**. Fifth cervical. **K**. Dorsal vertebra. Left lateral view.

centrum are offset in relation to one another. This slope is manifested in the anterior view of centra (Fig. 3A, B, D), so that both the posteroventral profile of the centrum and posteroventral margin of the neural arch are exposed in the cervicals, but not in the dorsals. In dorsal vertebrae the posterodorsal margin of the centrum is visible (Fig. 3F, H). The neck had probably an elevated rest position, but it levelled out within the anterior part of the dorsal series. Cervical centra bear an acute ventral keel (that fades posteriad beginning about the middle of the dorsal series). Because of the keel, the anterior facet of the centrum tends to be subtriangular, but it may be subpentagonal (because of the diapophyses) or even subseptagonal (because of parapophyses), while changing to subcircular in posterior dorsals (Fig. 3F, H), partly as a preservational effect. However, some cervical centra of *Osmolskina* type have the ventral side more flattened than usual, the ventral keel being little more than slight ridge along the blunt surface of the centrum. This is tentatively regarded as an intraspecific variability, but it remains poorly understood.

The ventral profile of the cervical centra is concave along the longitudinal axis and beveled both anteriorly and posteriorly (Figs 2D, F, 5F, G) to enclose triangular intercentral spaces. These may have housed intercentra, but could also result from poor ossification of the margins of the articular surfaces. However, the spaces are absent or very small in the dorsal region.

The neural arches are almost equal in length throughout the column. The neural spines are usually damaged. In cervicals, they are subquadrangular, much taller than long. The spine tops are rarely preserved, but

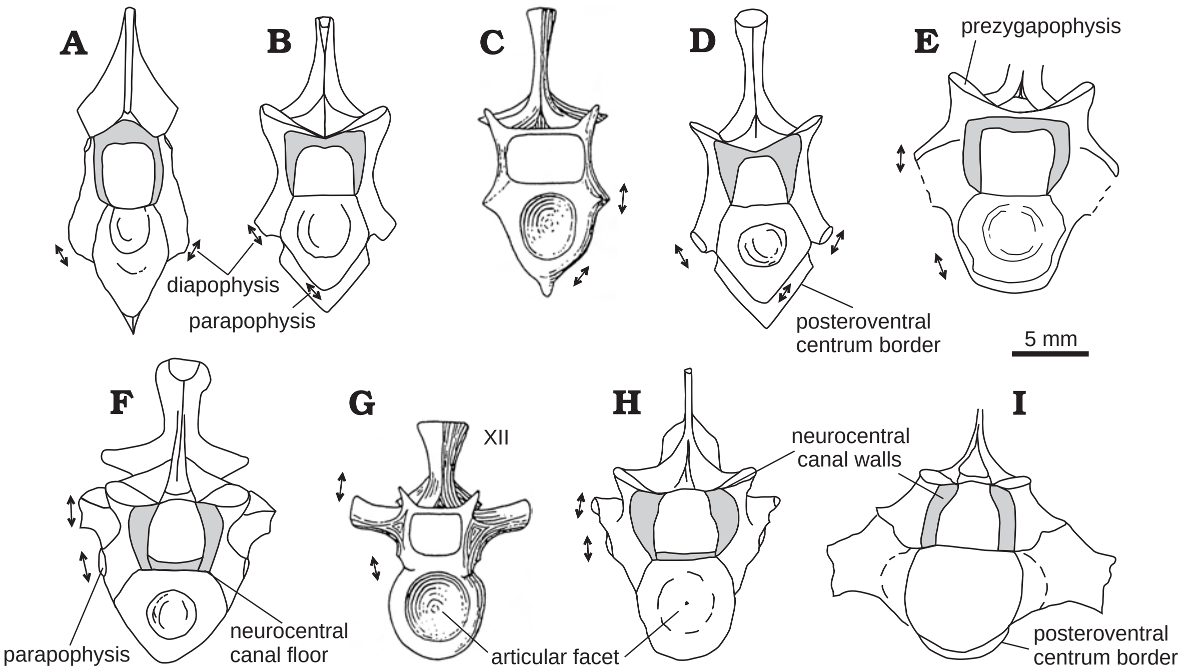

Fig. 3. **A**, **B**, **D**–**F**, **H**, **I**. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A**. Axis ZPALRV/570. **B**. Cervical IV ZPALRV/577. **D**. Cervical IV ZPALRV/571. **E**. Posterior cervical ZPALRV/634. **F**. Anterior dorsal ZPALRV/633. **H**. Posterior dorsal ZPALRV/575. **I**. First sacral based on ZPALRV/639 and 642. **C**, **G**. *Euparkeria capensis* Broom, 1913 (after Ewer 1965). **C**. Cervical III. **G**. Dorsal. Cranial view; arrows denote the positions of diapophyses and parapophyses.

the presence of spine tables is documented in some cervical and anterior dorsal vertebrae (*e.g.*, ZPAL RV/1229; Fig. 4H). In some better preserved specimens the height of the spine is almost half the total height of the vertebra. The position of the neural spines changes along the column. By comparison with *Euparkeria*, the *Osmolskina* cervicals with anteroventrally sloping spines are considered to be anteriormost of the series (Fig. 2C, D). In the middle of the series, the spines became vertical (Figs 2E, F, 5F), and then sloped posteroventrally in the last cervicals (Figs 2H, I, 5G), and possibly in the anterior dorsals. Based on this reasoning, specimen ZPAL RV/573 (Fig. 4A) which has a more posteroventrally sloping spine than other cervicals, would be a posterior cervical, but it is longer than would be expected at the cervical-dorsal transition. Its position is therefore questionable. Anterior dorsals have lower, more vertical spines. When preserved the dorsal and sacral spines are subvertical and have no spine tables (Fig. 4B, C).

The anterior and posterior zygapophyses are subhorizontal and bear ovoid facets. Anteriorly, they sit at the anterior corners of a triangular shelf, apex posterior, that is laterally delimited by low subhorizontal crests converging toward the spine base. The articular facets are separated from each other by an incision, while uniting at the base by a dorsally concave blade that received a ventrally convex projection bridging the postzygapophyses, but an accessory articulation probably did not exist. The postzygapophyses protrude only slightly beyond the posterior edge of the centrum, but more so than do the prezygapophyses on the other side of the vertebra. They are suspended dorsally on the crests that converge toward the spine base. The crests delimit a deep triangular cleft that presumably received intervertebral ligaments. The articular facets are usually more or less oblique ventromedially, while being apparently more horizonatal in the posterior half of the dorsal series.

As usual for reptiles, the cervicals have the diapophyses situated about the level of the neurocentral suture and close to the anterior margin of the centrum, whereas they are more posteriorly positioned on the dorsals, and lie on the neural arch. In the cervicals, the diapophyses are strongly protuberant and curve ventrolaterally towards the parapophyses so that the lateral walls of the centra are excavated. In dorsal vertebrae, the diapophyses extend horizontally, but their lateral extent is unknown because the distal parts are always damaged. On cervicals, the posterior border of the diapophysis passes into the centrodiapophyseal crest, concave both ventrally and laterally, that roofs the lateral excavation of the centrum. On the dorsals, the diapophysis is supported by three crests: the centrodiapophyseal crest reduced to a straight posterolateral border of the diapophysis, an anterior crest extending to the prezygapophysis, and a ventral crest extending to the parapophysis (Figs 2L–N, 4B).

In cervicals, the parapophyses are situated very low, just above the level of the keel, and far anterior, so that they touch the border of the centrum (Figs 2C–F, 3B, D). As the anterior central region is usually damaged, the presence of the parapophyses is marked by a wavy margin. In the anterior dorsals, the parapophyses are positioned beyond the neurocentral suture (Fig. 3E, F) and then gradually more and more posterodorsally along the dorsal series (Fig. 2N). The gap between the parapophysis and diapophysis, bridged by the sharp crest, gradually decreases. In posterior dorsals, the diapophysis and parapophysis are close together (Fig. 4C), but the exact vertebral level at which they fuse cannot be determined.

Among 32 sufficiently well preserved archosauriform postaxial cervicals considered mature, the *Osmolskina* cluster encompasses 26 vertebrae (Appendix 2). Limited as they are, their measurements show a normal distribution (Figs 22, 23). Within this unifom group, there is some variation in central section whereby additional crests lateral to the ventral sagittal crest (posterior centroparapophyseal lamina of Wilson 1999) may be absent or variably developed. Nesbitt (2005) described similar variability within the vertebral series of *Arizonasaurus babbittini*. Depending on the presence v. absence of the lateral crests the ventral side of the centrum is narrow to acute or rather broad. However, no correspondence between this variability and the position of the vertebra along the spine has been observed.

Sacral and caudal vertebrae. — Among numerous sacrals attributed to *Osmolskina czatkowicensis*, two morphotypes, corresponding to the first and second sacral, have been recognized, both of them with conjoint sacral ribs. Both sacral centra are rather long (see Supplement 1C). The anterior articular facet of the first sacral centrum (Fig. 4D) often appears very broad, in contrast with the subcircular shape of the dorsal centra and that of the second sacral. This condition results from the large size and anterior position of the first sacral rib, as exposed by damage (see Gower 2003, p. 51 and fig. 25, for a similar structure in *Erythrosuchus*). The dorsal surface of the first sacral centrum slopes slightly posteroventrally (Fig. 3I), but there is no equivalent slope in the second sacral vertebra. Sacral ribs completely fuse with the centrum before the ossification of their distal ends and those of the neural spines.

In the first sacral the length of the base of the diapophysis almost equals that of the neural arch, the latter being relatively short and the former more expanded than in presacral vertebrae. The diapophysis is completely fused with a parapophysis that is unexpectedly low and anterior in position, given its posterodorsal position in the last dorsals. Together, the diapophysis and parapophysis create a subvertical facet that extends from a point at about half the height of the neural arch onto the dorsolateral side of the centrum. The second sacral rib is less deep, and more horizontally extended than the first one, and it does not invade the centrum as much. The distal ends of the sacral ribs are never preserved, but their general shape, subvertical in the first sacral and subhorizontal in the second (Fig. 2O, P) correspond to the sacral facet on the ilium (Fig. 10A_2, A_3).

The anterior caudal centra (Fig. 4F) are no longer than those of the dorsals, and correspond to them in proportions and overall shape (Supplements 1C, 2E–G). They are ventrally beveled, and probably bore chevrons. In the first caudal, the base of the transverse process retains a horizontal position and is equal to the neural arch in length. Posteriorly, the processes become shorter and thinner (Fig. 4F). They level with the base of the neurocentral canal. Attributed posterior caudals of *Osmolskina* (*e.g.*, ZPAL RV/1300, 1301) become very narrow and elongate as the spines and diapophyseal crests are gradually reduced.

Chevron bones. — The largest of the numerous, usually damaged, chevron bones from Czatkowice 1 material, are considered to belong to archosauriforms. The chevrons are more than twice the length of the caudal centrum in *Proterosuchus vanhoepeni* (Cruickshank 1972) and are even longer in *Ticinosuchus ferox* (Krebs 1965), but no measurements are available for *Euparkeria capensis* (Ewer 1965). Given an estimated mean length of about 8.5 mm for the caudal vertebrae in *Osmolskina* (Supplement 1C), the expected length of the chevrons would be over 20 mm. ZPAL V/1349 (Fig. 4I) is a chevron that corresponds to this size range. It consists of a pair of distally fused haemal arches with a bilaterally flattened distal end. The arches are linked proximally by a dorsally concave transverse bar homologous to the intercentrum. The specimen thus closely corresponds to Ewer's (1965) description for *Euparkeria*, but this is not a phylogenetically useful element.

Osteoderms. — Numerous osteoderms of a fairly uniform size (about 5 mm in length) occur in the Czatkowice 1 material (Fig. 5B, C, H–O). They are mostly symmetrical, more or less cordate, the apex anterior (orientated by comparison with *Ticinosuchus* and *Euparkeria* Krebs 1976, pp. 62 and 70 respectively),

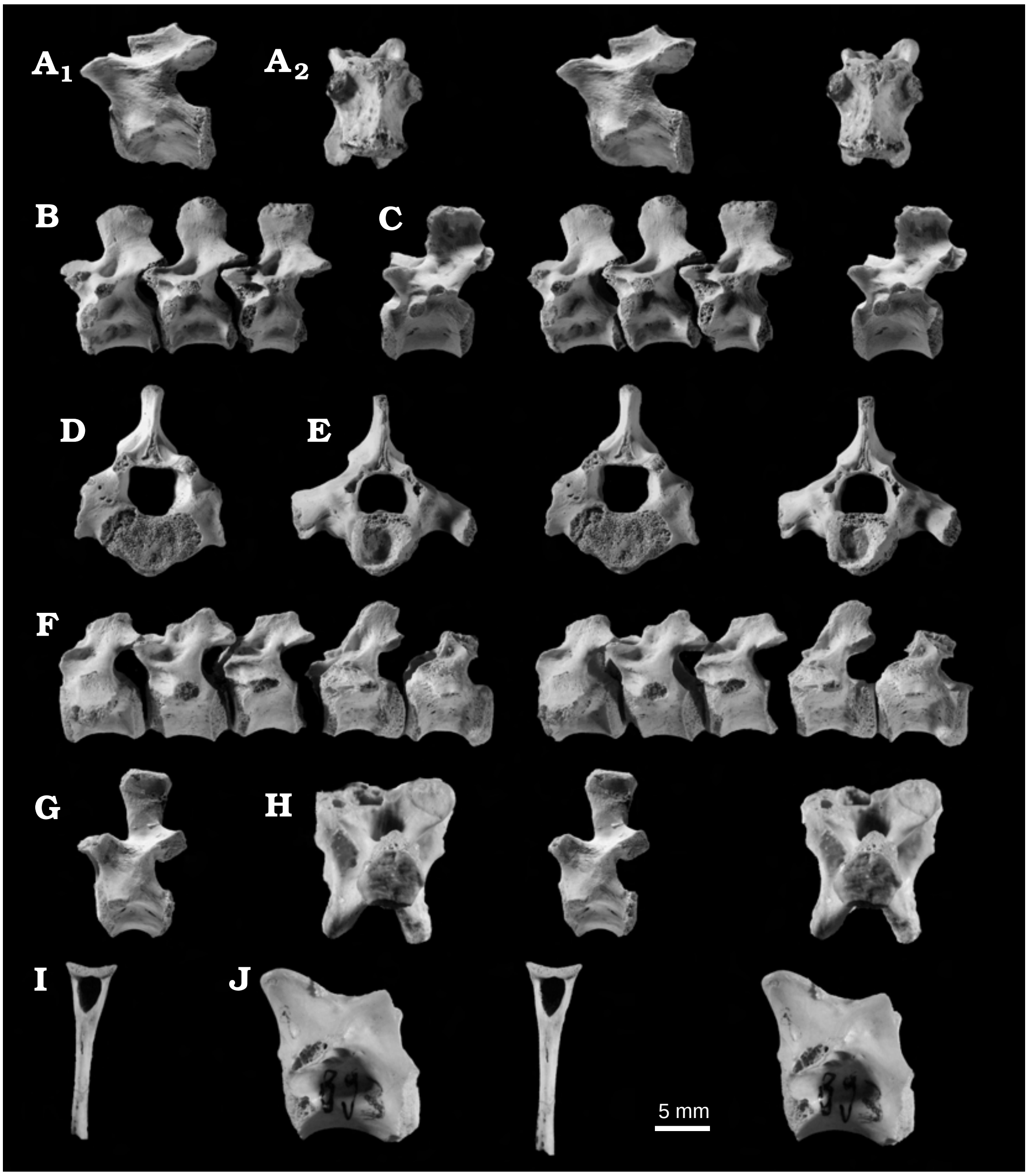

Fig. 4. **A**–**L**. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A**. Cervical vertebra ZPAL RV/573. **B**. Middorsal vertebrae ZPAL RV/572, 632, 633 in a possible sequence. **C**. Posterior dorsal vertebra ZPAL RV/572. **D**. First sacral ZPALRV/639. **E**. Second sacral ZPALRV/640. **F**. Possible series of consecutive caudals ZPAL RV/659, 657, 658, 576, 660. **G**. Midcervical vertebra ZPAL RV/571. **H**. Spine table in anterodorsal vertebra ZPAL RV/1348. **I**. Chevron ZPAL RV/1349. **J**. *Collilongus rarus* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Postcervical vertebra ZPAL RV/893. Left lateral (A_1, B, C, F, G, J), ventral (A_2), cranial (D, E), and dorsal (H) views. Stereo-pairs.

and incised at a posterior end (Fig. 5C, I, O). They vary in shape from very narrow to equilateral triangles. They have a more or less concave ventral surface and a longitudinal dorsal crest extending along the sagittal axis. Both surfaces are pitted, and many show traces of resorption. The anterior tip of the osteoderm is bordered posteriorly by a transverse furrow, and is slightly upturned (Fig. 5C_2, M), forming a tubercle that matches a small fossa on the posteroventral tip of the preceding osteoscute (Fig. 5O). The resulting articulation is similar to that described by Ewer (1965, p. 414) in *Euparkeria*, and suggests these elements formed a single row of osteoderms with no trace of a transition from an unpaired to a paired arrangement. Nor is there any trace on these elements of a lateral overlap or any straight border that could have made a sutural contact with neigbouring scutes. They may belong to an unpaired series of the anterior neck or posterior tail, but it is difficult to envisage a smooth transition between the unpaired and paired rows of osteoderms, similar to that reconstructed in *Ticinosuchus* (Krebs 1965, 1976, p. 62)). Alternatively they may belong to a flank series.

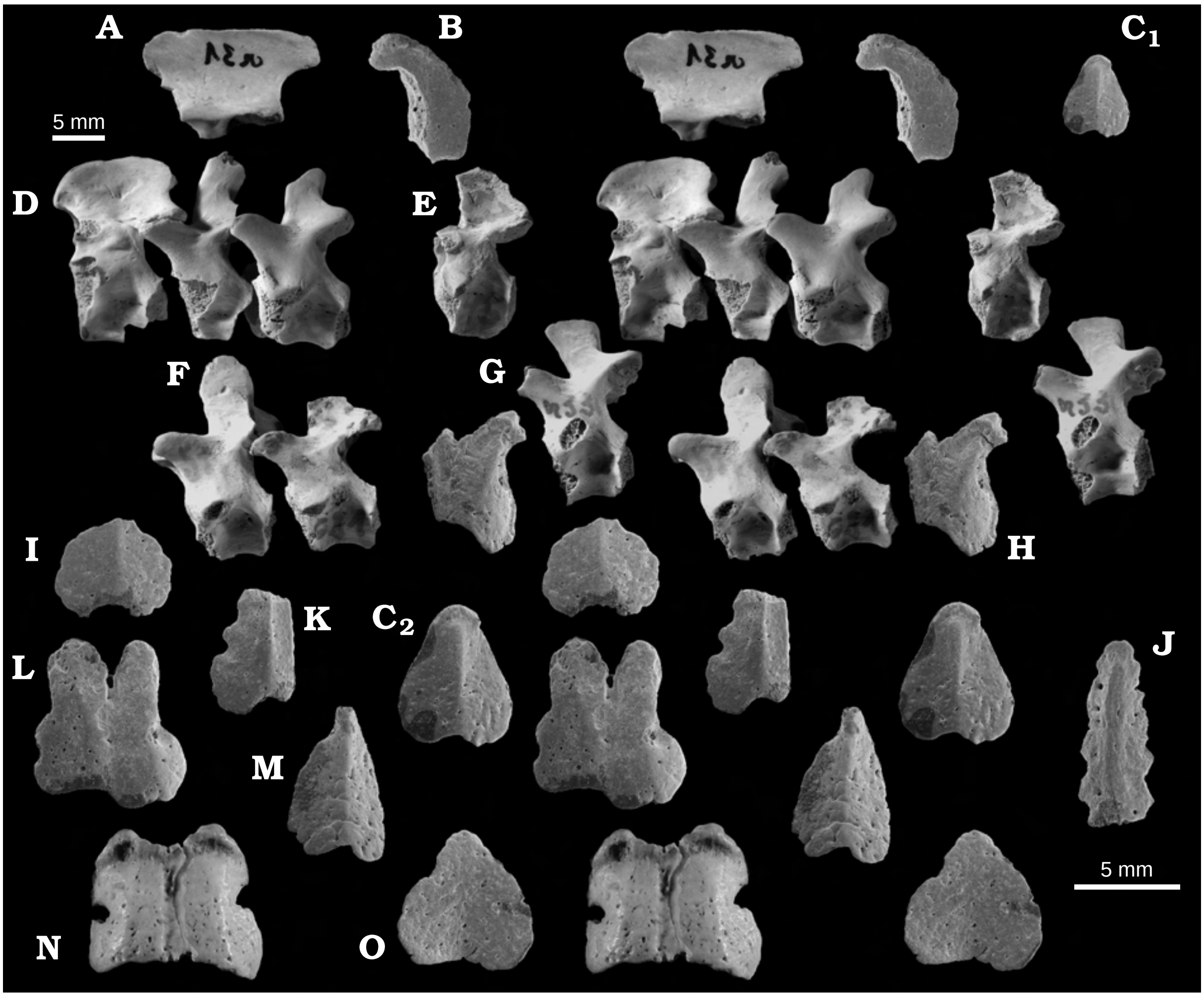

Fig. 5. Archosauriform remains, Early Triassic of Czatkowice 1, Poland. **A**. *Collilongus rarus* gen. et sp. n. Neural spine of axis ZPAL RV/587. **C**–**G**, **I**, **J**, **M**, **O**. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003. **C**. Simple osteoderm ZPAL RV/1338 in natural size (C_1), enlarged (C_2). **D**. Axis ZPAL RV/570, with two postaxial cervical vertebrae ZPAL RV/635 and 636 in a possible sequence. **E**. Cervical vertebra ZPAL RV/637. **F**. A possible sequence of midcervicals ZPAL RV/577 and 681. **G**. Posterior cervical vertebra ZPAL RV/607. **I**, **J**, **M**, **O**. Osteoderms: ZPAL RV1342 (**I**), ZPAL RV/1341 (**J**), ZPAL RV/1339 (**M**), and ZPAL RV/1335 (**O**). **B**, **H**, **K**, **L**, **N**. Archosauriformes gen. indet. **B**. Left side of a compound osteoderm ZPAL RV/1345. **H**. ZPAL RV/1344. **K**. ZPAL RV/1336. **L**. ZPAL RV/1337. **N**. ZPAL RV/1340. Left side (A, D–G) and dorsal (B, C, H–O) views. SEM micrographs; all but C_1 stereo-pairs.

Some small, very narrow specimens (*e.g.*, ZPAL RV/1341) might belong to the unpaired posterior tail armour (Fig. 5J). Much less numerous are asymmetric osteoderms bearing a paramedian, instead of a median, keel and having one straight border (Fig. 5K) to make a sutural contact with a contralateral osteoderm. These elements closely correspond to the description of *Euparkeria* osteoderms (Ewer 1965, p. 414). They are usually strongly angled, the parasagittal part being rather narrow, thus indicating a slender back, the lateral part extending down the body flank. The third morphotype is represented by fused pairs of slightly asymmetric elements that are the largest and heaviest osteoderms (Fig. 5L, N). Some of these heavy osteoderms display a laterally twisted tip (Fig. 5B) that is rather difficult to interpret. One possibility is that such osteoderms fused with others to form an unpaired (*e.g.*, cervical) shield of a type known in some crocodiles (Rogers 2003). They seem to be a variant of the fused pair (Fig. 5L, N).

The extremely small percentage of the heavy compound osteoderms (Fig. 5B, L, N) and the high percentage of the perfectly symmetric ones might reflect systematic differences. On the size and frequency criteria, the osteoderms of the first morphotype are tentatively considered to belong to *Osmolskina czatkowicensis*. If it is true, the dorsal armour over the vertebral column in *O. czatkowicensis* would be essentially unpaired, which is at odds with the data on *Euparkeria* armour (Ewer 1965; Krebs 1976). A close similarity between osteoderms of the small, asymmetrical, morphotype described above (Fig. 5K) and those described by Ewer (1965) suggests paired construction of the armour over the spine, probably within the trunk, but the heavy compound osteoderms are relegated to Archosauriformes gen. indet.

PECTORAL GIRDLE AND FORELIMB

Scapula. — The archosauriform scapulae from the Czatkowice 1 material are elongate bones (Fig. 6G) about three times longer than wide at the distal end, and widening at the glenoid. The best preserved specimen, ZPAL RV/902 (Fig. 6H), exceeds 34 mm in length, and is about 11 mm in distal width.

The bone is medially concave (Fig. 7A) but becomes flatter towards the distal end. It suggests the thorax was fairly deep and narrow. The coracoid surface tapers anteriorly but is usually damaged. The glenoid facet is roughly semicircular and is perpendicular to the posterior border of the scapula (Figs 6F, 7A). More dis-

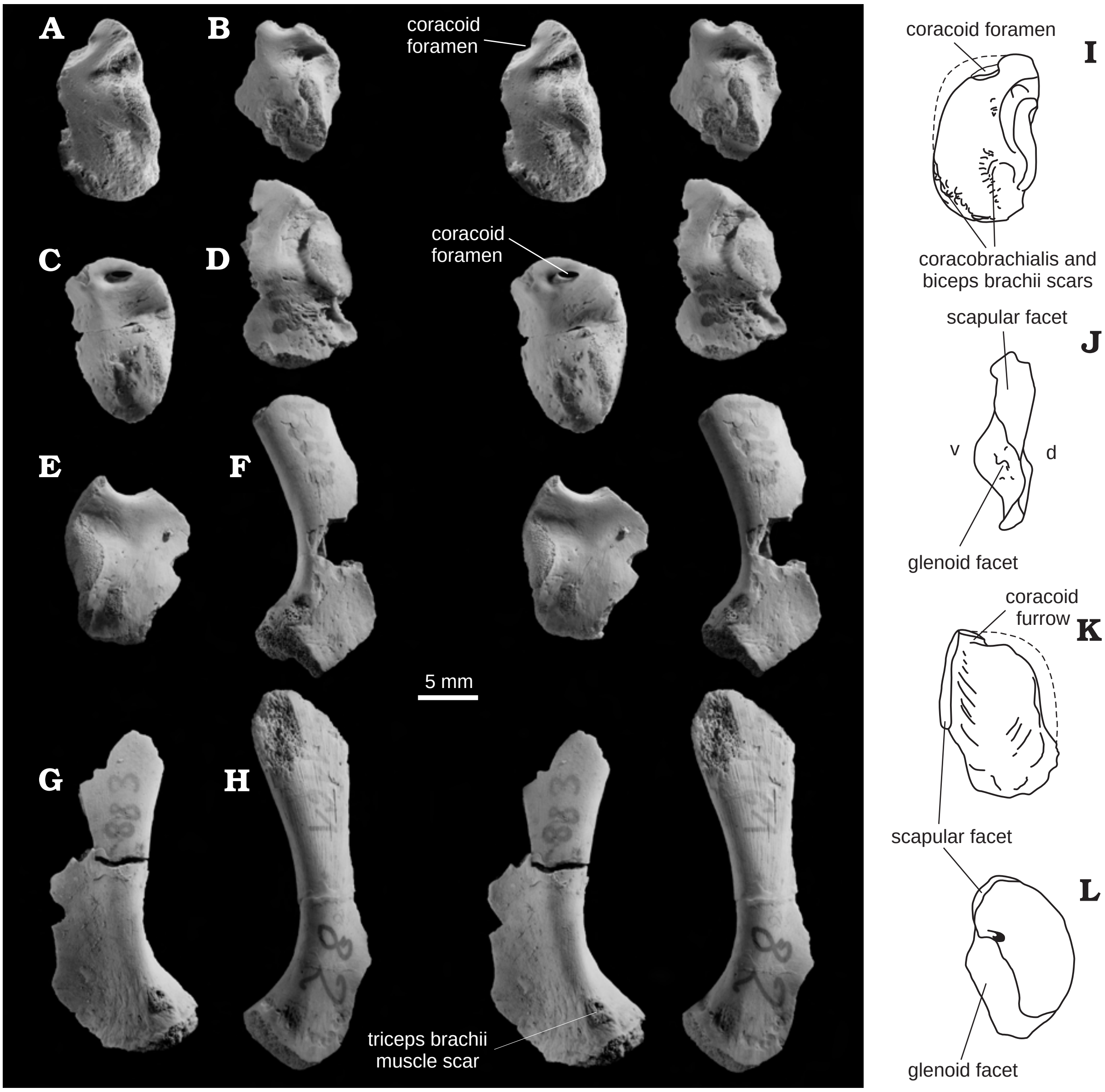

Fig. 6. **A**–**K**. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A–D**. Left coracoids: ZPAL RV/903 (**A**), ZPAL RV/1169 (**B**), ZPAL RV/1311 (**C**), and ZPAL RV/1166 (**D**). **E**. A fragment of right coracoid ZPAL RV/1167 with largely open coracoid foramen. **F**. Right scapula ZPAL RV/881. **G**. Left scapula ZPAL RV/883. **H**. Right scapula ZPAL RV/1161. **I**. Left coracoid. **J**. Articular border of the left coracoid. **K**. Left coracoid. **L**. *Erythrosuchus africanus* Broom, 1905. Left coracoid (after Gower 2003, fig. 29). Ventral (A–E, I), lateral (F–H), and dorsal (K, L) views. A–H, stereo-pairs.

tally, this border arches strongly posteriorly, but becomes straighter distally. ZPAL RV/881 (Fig. 6G), shows that the proximal region was antero-posteriorly much wider (Fig. 7A_3) than preserved in most specimens, as it was in *Euparkeria* (Fig. 7E). The bone thins anteriorly, but probably gets thicker again (as does the scapular facet of the coracoid (Fig. 6J) to create a cavity on the lateral side of the scapula, anterior to the glenoid. Directly above and posterolateral to the proximal end, there is a scar probably left by the scapular head of the triceps muscle (Figs 6G, 7A).

The best preserved scapulae cluster about 30 mm in length, but there are many smaller specimens that are too fragmentary to be measured. There is no indication of heterogeneity in the sample, so the morphology described above may safely be ascribed to *Osmolskina*. Based on skull to scapula length proportions in *Euparkeria* (Appendix 1), the scapula appears relatively longer in *Osmolskina*. However, direct comparisons (Fig. 7A, E) show that the difference is not significant.

Coracoid. — The coracoid is considerably longer (15–21 mm N = 3) than wide (10–13 mm N = 3), and has thickened lateral and posterior borders (Fig. 6). Both the anterior and medial borders are usually damaged. As a rule, the fracture passes through the coracoid foramen, leaving it as an incision rather than an enclosed perforation. The slightly concave surface of the bone is considered dorsal. It is sculptured by posteriorly converging V-shaped ridges. The other side is a folded ventral or external surface. The folds probably correspond to what Ewer (1965, p. 407) described in *Euparkeria* as radiating struts buttressing the articular facets of the lateral border. The anteriormost of these supports the elongated scapular facet, extending down the anterior half of the coracoid (Fig. 6A–D, I), the middle one supports the glenoid, and the posterior one makes the coracoid blade more resistant to breakage. The scapular facet tapers posteriad and broadens at the anterior end (Fig. 6J). Its posteroventral half faces laterally and forms a complicated pitted facet that contributed to a glenoid. It has a swollen ventral border (*e.g.*, Figs 6A, 7A_3) that probably served for the attachment of the joint capsule. The swelling is bordered by two furrow-like depressions, exactly as it is in *Euparkeria*. The anterior one bears circular traces probably left by the origin of the supracoracoideus muscle. In rare instances, there is a vascular foramen or a trace of perforation (ZPAL RV/1169; Fig. 6B) in this concavity. The posteroventral surface of the coracoid bears two rugosities, lateral and posteromedial, probably for the coracobrachialis and the biceps brachii muscle respectively (Fig. 6I).

The coracoid foramen usually appears as a subhorizontal furrow (Fig. 6A, I) that incises the anterior border. The furrow enters ventrally, well anterior to the glenoid, and then slopes dorso-laterally to continue onto the dorsal surface of the bone (Fig. 6K). Only in rare specimens is the passage fully enclosed anteriorly. ZPAL RV/1168 (Fig. 6C) is an example, but the closing bridge is anteriorly damaged and none of the original bone edges are preserved. Specimens ZPAL RV/903 and 1168 (Fig. 6A and C respectively) are better preserved anterolaterally, and show that the usually missing anterior part of the coracoid was not extensive. This indicates a comparatively anterior position of the foramen, far from the posterior margin of the bone. ZPAL RV/1167 suggests that there was no anterior part (Fig. 6E), and the coracoid passage was open.

In terms of outline, *Osmolskina* coracoids are exactly the same as those of *Euparkeria* (Ewer 1965) and other basal archosauriforms such as *Sarmatosuchus* (Gower and Sennikov 1997, fig. 10), *Erythrosuchus* (Gower 2003), and the rauisuchids *Batrachotomus* (Gebauer 2004), *Ticinosuchus* (Krebs 1965), and *Postosuchus* (Long and Murry 1995). The *Osmolskina* coracoid (Fig. 7A_3) differs from that of *Euparkeria* (Fig. 7E_1) in that the glenoid part is more elongate relative to the preglenoid portion than in the latter (as presented by Ewer's 1965, fig. 9), while being similar to *Erythrosuchus* and *Sarmatosuchus* in this respect. A comparison with *Erythrosuchus africanus* is noteworthy. In this species (Gower 2003, fig. 29), the glenoid facet is widely exposed in dorsal view (Fig. 6L) in contrast to *Osmolskina* where it is almost hidden under the lateral border (Fig. 6K). This means a difference in position of either the coracoid, which is more probable, or the humerus. In *Osmolskina*, the coracoid probably angled ventromedially, suggesting a bilaterally flattened thorax, whereas *Erythrosuchus* had a more horizontally placed coracoids, indicating a more dorsoventrally flattened ribcage. As reconstructed by Ewer (1965, fig. 9) in *Euparkeria*, the coracoid was subhorizontal in orientation, but it is much more oblique in her fig. 20. The putative differences between *Osmolskina* and *Euparkeria* in the length and orientation of the glenoid (the glenoid being much shorter and more posterior in orientation in *Euparkeria*) might be artefacts.

Osmolskina is distinguished from all other basal Archosauriformes, and from most outgroup taxa (the rhynchosaur *Hyperodapedon* is an exception; Benton 1983), in that the coracoid foramen is situated close to the anterior border of the coracoid and is anteriorly open in at least some cases. This difference (the foramen

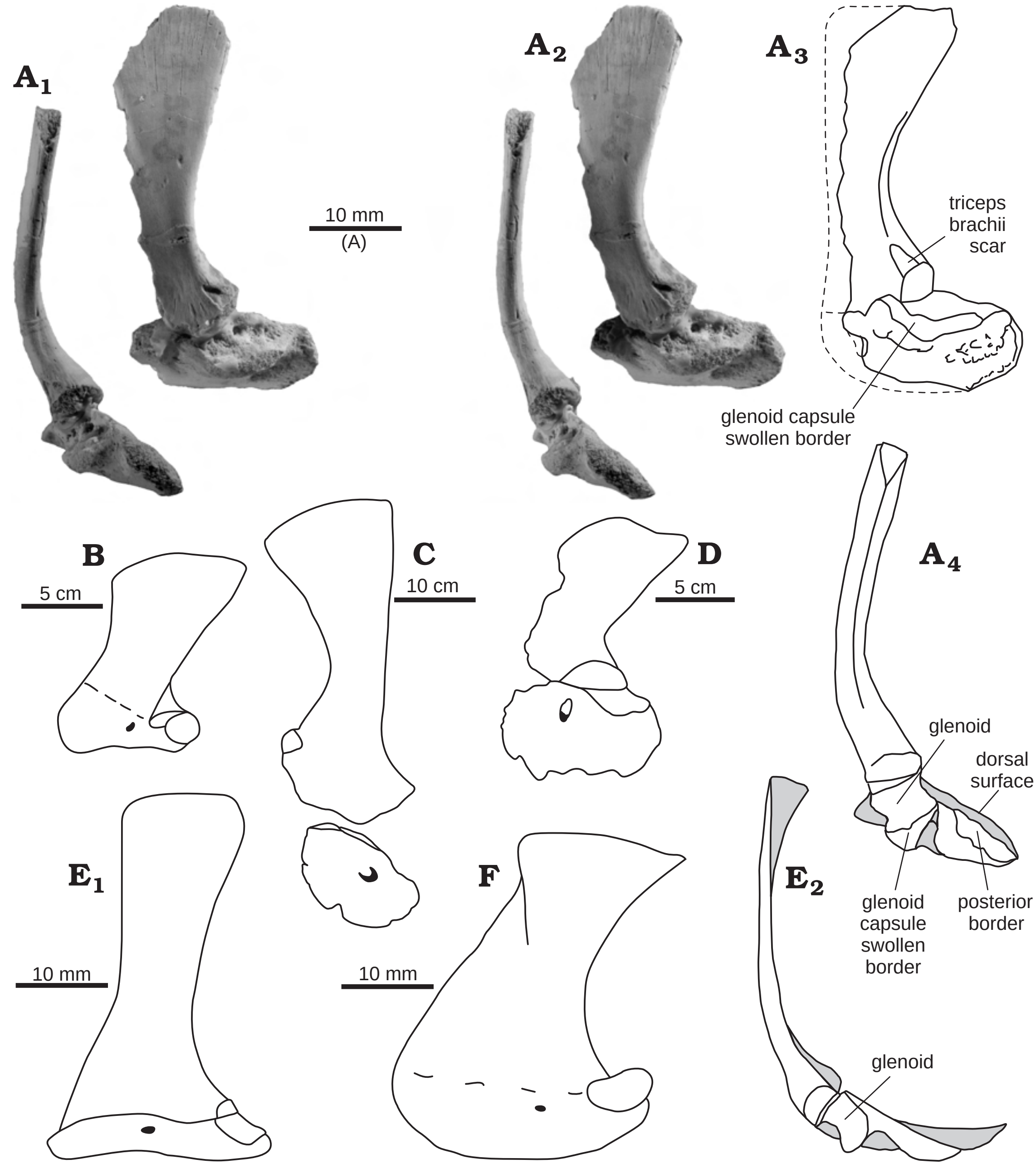

Fig. 7. Left scapulocoracoids. **A**. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. Combined from ZPAL RV/903 (scapula) and ZPAL RV/902 (coracoid). **B**. *Proterosuchus vanhoepeni* (Haughton, 1924) (after Cruickshank 1972). **C**. *Erythrosuchus africanus* Broom, 1905 based on Gower (2003, fig. 29). **D**. *Sarmatosuchus otschevi* Sennikov, 1994 (after Gower and Sennikov 1997). **E**. *Euparkeria capensis* Broom, 1913 (after Ewer 1965). **F**. *Prolacerta broomi* Parrington, 1935 (after Gow 1975). All but A_1, A_4, E_2 in left side view. A_1, A_4, E_2 in posterior view. A_1, A_2, stereo-pairs.

enclosed or open anteriorly) may well be ontogenetic, as demonstrated *e.g.*, by Currie and Carroll (1984) in the younginiform reptile *Thadeosaurus colcanapi*, but the decidedly anterior position is certainly an apomorphy of *Osmolskina*. Interestingly, anterior emargination of the coracoid is a phytosaurian character (Romer 1956; Westphal 1976; Chatterjee 1978; Long and Murry 1995, fig. 30), but an anterior position of the coracoid foramen is also found in the rauisuchid *Arizonasaurus babbitti* (Nesbitt 2005, fig. 27).

Humerus. — All Czatkowice 1 humeri of a size consistent with *Osmolskina* (see Appendix 1) display essentially the same structure. They are derived in terms of a weak twist of the shaft, a weak enlargement of the extremities, and the absence of both entepicondyle and ectepicondyle foramina. The proximal articular head is protuberant, and probably earlier to ossify than the internal tuberosity and the most proximal part of the

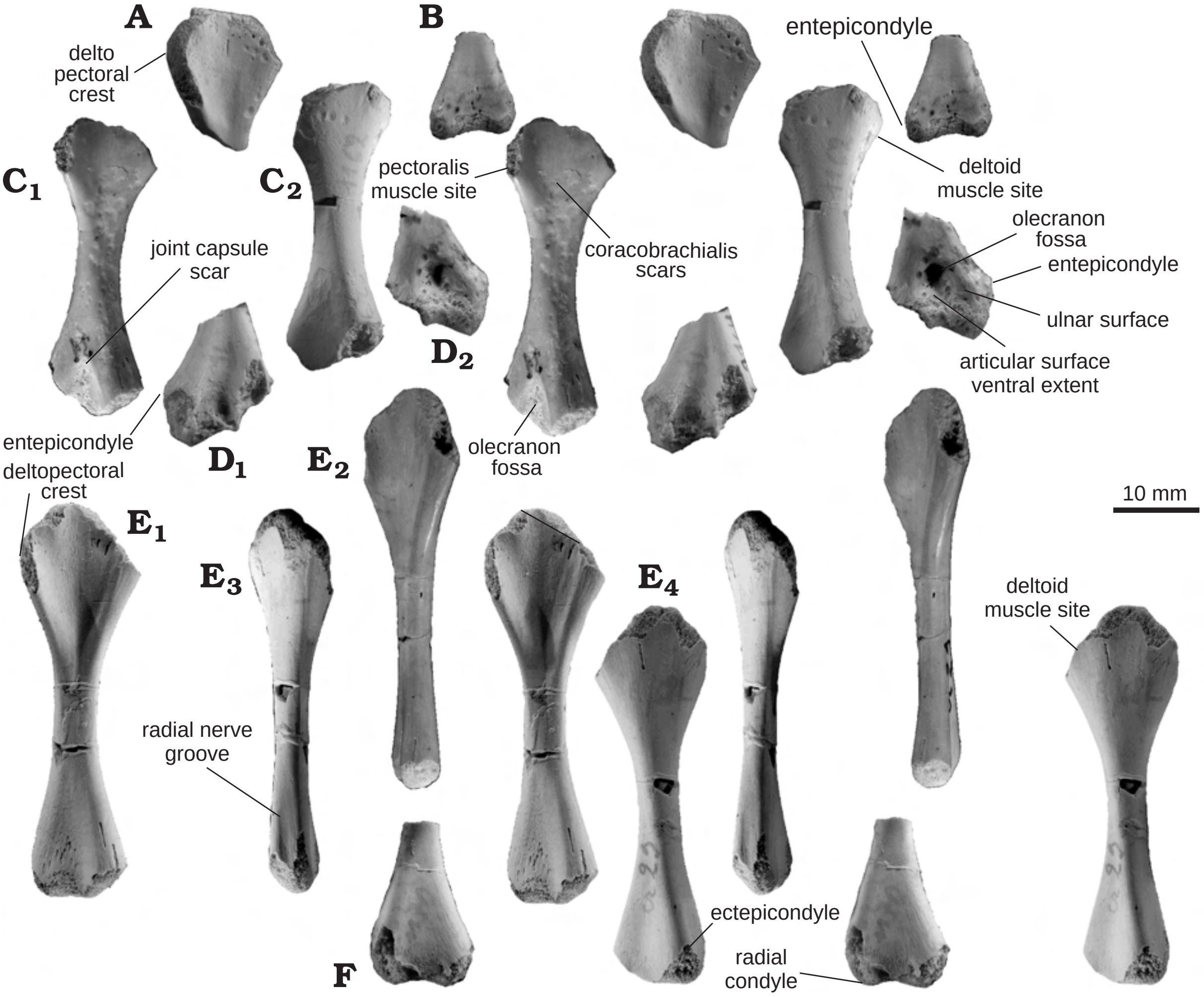

Fig. 8. **A**, **C**, **D**. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A**. Proximal end of the right humerus ZPAL RV/1172, in ventral view. **C**. Left humerus ZPAL RV/1262 (reversed), in proximal ventral (C_1) and proximal dorsal (C_2) views. **D**. Distal end of the right humerus ZPAL RV/1164, in dorsal (D_1) and ventral (D_2) views. **B**, **E**, **F**. Archosauriformes gen. indet., Early Triassic Czatkowice 1, Poland. **B**. Distal end of the right humerus ZPAL RV/1173, in dorsal view. **E**. Right humerus ZPAL RV/877, in proximal ventral (E_1), distal medial (E_2), distal lateral (E_3), and proximal dorsal (E_4) views. **F**. Distal part of the left humerus ZPAL RV/1170, in dorsal view. Stereo-pairs.

deltopectoral crest which are less ossified and always damaged. The concave ventral surface of the proximal end bears slight scars that probably relate to the insertion of the coracobrachialis muscle. The dorsal face is slightly convex.

Humeral lengths and proportions, both suggest the presence of two morphotypes in the Czatkowice 1 material. The first morphotype is shorter and more robust, the second one is longer and slimmer. Based on rough estimates from damaged bones, most humeri cluster between 25 and 36 mm in length, which corresponds to the first morphotype. On the basis of frequency we consider it as belonging to *O. czatkowicensis*. The longest and best preserved specimen, ZPARV/877 (Fig. 8E) represents the second morphotype. It exceeds the next in length by more than 20% and is more slender. The possibility of negative allometry during ontogeny (McGowan 1999), the humerus becoming more slender with increasing length, is improbable. The longer morphotype, although more closely similar in proportions to *Euparkeria capensis,* is relegated to *incertae sedis*.

Also the proximal and distal ends detached from the shafts display two different morphologies, the more expanded ends (Fig. 8A, D) matching the shorter bones (Fig. 8C) belonging to *O. czatkowicensis* and *vice versa* (Fig. 8B, F and E). The distal end of *O. czatkowicensis* (Fig. 8D), has a more protruberant entepicondyle than the second morphotype (compare Fig. 8D and E). The flattening of one of its sides corresponds to the position of the radial nerve groove that usually runs laterally and separates the ectepicondyle from the supinator muscle origin. The other side, which is thus considered medial, is evenly convex in section, and ex-

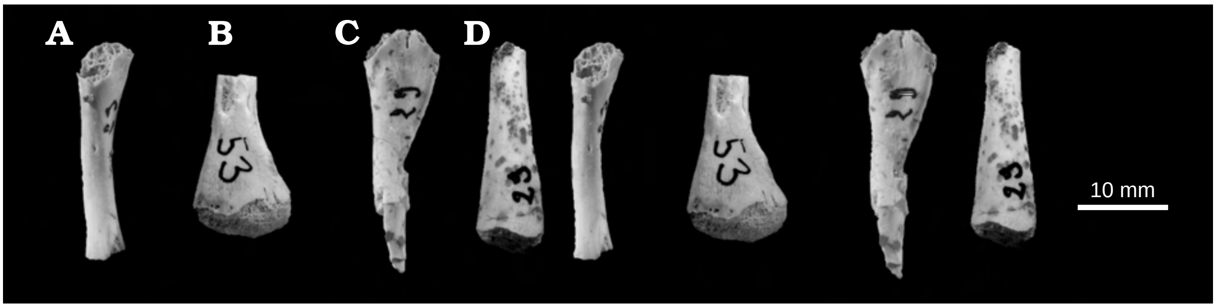

Fig. 9. **A**, **C**, **D**. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A**. Proximal part of the left ulna ZPAL RV/1230, in ventromedial view. **C**. Proximal part of the left ulna ZPAL RV/1179, in medial view. **D**. Distal part of the radius ZPAL RV/1235. **B**. Archosauriformes gen. indet., Early Triassic Czatkowice 1, Poland. Distal part of the radius ZPAL RV/1232. Stereo-pairs.

tends into the entepicondyle. The central part of the articular surface extends onto the lateral wall of the ulnar condyle, and only slightly onto the ventral surface of the bone (Fig. $8D_2$). The preserved part probably received the ulna. The radial condyle is broken off. There is a deep concavity proximal to the trochlea, corresponding to the olecranon fossa on the ventral side of the bone. Attributed to Archosauriformes, ZPAL RV/1170 (Fig. 8F) has a shallower olecranon fossa, and a less prominent entepicondyle, suggesting that this specimen belongs to the longer morphotype (ZPAL RV/877; Fig. 8E).

The twist in the proximo-distal axis is roughly 30–40° for the whole Czatkowice 1 archosauriform group, being slightly more in the shorter ones, assigned to *O. czatkowicensis*, and slightly less in the longest bone. The deltopectoral crest is always smoothly rounded and has its apex at a point roughly 20% down the length of the humerus. In spite of some differences, both Czatkowice 1 humeral morphotypes correspond to a lightly built animal and are closely similar to those of *Euparkeria*.

Radius. — Several fragments (*e.g.*, ZPAL RV/1231, 1233, 1234, 1235; Fig. 9D) of slender columnar bones with slightly convex articular ends are considered to be the distal parts, possibly less than half the length, of the radius. The bones are featureless, circular in section, and only slightly waisted. They are considered to belong to *O. czatkowicensis* because they are more numerous and smaller than the second morphotype from the Czatkowice 1 material (ZPAL RV/1232; Fig. 9B).

Ulna. — Only those ulna fragments that have the proximal part preserved (ZPAL RV/1178, 1179) are readily recognizable (Fig. 9A, C), but no specimen has its articular surface and olecranon preserved. The distal parts are less characteristic anatomically and have yet to be recognized. On the basis of Ewer's (1965) data on *Euparkeria,* and specimens of crocodile antebrachii (ZPAL RI/75, 76), the acute proximal apex is regarded as medial, and the two blunt ones are considered dorsal and lateral. The proximal parts of the ulna are short along the dorsoventral axis and expanded transversally, being slightly concave ventrally and convex dorsally. Proximally, the dorsal wall turns into a blunt margin that probably continued as an olecranon. The ulnar head is triangular in transverse section. As a whole, the bone is twisted, the ventral concavity probably facing towards the radius, as it does in the crocodilian antebrachium. Mid-shaft, the transverse section becomes circular. Distally, the shaft is twisted at about 50° to the proximal end, the ventral surface of the bone passing into the lateral side of the distal end. These specimens match the size of radii and humeri assigned to *O. czatkowicensis*.

PELVIC GIRDLE AND HINDLIMB

The pelvis is represented by more than 100 iliac specimens of which about ten are complete, and by a large number of fragmentary pubes and ischia, none of them complete.

Ilium. — The subtriangular iliac blade and subcircular acetabular region (Fig. 10) are separated by an antero-posteriorly constricted neck, at the level of the dorsal half of the acetabulum. The preacetabular process of the iliac blade hardly extends beyond the anterior margin of the iliac neck. The postacetabular process is a stout elongate blade that is triangular in lateral aspect and tapers posteriad, slightly excavated ventrally in its distal half. The ventrolateral margin of the excavation is thickened and featureless. The ventromedial margin is acute and protrudes mediad. Bordered by these two margins, the elongate ventral excavation is a possible site of

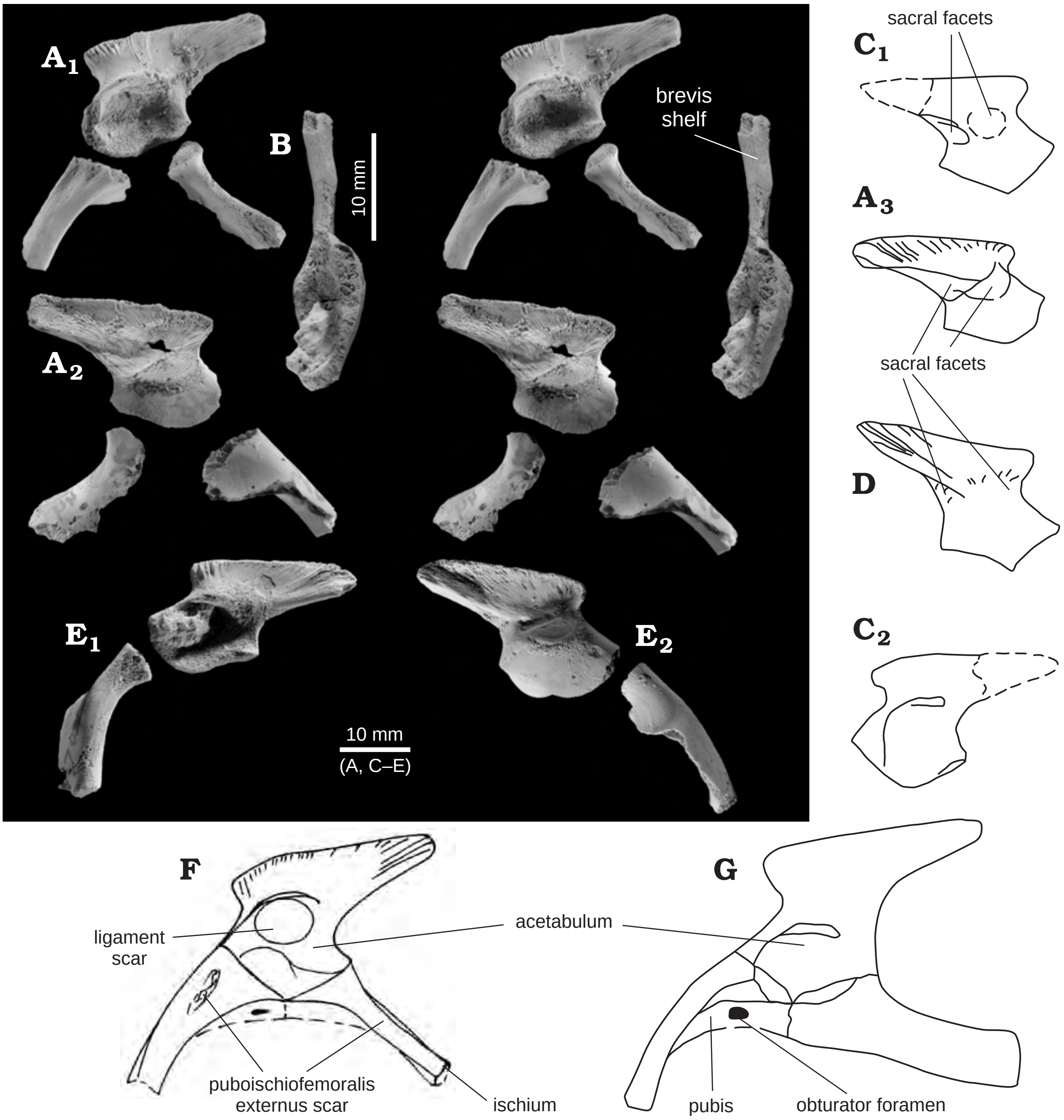

Fig. 10. **A**, **B**, **E**, **F**. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A**. Right pelvis (reversed) combined from different individuals: ZPAL RV/678 (ilium), ZPAL RV/910 (pubis), and ZPAL RV/908 (ischium), in lateral (A_1) and medial (A_2) views; A_3, the same ilium in medial view. **B**. Left ilium ZPAL RV/630, in ventral view. **E**. Left ilium ZPAL RV/630 combined with a reversed right pubis ZPAL RV/905, in lateral (E_1) and medial (E_2) views. **F**. Reconstruction of the left pelvis, in lateral view. **C**. *Dorosuchus neoetus* Sennikov, 1989. Left ilium, in medial (C_1) and lateral (C_2) views, after Sennikov (1995). **D**, **G**. *Euparkeria capensis* Broom, 1913. **D**. Left ilium, in medial view, after Ewer (1965). **G**. Left pelvis, in lateral view, after Ewer (1965). A, B, stereo-pairs.

origin of the caudifemoralis brevis muscle (Romer 1923; Hutchinnson 2001). This position is essentially the same as that of the "brevis shelf" (Romer 1927; Gauthier 1986; Novas 1996), as demonstrated by Langer and Benton (2006, fig. 9) in the dinosaurs. In the dinosaurs the brevis shelf extends more anterior and faces more ventrolateral than ventral, while being more distal, tapering toward the acetabulum (Fig. 10B), and facing ventrally in *Osmolskina*. According to Novas's (1996) definition, the brevis shelf is "a prominent shelf on the posterolateral margin of the iliac blade, placed external to the posteroventral margin", which corresponds to its lateral inclination. In *Osmolskina* the surface is more or less horizontal and its medial margin corresponds to the posteroventral one of the Dinosauria. Novas (1996) supported the view that the lateral of the two margins of the brevis shelf was a neomorphic structure, whereas the medial margin was original. The presence of the shelf, although narrower and less excavated, in *Osmolskina* is more consistent with Hutchinson's (2001) view that the shelf is a pre-existing (*i.e.*, plesiomorphic) structure which was subjected to variability in the archosauriform evolution. The ventromedial margin continues towards the middle of the anterior sacral rib scar, and it probably received the second sacral rib. The ventral profile of the posterior ilac process makes an open angle (about 120°) with the posterior wall of the acetabulum.

A major part of the acetabulum is produced by the ventral portion of the ilium. Its ventral border bears elongated articular facets for the pubis and ischium, the axes of which close an angle of about 120°. The apex of the angle protrudes ventrally, exactly as it does in most basal Archosauriformes (Charig and Sues 1976), but hardly so in *Shansisuchus* (Young (1964, fig. 41). It also protrudes in basal archosaurs such as parasuchians and aetosaurs (Krebs 1976; Long and Murry 1995) on the one hand and in *Lagerpeton* (Sereno and Arcucci 1993) on the other. In all these taxa, the pubis and ischium facets touch each other leaving no space for an acetabular perforation, in contrast to *Marasuchus* where they are wide apart (Sereno and Arcucci 1994). In *Osmolskina*, the ischium and pubis facets are subperpendicular to the plane of the acetabulum, which suggests a vertical position of the ilium. In contrast, in rauisuchids, the facets face ventrolaterally (personal observation on *Batrachotomus kupferzellensis* SMNS 80273, and *Stagonosuchus nyassicus* GPIT 325, see also Gebauer 2003), which is consistent with a subhorizontal position of the ilia (Bonaparte 1984; Parrish 1986).

In *Osmolskina*, the lateral surface of the iliac blade is slightly concave, but anteriorly, it turns into a convex surface facing anterolateral. This angulation is not associated with the presence of the rugose swelling or crest in contrast to most rauisuchid ilia (Gower 2000). A thick, laterally protruding supraacetabular ridge overhangs the acetabulum. It encircles the acetabulum anterodorsally, and protrudes mostly above the acetabulum, while leaving its posterior side open with no trace of an antitrochanter (*e.g.*, see Sennikov 1995, pp. 63–64 for terminological discussion). Two circular scars of porous bone marking the attachment of the ilio-femoral ligaments are situated within the acetabulum. The larger one, about one third the diameter of the acetabulum, occupies the ventral-most position, the second slightly smaller one, is dorsal and directly underlies the supraacetabular ridge.

The acetabular portion of the ilium is medially convex. Its dorsal part bears a flat, step-wise subcircular sacral facet facing dorsomedially (Fig. $10A_2$, A_3). The facet passes onto the iliac blade and is radially ridged. Posterior to it, there is a triangular scar for the posterior sacral rib bordered dorsally by a longitudinal crest that passes into the ventro-medial border of the posterior process.

The dorsal border of the ilium is thin and bears heavy striations (Fig. $10A_1$). They are most likely traces of tendons of the axial muscles, particularly of longissimus dorsi and iliocostalis muscles that fill the gap between the ilium and the neural spines (Romer 1956, p. 317). Anteriorly, the striations are vertical. They attenuate posteriorly to become distinct again on the lateral side of the posterior process. They also occur on the medial surface of the iliac blade and are oriented in a similar fan-shaped manner, subvertical in the anterior part then increasingly oblique.

The fairly large sample of ilia from Czatkowice 1 attributed to archosauriforms is morphologically quite uniform, and does not suggest any taxonomic heterogeneity. As there is more than one archosauriform taxon in the Czatkowice 1 material (see p. 316), this suggests that the ilium must have been identical in all of them. It seems useful to stress that the morphology differs from that of the rauisuchids (Sennikov 1988, Gower and Sennikov 2000) in the absence of a buttress above the rim of the acetabulum, a character unique to this group (Parish 1993, Gower 2000), and in the weak, rather than strong (Gower 2000), dorsal reorientation of the anterior sacral facet that indicates a weak, instead of strong, ventral deflection of the sacral ribs.

Comments: In the overall shape of the iliac blade, the iliac contribution to the acetabulum, the shape and depth of the acetabulum, and the development of the supraacetabular ridge, the *Osmolskina* ilium (Fig. 10A) corresponds to that of *Euparkeria* (Fig. 10G) as well as to that of *Dorosuchus neoetus* (Fig. $10C_2$). This type of ilium is typical of archosauriforms in that (1) the acetabulum is deep, overhung by an anterodorsal, but mostly dorsal, supraacetabular ridge, and (2) the sacral facets are situated on the ventral (acetabular) and anterior parts of the ilium whereas they lie above the acetabulum level in prolacertiforms, and posterodorsal to it in lepidosaurs (Borsuk-Białynicka 2008). The non-perforated state of the acetabulum, and the weak development of the anterior process of the blade (Fig. 10A, E), both suggest a basal position for *Osmolskina* within the Archosauriformes.

Pubis. — All pubic specimens are damaged, and are usually represented by their middle sections. None has the acetabular part preserved. A roughly estimated length for the best preserved specimen, ZPAL

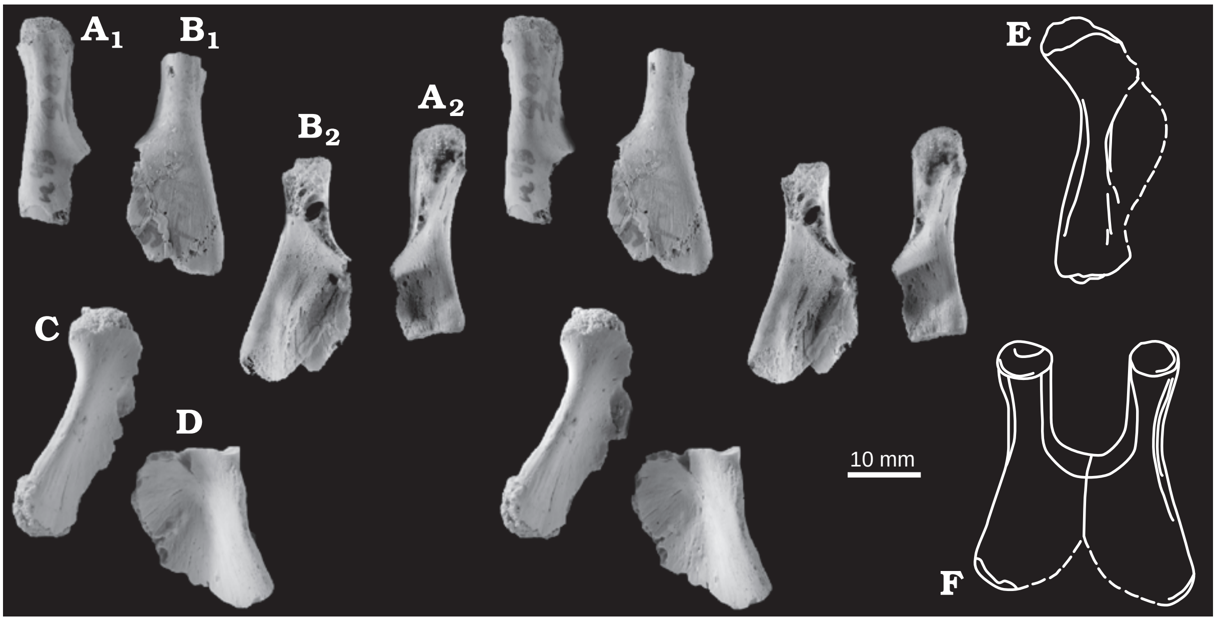

Fig. 11. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A**. Right pubis ZPAL RV/905. **B**. Left pubis ZPAL RV/906. **C**. Right ischium ZPAL RV/908. **D**. Distal part of the left pubis ZPAL RV/904. **E**. Reconstruction of pubis of both sides with a symphysis based on ZPAL RV/905 and 906. **F**. Reconstruction of right ischium based on ZPAL RV/908. Anterior (A_1, B_1), posteroventral (A_2, B_2), anteroventral (C), posteroventral (D), anteroventral (E), and anterodorsal (F) views. A–D, stereo-pairs.

RV/906, is about 20–25 mm. The pubis is bilaterally flattened proximally, but distally it passes into the medial symphyseal blade that forms the so called "pubic apron" (Fig. 11A, B, F). As a whole the bone is bowed antero-ventrally. The proximal part extends towards the ischium. A pubic foramen or an incision is expected to occur in that region, but neither it nor the pubic symphysis is ever preserved. Laterally, the proximal end of the bone bears a scar that probably reflects the origin of the puboichiofemoralis externus muscle.

Ischium. — The columnar shaft of the ischium is straight in posterior aspect but is arched transversely. The concave surface was probably oriented ventrolaterad in life, but the structure of this part of the pelvis is far from clear. Two specimens (ZPAL RV/908 and 892) are both 20 mm in length. Numerous fragmentary specimens are about the same size. The acetabular end is heavy. As suggested by the remnants of the acetabular part, the bone extended straight posteroventrad whereas the pubis turned more sharply ventrad. The shaft extends into a medial blade (Fig. 11C, E) that thins toward a symphyseal part, never fully preserved in the Czatkowice 1 material. The lateral border of the ischium bears rugosities that probably relate to the origin of the puboischiofemoralis externus muscle (Fig. 11C). They are situated about the mid-length of the bone.

Femur. — Femora are amongst the most common elements in the postcranial material from Czatkowice1, but even the largest are incomplete (Fig. 12A, G) with the proximal and distal ends always damaged. Very few specimens (*e.g.*, ZPAL RV/1188 and 1189; Fig. 12E and F respectively) preserve the region of the head. Contrary to expectations, they belong to the smallest individuals, but morphologically they are identical with the larger bones in the sample. The distal ends are more numerous but always detached from the shafts.

The *Osmolskina* femur (Fig. 12C) is similar to that of *Euparkeria* (Fig. 12D) and of *Dorosuchus* (Fig. 12I)), but seems more twisted. It is expressed by a proximal end relatively narrow (Fig. 12C) in distal ventral view as compared to *Euparkeria* (Fig. 12D). The roughly estimated angle between the main axis of the distal end and that of the proximal end is as much as 55° in *Osmolskina*, compared to 25° in *Erythrosuchus* (Gower 2003, p. 63), slightly more than this in *Euparkeria* (32° according to Ewer 1965, p. 413), about 40° in *Dorosuchus* (Sennikov 1989) and up to 60° in crocodiles (*Crocodilus niloticus* ZPAL RI/76 and juvenile *Alligator* sp. ZPAL RI/74).

The proximal part of the shaft is widely subtriangular in transverse section, the ventrally located fourth trochanter (site of attachment of caudifemoralis musculature, Romer 1923), being at the top of the triangle. The

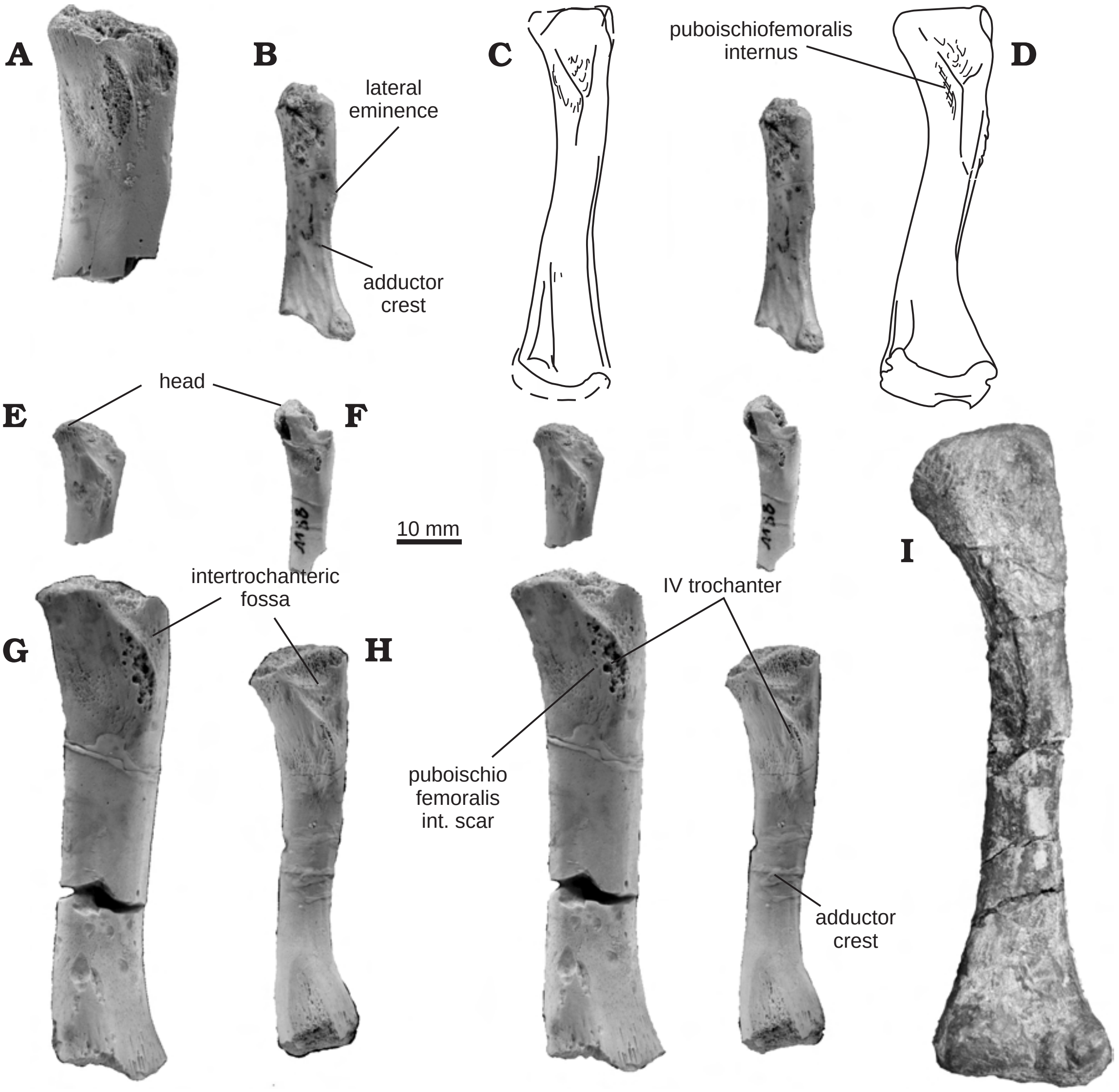

Fig. 12. Right femora. **A**, **G**. Archosauriformes gen. indet. **A**. Proximal part ZPAL RV/1174 (left reversed). **G**. ZPALRV/1332. **B**, **C**, **E**–**H**. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **B**. ZPAL RV/1184 (left reversed). **C**. Reconstruction of the bone. **E**. Proximal end ZPAL RV/1189 (left reversed). **F**. Proximal part ZPAL RV/1188. **H**. ZPALRV/940. **D**. *Euparkeria capensis* Broom, 1913 (left reversed), drawing after Ewer (1965, fig. 31). **I**. *Dorosuchus neoetus* Sennikov, 1989 PIN/1579/61, in distal ventral view. All but I in proximal ventral view. B, E–H, stereo-pairs.

distal end is roughly quadrangular in transverse section. The presence of an intercondylar fossa (Fig. 13G) on the dorsal side, and of the popliteal space on the ventral side (Fig. 13F) make both sides of the distal end slightly concave. The posterior (or lateral) surface bears a short furrow extending along its ventral border.

On the ventral surface, a triangular sculptured region, extending over a proximal one fifth the length of the shaft, and tapering distally (Fig. 13F), corresponds to the intertrochanteric fossa, the site of attachment of puboischiofemoralis externus (Romer 1922, 1923). The fourth trochanter lies at the apex of a sharp V-shaped crest, widely open anteriorly and pointing towards the tail. It is weakly expressed, and lies at no more than the proximal 1/4 of the femur length, slightly more proximal than in *Euparkeria,* and slightly more distal than in *Dorosuchus*. Anteromedial to the trochanter, a subcircular scar probably marks an attachment point of a part of the puboischiofemoralis muscle. The adductor crest extends diagonally along the ventral side of the shaft, beginning from the fourth trochanter and fading out at the ectepicondyle. Distally the adductor crest is confluent with a sharp crest that follows the lateral border of the bone. Proximally, at about one third the length of the shaft, this border produces an eminence (Figs 12B, 13F, G) which gives the bone a slightly humped lateral profile. In *Erythrosuchus*, the ilofemoralis muscle was inserted proximal of this eminence and the

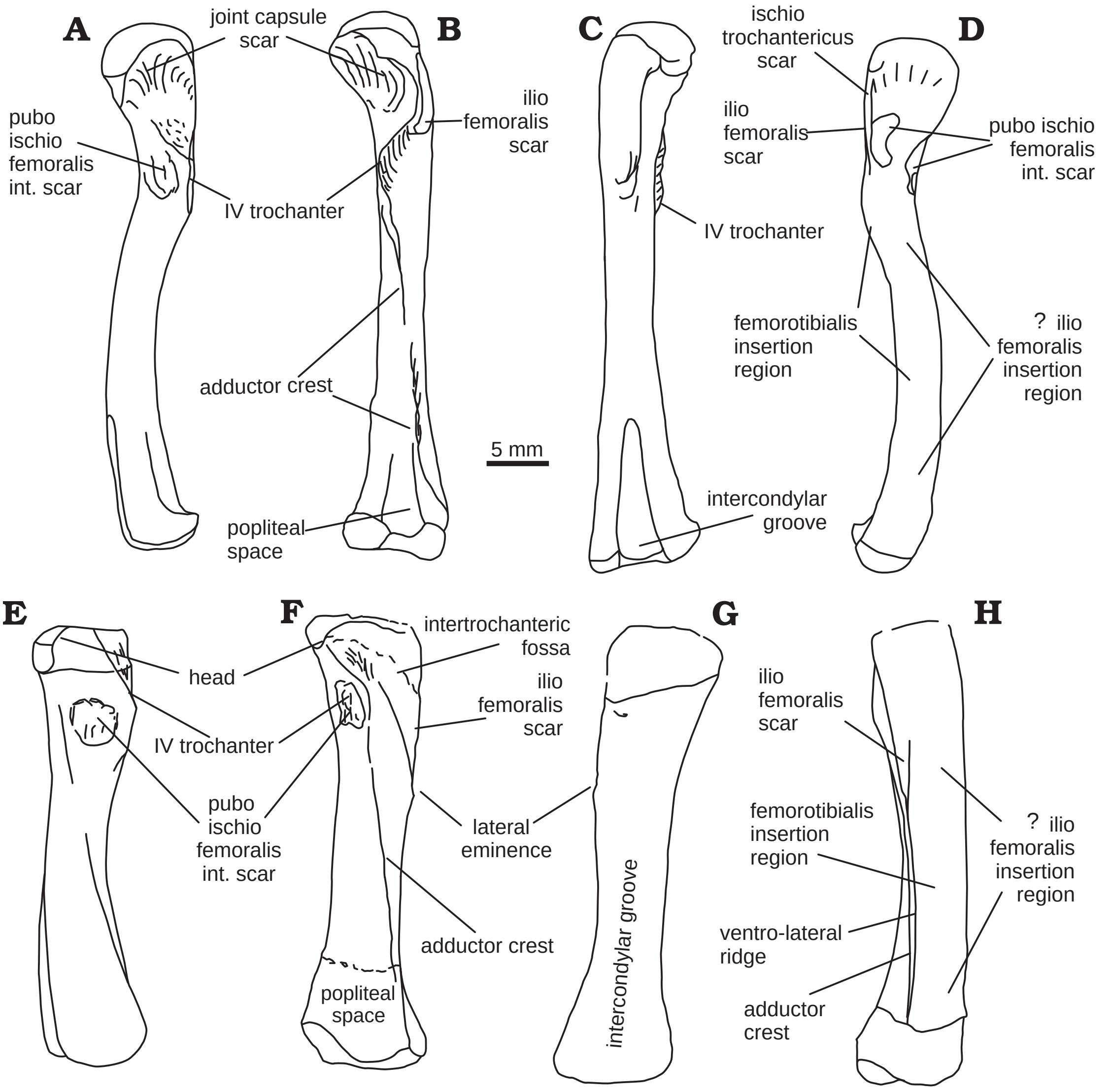

Fig. 13. **A**–**D**. Extant juvenile *Alligator* sp. Right femur ZPAL RI/74. Muscle scars according to Romer (1923). **E**–**H**. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. Right femur. Distal medial (A, E), distal ventral (B, F), distal dorsal (C, G), and distal lateral (D, H) views.

femoro-tibialis muscle distal of it (Gower 2003, fig. 34). The dorsal surface of the femur in *Osmolskina* (Fig. 13G) is quite smooth.

The *Osmolskina* femora range in size. The modal length is estimated at about 40 mm, but fragments of larger individuals show that the bone may have attained twice this length. As estimated for one of the more complete bones, ZPAL RV/940, the length to width index is about 4.5 for both proximal and distal ends. In 26 specimens, the width of the proximal end measured directly above the fourth trochanter, is mostly between 9 and 11 mm. Some much larger specimens reach 15–19 mm in width (Fig. 12A, G). They are separated by a hiatus (Supplement 2H and Fig. 14) from the rest of the sample, and, on this basis, are relegated to Archosauriformes gen. indet., but they cannot be distinguished from the femora attributed to *O. czatkowicensis* on any morphological features.

The dorso-ventral flattening of the proximal part of the shaft is expressed by the ratio of the bi-lateral diameter to the dorso-ventral diameter, and is 1.4:1 in ZPAL RV/940 and 1.7:1 in one of the largest femora, ZPAL RV/1174. This either shows negative allometry (the flattening increasing in ontogeny) or systematic difference. According to Parrish (1986), the femora are markedly anteroposteriorly (= dorsoventrally) flattened in both ornithosuchids and rauisuchids while being more nearly circular in other archosauriforms. The width to height ratio is 1:1 in both the older and the younger *Crocodilus niloticus* (ZPAL RI/76 and 75 respectively) examined.

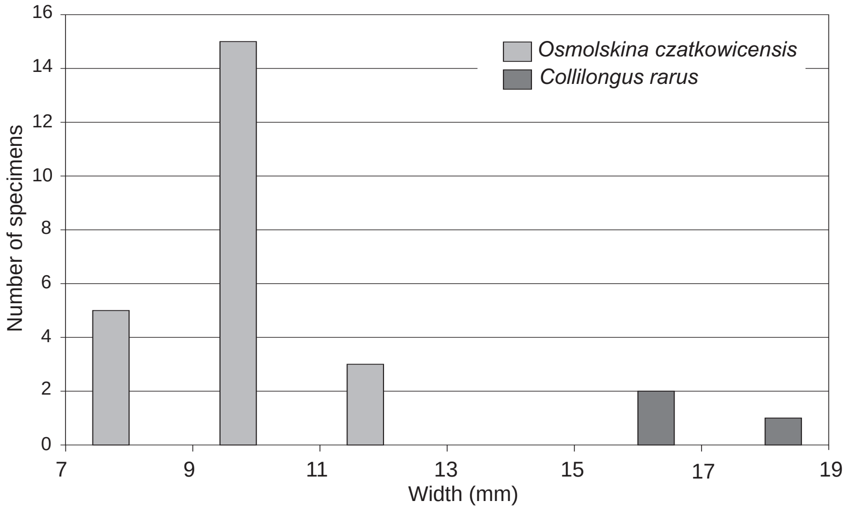

Fig. 14. Frequency distribution of femur width. Archosauriformes from the Early Triassic Czatkowice 1, Poland.

Tibia. — All the archosauriform tibia from Czatkowice 1 are simple long bones that are slightly expanded at both ends, especially proximally, the transverse section being a flattened oval rather than a circle. They are represented by several fairly well preserved but never complete specimens (Fig. 15A–C), and numerous fragments. The roughly estimated lengths suggest the same hiatus in the variability ranges of this bone as in the case of the femur. Moreover, the size differences combine with morphological differences that suggest the variablity has systematic significance.

The main morphotype, about 30 mm in length, and flattened dorso-ventrally, is considered to belong to *Osmolskina.* The shorter side of the *Osmolskina* tibia bears a distinct oval muscle scar probably left by the puboischiotibialis muscle. In lizards, the tendon of this muscle inserts on the medial wall of the tibia near the proximal end (Romer 1942). The side bearing this scar is thus considered medial, and the flattening of the bone is correspondingly dorso-ventral. A similar scar that appears (although not described) on the medial side of the tibia in *Euparkeria* (Ewer 1965, fig. 32) and in *Erythrosuchus* (Gower 2003, fig. 35B), is considered homologous. One of the larger surfaces of the shaft, which is slightly convex, is considered dorsal. The opposite side, which is slightly concave, is ventral. A vertical crest extending from the proximal end of ZPAL RV/1221 (Fig. 15B_3, B_4) for a short distance down the ventrolateral side of the shaft probably denotes the fibular contact. The proximal and distal articular surfaces are never preserved. In *Euparkeria* (Ewer 1965, fig. 32) the proximal end of the tibia bears a rough triangular field tapering distally and laterally which may reflect the attachment of the common tendon of the knee joint extensors (extensor tibialis, ambiens and femoro-tibialis), and is thus a substitute of the cnemial crest. No such field occurs in *Osmolskina.*

Fibula. — The fibula has been reconstructed (Fig. 16E) from two sets of fragments considered as proximal and distal parts (Fig. 16A, C respectively). They come from the same sample, correspond in size and state of preservation, and are probably complementary to each other. The bone is very narrow, the shaft being flat on one side, considered ventral, and slightly convex in transverse section on the opposite side. The flat wall (Fig. 16E_1, E_3) is bordered by faint crests. The flattening continues over both parts of the fibula thus providing a basis for reconstruction. The anterior trochanter (*i.e.*, iliofibularis trochanter of Parrish 1986) protrudes from the shaft at around one third its length. It makes the bone crooked. As reconstructed, the fibula is slightly bowed medially and the distal end is enlarged.

According to Sereno (1991), the anterior trochanter of the fibula in basal archosauriforms is represented by an oval rugosity or a low vertical crest, in contrast to the strongly protruding trochanter in most basal crurotarsians (phytosaurs, ornithosuchids, aetosaurs, rauisuchids and primitive crocodylomorphs) that makes the fibula crooked in shape. As illustrated by Sereno (1991, fig. 21), the shape of the fibula in *Euparkeria* is speculative, because it is only preserved distally. Ewer (1965) did not comment on this feature. Reconstructed from Czatkowice 1 material, the fibula corresponds in length to the tibiae of *Osmolskina czatkowicensis,* and is tentatively assigned to this species. However its crooked appearance resembles basal crurotarsians rather than *Proterosuchus* (Cruickshank 1972) and most erythrosuchids (Charig and Sues

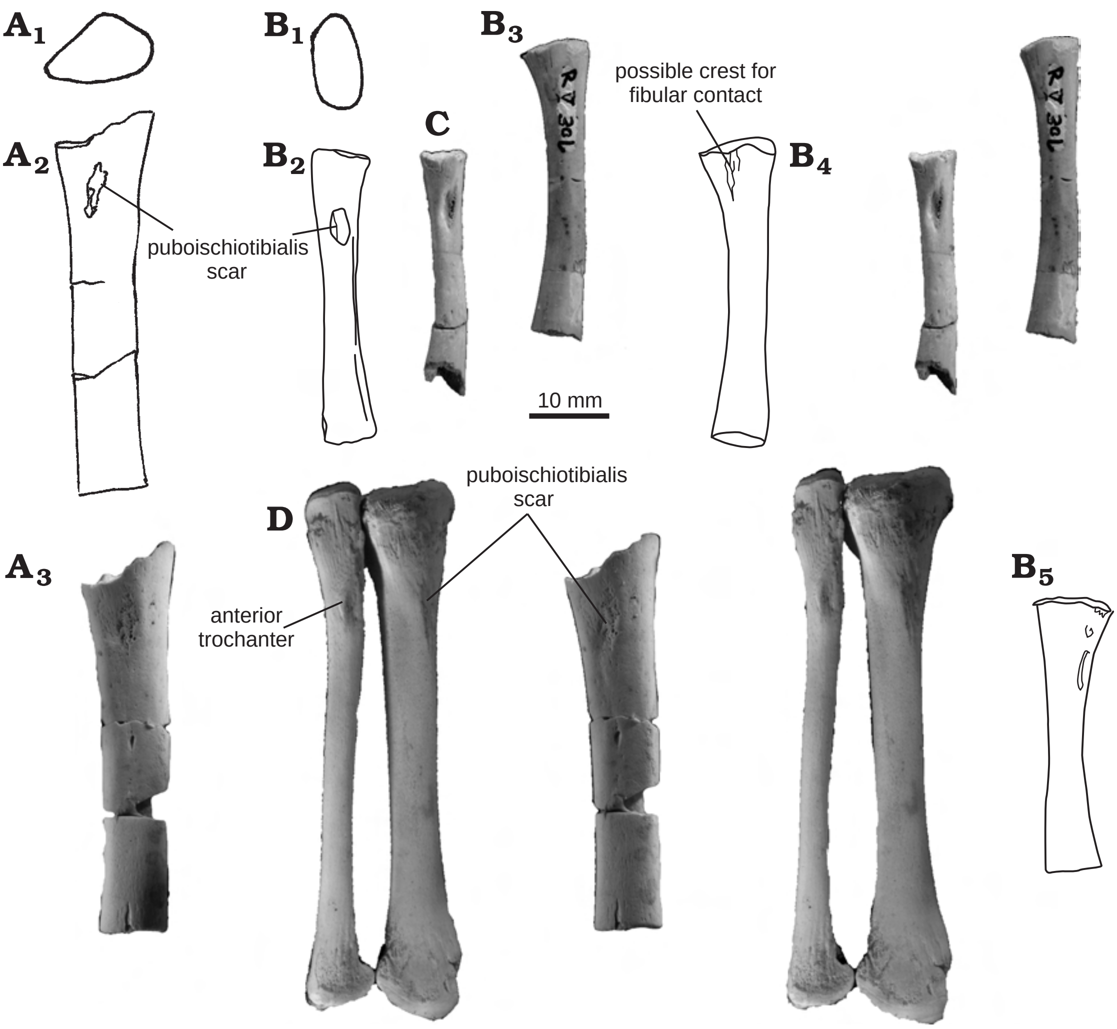

Fig. 15. **A**. Archosauriformes gen. indet. 2003, Early Triassic of Czatkowice 1, Poland. Tibia ZPAL RV/1175, in ?medial view (A_2, A_3). The outline of the proximal end with medial side down (A_1). **B**, **C**. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **B**. Right tibia ZPAL RV/1221, in medial (B_2) view; with the outline of the proximal end with medial side down (B_1); the same tibia in lateral (B_3, B_4) and dorsal (B_5) views. **C**. Left tibia ZPAL RV/1222, in medial view. **D**. Extant crocodile *Crocodilus niloticus*, crus ZPAL RI/76. A_3, B_3, C, D, stereo-pairs.

1976) as far as they are known. As reconstructed, the fibula suggests either that the crooked shape appeared in basal archosauriforms, or that it does not belong to *Osmolskina* and demonstrates the presence of the crurotarsians in the material.

Tarsus. — Among the very small disarticulated tarsal and carpal elements in the Czatkowice 1 material, the largest, most frequent, and least variable in size are considered to belong to *Osmolskina czatkowicensis*. They usually look like small bodies of spongiosa mostly lacking a surface of finished bone. If preserved at all, the joint facets are damaged all around the margins. However, a few more complete specimens (an astragalus: ZPAL RV/811, a calcaneum ZPAL RV/810, and a fourth distal tarsal ZPAL RV/812) permit a more detailed description. Other than the fourth, the distal tarsals have not been identified.

The astragalus is an ovoid body bearing two slightly concave proximal facets for the fibula and tibia, respectively, on the proximolateral and proximomedial sides. They are approximately perpendicular to each other and separated by a nonarticular surface. This surface is slightly concave in its transverse axis. It extends from the dorsal surface to the ventral one, turning distally into the ventral groove system (Cruickshank 1978, 1979; Sereno 1991; Gower 1996), and running down the ventral surface to end at the distolateral corner in a deep pit (referred to as the "perforating foramen component of the astragalar groove system" by Gower 1996). The exact shape of the ventral groove system is difficult to assess, because of poor preservation of the surface.

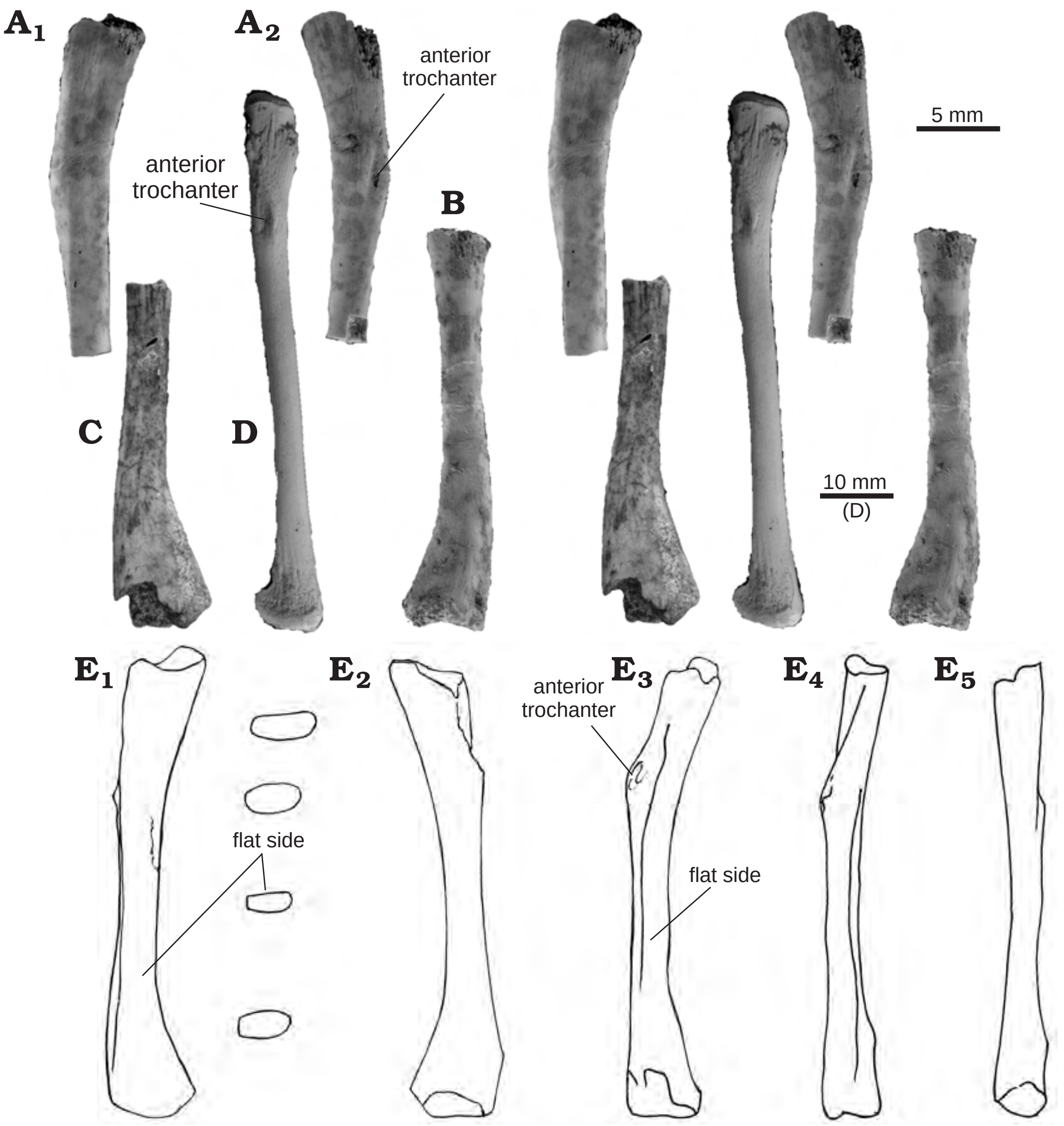

Fig. 16. **A**, **B**, **C**, **E**. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. Possible left fibula. **A**. Proximal part ZPAL RV/1225. **B**. Almost complete shaft ZPAL RV/1247 with the distal end. **C**. Distal part ZPAL RV/1182. **E**. Reconstruction of the whole bone. **D**. *Crocodilus niloticus*, left fibula ZPAL RI/76. Ventral (A_1, C), dorsal (A_2, B, D, E_2) views; E_1, ventral view and transverse sections on different levels (ventral side upwards); ventro-lateral (E_3), lateral (E_4), and medial (E_5) views. A–D, stereo-pairs.

In the lateral half of the dorsal surface, finished bone is sometimes preserved in a slightly concave and pitted field (Fig. 17A) (dorsal hollow of Gower 1996). The tibial facet is a transversely widened oval (Fig. 17) whereas the fibular facet is subcircular with the lateral part of the outline slightly concave (Fig. 17F). Distally the fibular facet passes along the lateral side of the bone into a calcaneal facet Fig. 17B) of approximately the same diameter. The calcaneal facet faces distolaterally. It is incised posteriorly by the distolateral branch of the ventral groove mentioned above (Fig. 17B). Apart from this, there is no indication of any subdivision of this facet into dorsal and ventral parts as recognized in *Proterosuchus* (Sereno 1991, fig. 3D). Neither is there any astragalo-calcaneal canal. Obviously, the pit of the ventral groove is a rudiment of this canal. The calcaneal facet is saddle-shaped and slightly convex (Fig. 17B), along the antero-posterior axis (because ventrally it turns toward the perforating foramen of the ventral groove system). The posterior incision probably received the ventromedial process of the calcaneum (Fig. $18B_3$, E), the joint allowing a slight mobility in two planes.

The distal facets of both astragalus and calcaneum contribute to the articular surface for distal tarsal four (Figs 17J, $18B_3$, B_2), as they do in *Erythrosuchus* and *Euparkeria* (Gower 1996). If properly identified here, the facet for distal tarsal four covers the medial one third of the distal surface of the astragalus. It is almost flat

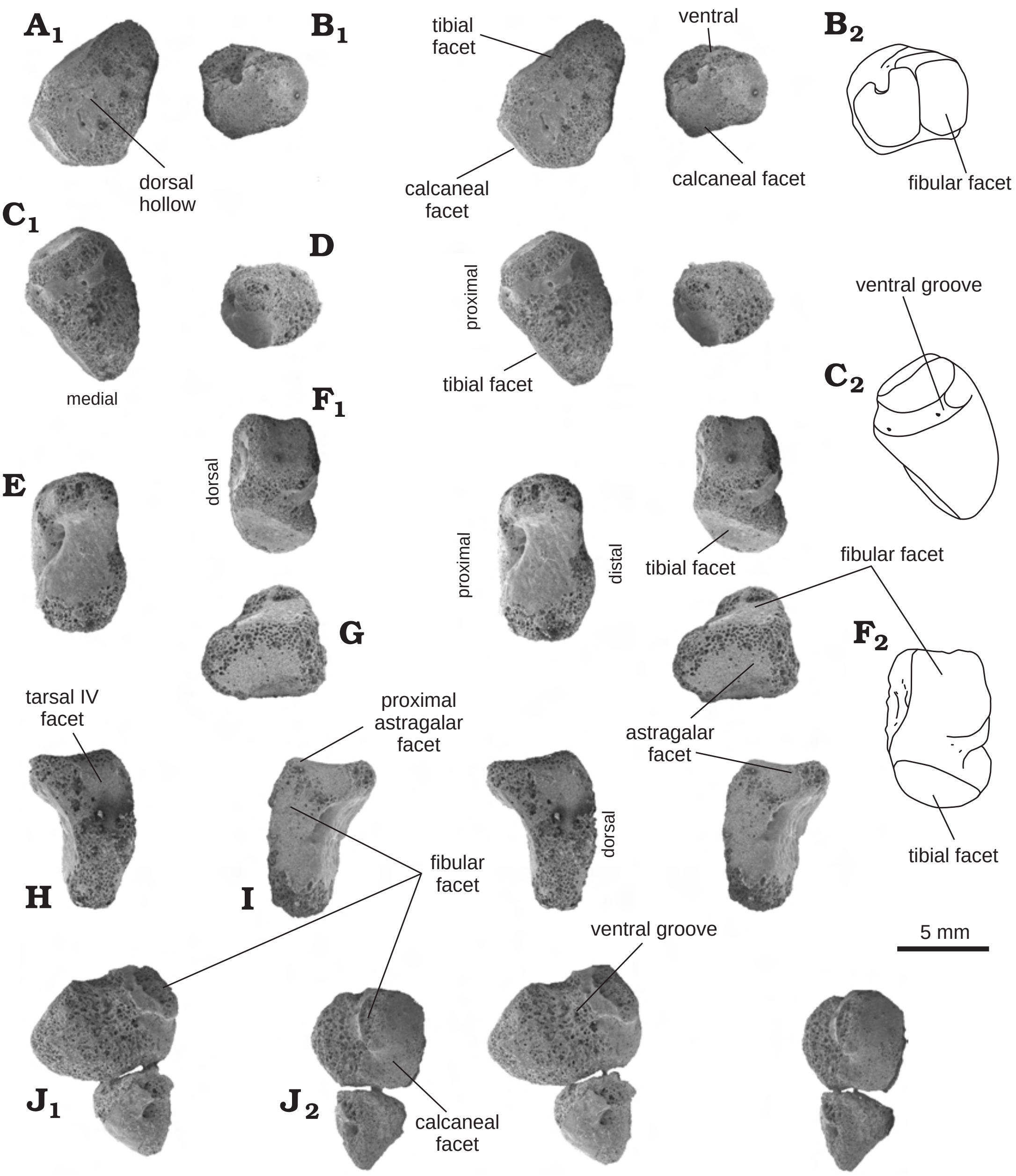

Fig. 17. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A**–**C**, **F**. Right astragalus ZPAL RV/811. **D**. ?Right distal tarsal IV ZPAL RV/812. **E**. Left calcaneum ZPAL RV/810. **G–I**. Left calcaneum ZPAL RV/810. **J**. Right astragalus ZPAL RV/811 combined with ?right distal tarsal IV ZPAL RV/812. Dorsal (A), lateral (B$_1$, B$_2$, J$_2$), ventral (C, E, J$_1$), proximal (D, I), proximolateral (F), medial (G), and distal (H) views. All but B$_2$, C$_2$, F$_2$ SEM stereo-pairs; B$_2$, C$_2$, F$_2$ corresponding schemes.

and subtriangular in outline. The remaining two thirds of the distal astragalus form an ovoid surface that is distally convex. This surface extends onto the ventral side. Faint subdivisions probably mark the separation of facets for tarsal III and metatarsals II and I, as in *Euparkeria* (Fig. 19C).

The calcaneum (Fig. 17E, G–I) is a wedge-shaped bone with an almost flat dorsal face and a concave ventral face; the medial portion of the bone protrudes ventrad (corresponding to medial posterior pyramid of Cruickshank,1979 and Cruickshank and Benton 1985. The best preserved specimen, ZPAL RV/810, is largely surfaced with compacta. The orientation of the bone is based on comparative data from Sereno (1991) and Gower (1996). The ventral surface of the calcaneum bears a step-like groove directly below the proximal edge of the bone (Fig. 17E, I). This groove is perforated by a large vascular foramen. The same structure in *Erythrosuchus africanus* is referred to as a proximoventral groove (Gower 1996; p. 354). According to the

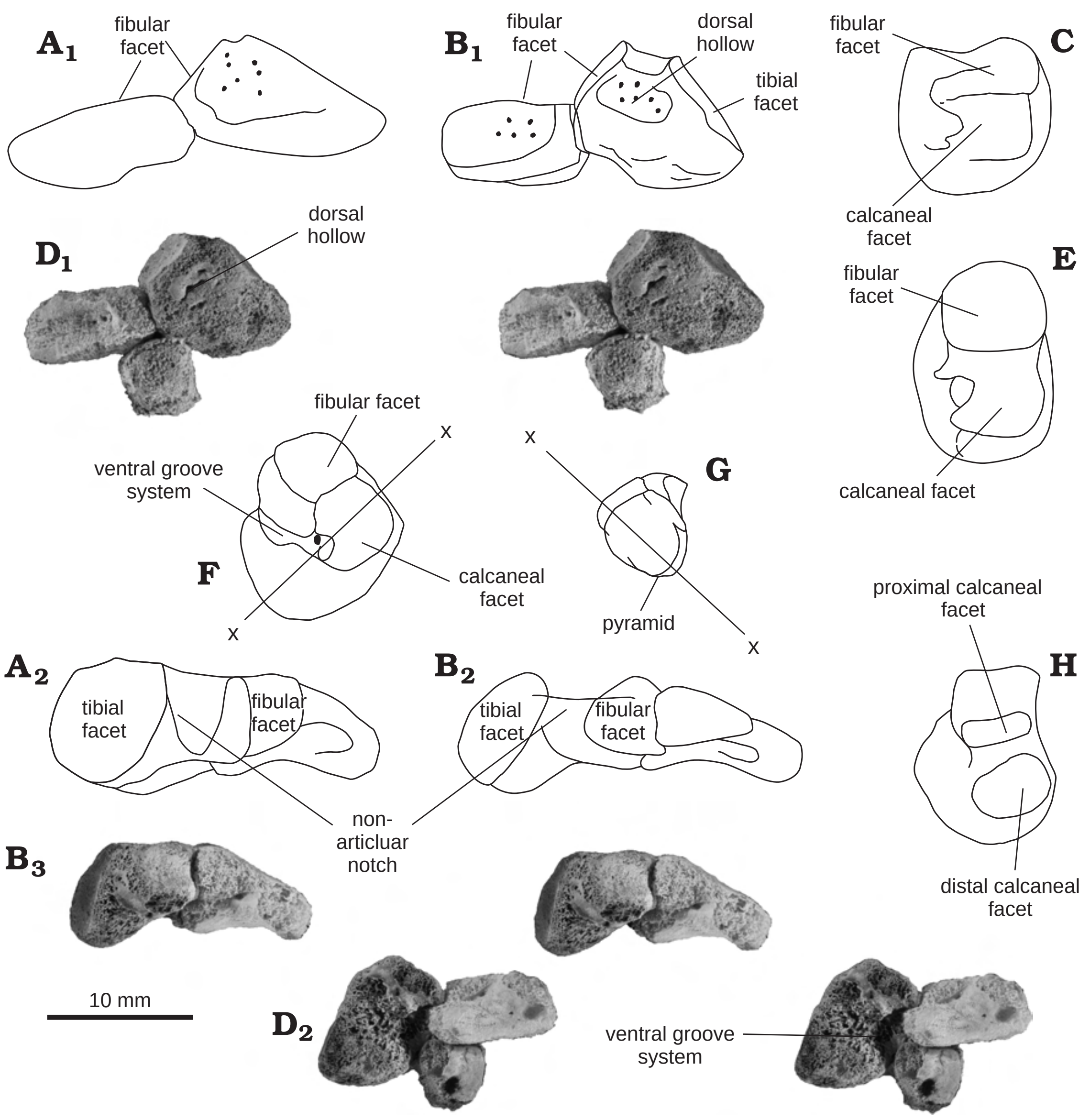

Fig. 18. **A**, **C**. *Euparkeria capensis* Broom, 1913. Right astragalus and calcaneum. **B**, **D**–**G**. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **B**. Right astragalus and calcaneum. **D**. Right astragalus ZPAL RV/811 combined with calcaneum ZPAL RV/1253 and distal tarsal IV ZPAL RV/812. **E**, **F**. Right astragalus. **G**. Right calcaneum. **H**. *Proterosuchus vanhoepeni* (Haughton, 1924), right astragalus. A_1, A_2, C, H after Sereno (1991), but A_1 slightly changed. Dorsal (A_1, B_1, D_1), proximal (A_2, B_2), ventral (D_2), directly lateral (C, E, H), distolateral (F), and medial (G) views. B_3 D_1, D_2, SEM stereo-pairs.

latter author this groove, which is also present in other erythrosuchids and in *Proterosuchus,* probably housed soft tissue binding the fibula to the calcaneum on the plantar surface of the foot. The dorsal part of the bone is covered by a slightly concave surface of compacta perforated by small nutrient canals.

The proximal surface of the calcaneum bears a flat, subtriangular facet that would have combined with the fibular facet of the astragalus to receive the fibula. The fibular facet is extended laterally and then ventrally (Figs 17I, 18B_2, B_3). The extension is covered with a sheet of compacta, and is medially separated by the proximoventral groove mentioned above. The groove extends along and below the posterolateral border of the facet.

The astragalar facet on the calcaneum (Fig. 17G, I) is subrectangular and slightly saddle-shaped. It is weakly convex in the shorter proximodistal axis and slightly concave along the subhorizontal axis (Fig. 18F: X-X axis). It extends onto the ventrally protruding part of the calcaneum (Fig. 17G) to articulate with the incision on the corresponding calcaneal facet of the astragalus, along the X-X axis (Fig. 18F). This articulation results in the fibular facet of the calcaneum being turned a little posteroventrally from the plane of the astragalus. There would have been a limited mobility at this joint in the horizontal plane, around a vertical axis, and probably some in a vertical plane, but no subdivision of the tarsus into crus-connected and pes-connected units is evident.

The lateral portion of the calcaneum is featureless. The tuber is directed laterally and only slightly ventrad. The lateral half of the distal surface (Fig. $18B_3$) lacks compacta whereas the medial half bears two facets. Of these, a narrow semilunar facet situated on the medial border of the bone is probably just an extension of the astragalar facet, and suggests a slight vertical mobility within the astragalo-calcaneal joint, as does a similar extension on the proximal side of the astragalar facet. A large flat surface lateral to the semilunar facet would have combined with the facet on the astragalus to receive distal tarsal four (Fig. 17H).

The width of calcaneum (8 specimens) varies from 7–13 mm, but the majority (7 specimens) cluster between 7–9 mm (Appendix 1). Again, as in the case of long bones, there is a hiatus within the size range, but the largest specimen (ZPAL RV/1281) does not differ from the remaining specimens in morphology.

Only one specimen of distal tarsal four (DT4), ZPAL RV/812, is sufficiently well preserved for description (Figs 18D, J, 19C). It is a pyramidal bone with one subtriangular flat facet covered with compacta that matches the distal facet of the best preserved astragalus, ZPAL RV/811. If this is a correct interpretation, then the adjacent slightly convex surface of the pyramid is for the calcaneum, whereas the base of the pyramid, covered with compacta and perforated by one deep pit, should be oriented ventrally. This would match the distoventral surface of the DT4 in *Erythrosuchus* as illustrated by Gower (1996, fig. 4B). Articulated in this way, DT4 leaves medial and lateral spaces that must have received DT3 and Metatarsal V respectively.

Comments: The reconstruction of the tarsus in *Osmolskina czatkowicensis* is broadly based on Cruickshank (1979) and Gower (1996), the latter describing the erythrosuchid ankle, the minute details of which provide a basis for homology. Only one calcaneum, ZPAL RV/1281, definitely exceeds the normal size range of the tarsal elements (Appendix 1), thus supporting the idea of sample heterogeneity, but the majority of tarsal bones are more or less uniform in size. The close match in size and shape of the respective articular facets (ZPAL RV/811 and 1253), albeit in different individuals, allows the reconstruction (Figs 18J and 19C).

According to this reconstruction, the overall structure of *Osmolskina* tarsus, including the relative widths of the distal articular surfaces of the calcaneum and astragalus (Sereno 1991) and lateral direction of the tuber calcanei, resembles that of other basal grade archosauriforms (Parrish 1993; Juul 1994). *Osmolskina* shares this structure with *Euparkeria* (Fig. 19A, C), proterochampsids (Cruickshank 1979), and erythrosuchids (Gower 1996), while differing from the latter mainly in size dependent details. It differs from that of *Proterosuchus* in having a relatively smaller calcaneum and in the absence of an astragalocalcaneal canal, the plesiomorphic features retained by *Proterosuchus*, and lost in all the remaining archosauriforms.

In *Osmolskina* the relative width of the astragalus to the calcaneum lies at roughly 1.12 (9 mm to 8 mm respectively), and 1.2 in *Euparkeria* (according to Ewer 1965, fig. 32), the difference being negligible. The astragalus and calcaneum are almost level distally, except for the distal concavity for distal tarsal four, but proximally, the astragalus protrudes strongly to contact the crus obliquely rather than terminally. The distal ends of the crural bones are never complete, but were probably also oblique to match the tarsus, as they are in crocodiles (Fig. 15D). The astragalus of *Osmolskina* shows no evidence of a depression at the medial end of the tibial facet (a feature mentioned by Gower 1996, p. 365, point 4).

The calcaneal facet of the astragalus in *Osmolskina* is quite similar to that illustrated for *Euparkeria* (Sereno 1991, fig. 4D), with a shallow pit incising the posterior margin (in the distolateral branch of the ventral groove system). In both genera, the shape of the ventromedial calcaneal protrusion that was received into a corresponding notch on the astragalus (Fig. 18C, E) is similar. This, in turn, suggests a similar, limited, range of mobility.

In *Osmolskina* the tibial and fibular facets of the astragalus are well separated from each other by the non-articular notch. The *Euparkeria* pes is represented by three articulated specimens; the unnumbered specimen of Broom (Ewer 1965, see also Broom 1913, pl. LXXV), SAM 6049, and GPTI 1681/1 (previously SAM 7698). According to Gower (1996, p. 365), the notch does not separate the fibular and tibial facets in *Euparkeria*. However, the stereophotographs of SAM 6049 (Ewer 1965) and Broom's (1913) unnumbered specimen (Ewer 1965, fig. 30 and Fig. 19C herein) as well as personal observations by one of us (MBB) on GPIT 1681/1, all suggest the facets may in fact be separated in the South African taxon.

In Broom's specimen (Fig. 19C), the proximal tarsals seem to be twisted counter-clockwise. We consider that the proximal tarsals turned as a single unit, instead of being disarticulated (contrary to Ewer 1965).

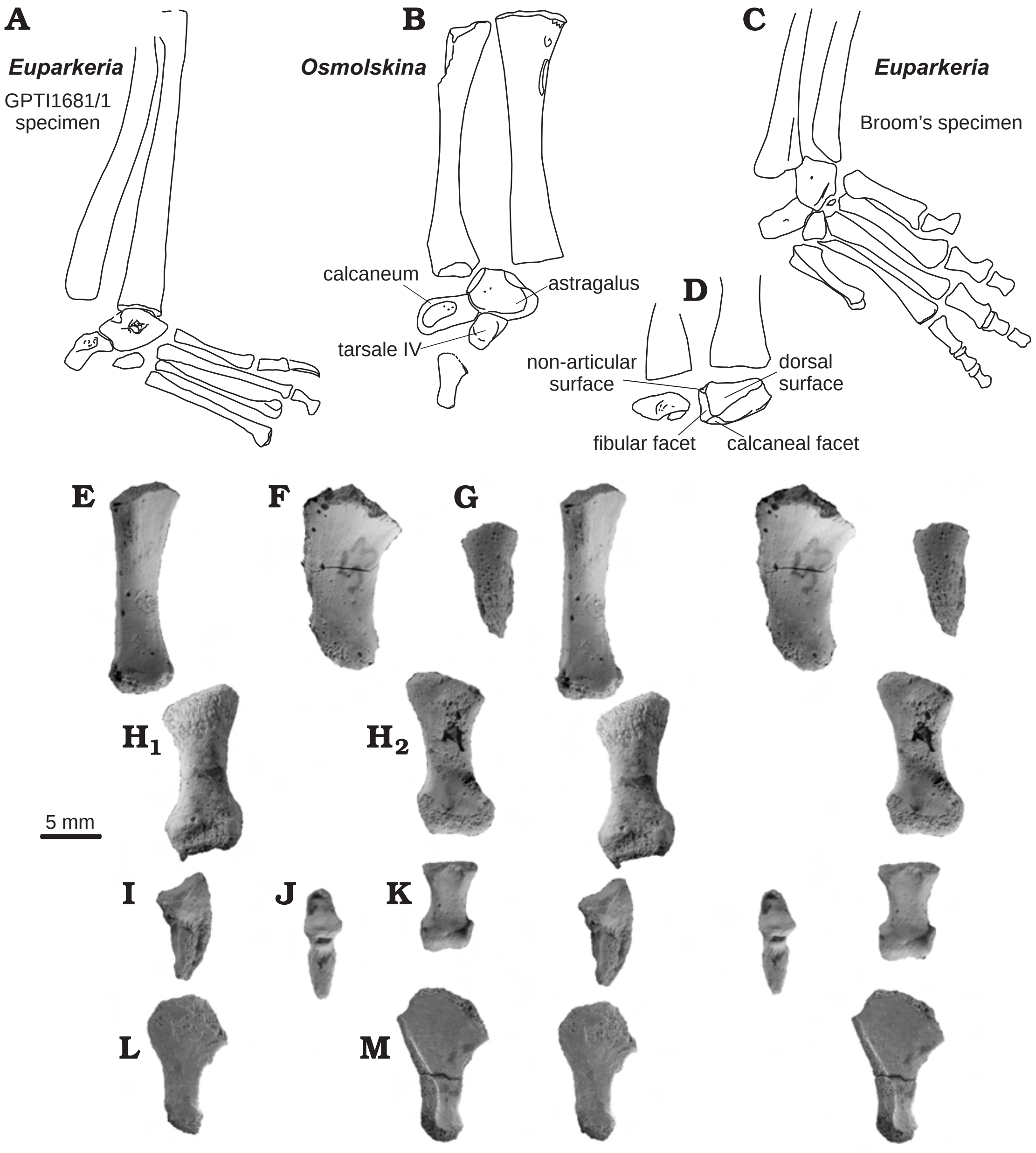

Fig.19. **A**, **C**, **D**. *Euparkeria capensis* Broom, 1913. **A**. Right crus and pes after GPIT 1681/1 (MBB's sketch drawing). **C**. Right crus and pes of Broom's (1913) specimen (after Ewer 1965, fig. 30). **D**. Distal part of right crus and partial tarsus of SAM 6049 (after Ewer 1965, fig. 32). **B**, **G**–**M**. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **B**. Reconstruction of the right crus, partial tarsus and Vth metatarsal. **G**. Ungual ZPAL RV/1244. **H**. Metatarsal ?I ZPAL RV/1238. **I**. Ungual ZPAL RV/1241. **J**. Ungual ZPAL RV/1242. **K**. A phalanx ZPAL RV/1243. **L**. Vth metatarsal V ZPAL RV/1247. **M**. Vth metatarsal ZPAL RV/1246. **E**, **F**. Archosauriformes gen. indet., Early Triassic of Czatkowice 1, Poland. **E**. Right metatarsal III or IV ZPAL RV/1236. **F**. Vth metatarsal ZPAL RV/1237. Dorsal (A–E, G, H_1), ventral (H_2, J, K), and side (I, L, M) views. All but A–D stereo-pairs.

Based on stereo-photographs of SAM 6049 (Ewer 1965, fig. 32), our interpretation (Fig. 18D) agrees with that of Gower (1996, p. 365) (in that the facet marked with a dot (Ewer l.c.) is for the calcaneum, and the one facing to the left is for the fibula) with one difference: what is a blunt proximo-lateral corner of the astragalus in Ewer's illustration is, in our opinion, the non-articular surface that separates fibular and tibial facets. The absence of this surface would be a significant difference between these otherwise similar genera, because its presence in *Osmolskina* is quite evident.

In the astragalus of *Osmolskina* (Fig. 18E), the fibular facet is broadly exposed in lateral view while being barely visible in *Euparkeria* (Fig. 18C) according to Sereno (1991, fig. 18). This suggests the astragalus is shallower in *Euparkeria* than in *Osmolskina*, and much less proximally protuberant. However, both SAM

6049 and Broom's unnumbered specimen (Fig. 19C) demonstrate that *Euparkeria* is quite similar to *Osmolskina* in the angulation of the crural facets and the degree of proximal protrusion of the astragalus (see also Gower 1996, p. 365).

In summary, the *Osmolskina* tarsus structure seems to be essentially the same as that in *Euparkeria*.

Metapodia and phalanges. — Within the small sample of more or less complete metapodia, five bones are recognized as metatarsals, and only one as a metacarpal. The metatarsals are longer and stouter than the metacarpal, but the size range is unknown and some overlap between them is possible. Specimen ZPAL RV/1236 (Fig. 19E), considered a possible right metatarsal III, is 18 mm long and about 3.5 mm in minimum width. It is thus longer than estimated on the basis of skull to metapodia length proportions (Appendix 1). The proximal end is oval with a dorso-laterally directed axis, probably to overlap metatarsal IV.

Two specimens, ZPAL RV/1238 (Fig. 19H) and ZPAL RV/1239, are considered right metatarsals I. Both are stout bones about 11mm in length and 3.7 in minimum width. The proximal articular facets are flat and triangular, the apex of the triangle directed dorsad. The putative lateral margin faces dorsomedially, perhaps to allow an overlap by metatarsal II. The distal end is markedly enlarged bilaterally. The medial condyle is more prominent, the end appearing slightly asymmetrical in dorsal aspect. Collateral ligament pits are present on each side wall. The distal articular facet extends slightly further ventrally than dorsally, but the latter surface bears a concavity, referred to as an extensor depression (in the manus Sereno 1993). The long axis of the bone is is slightly ventrally concave, especially in the distal part.

Among the metatarsals V of the Czatkowice 1 material, the largest specimens are considered archosauriform. Two specimens, ZPAL RV/1346 and 1347 (Fig. 19), match the *O. czatkowicensis* tarsus in terms of size (Fig. 19C), and are tentatively considered to belong to this species. A third, ZPAL RV/1237, is similar in morphology but about 25% longer and much stouter may be not conspecific. In accordance with Robinson's (1975, p. 464) terminology, the most probable metatarsal V of *Osmolskina* is both hooked and inflected. The hooking (*i.e.* medial angulation of the proximal end amounting to 90° in lizards) is about 70° in *Osmolskina*. The long axis of the shaft is rather straight in the transverse plane with both sides symmetrically concave. The inflexion (*i.e.* plantar-dorsal angulation of the long axis, Robinson 1975) is expressed by a ventral convexity of the bone in the long axis (and a corresponding dorsal concavity). The inflection increases the lever arm of the fifth digit flexors and is functionally similar to a convexity of the whole plantar side of the foot in lower tetrapods that serves as a pulley for the foot flexors (Schaeffer 1941; Robinson 1975). The lateral plantar tubercle that forms the protruding tip of the inflexion in lizards (and a partial substitute for the tuber calcanei of mammals, Robinson 1975) is represented in *Osmolskina* by an elongate tuberosity that borders the lateral side of the shaft. This served for the insertion of the femorotibial head of the gastrocnemius muscle, and probably for the fifth digit abductor and some parts of the peroneus muscle. There is no medial tubercle but the articular facet for DT4 (Fig. 20L) protrudes toward the plantar side, in contrast to lizards where it is angled dorsally relative to the proximal part of the metatarsal. The outer process of metatarsal V in *Osmolskina* is less protuberant than in lizards, but still developed.

Some shorter, flattened metapodia that are slightly bowed to one side (*e.g.*, ZPAL RV/1243; Fig. 19H) are considered metacarpal I or V. The outline of the proximal end is dorsoventrally depressed and ellipsoid, as in *Varanus niloticus* (ZPAL RI/31) and *Euparkeria* (Ewer 1965, fig. 10I). In *Varanus*, metacarpals I and V are slightly bowed towards the axis of the hand.

Manual and pedal phalanges are strongly waisted directly above their bilaterally expanded distal ends. As in metapodia, these ends bear deep collateral ligament pits on each side. The proximal surface is concave, but varies in its depth and symmetry, asymmetric facets probably belonging to outer digits. In some specimens the proximal surface is slightly subdivided. Dorsally, it is flanked by a protrusion (for the common digital extensor) that makes the articular surface deeper and subtriangular. In some specimens the whole surface extends ventrally to assure greater dorsiflexion.

The largest unguals of the Czatkowice 1 material range in size but are consistent in morphology. Most of them might belong to *Osmolskina czatkowicensis*. They are generally less bilaterally flattened, and less acute (Fig. 19G, J) than the small unguals of the Czatkowice 1 material (Fig. 19I), but vary in the degree of flattening, the depth of concavity and its symmetry. They are readily distinguishable by their porous surface texture, suggesting the presence of a particularly strong germinative layer of the keratinized claw. Extending along the distal 2/3 of both sides, deep furrows fastened the claw to the ungual. Relatively narrower unguals, probably belonging to side digits have a slightly asymmetrical proximal facet subdivided by a longitudinal ridge and bordered by a proximally protruding dorsal process for the common digital extensor tendon.

Family uncertain

Genus *Collilongus* gen. n.

Type species: *Collilongus rarus* gen. et sp. n.
Derivation of the name: From Latin, *collum* — neck, *longus* — long.

Diagnosis. — As for the species.

Collilongus rarus gen. et sp. n.

Holotype: Cervical vertebra ZPAL RV/580.
Type horizon: Early Olenekian.
Type locality: Czatkowice 1, southern Poland.
Derivation of the specific name: From Latin, *rarus* — rare in Czatkowice 1 material.

Material. — Four cervicals: ZPAL RV/579, 580, 581, 596; ?four dorsals: ZPAL RV/584, 585, 588, 694; one sacral ZPAL RV/1369; and twelve caudals: ZPAL RV/583, 594, 661, 662, 663, 1362, 1363, 1364, 1365, 1366, 1367, 1368.

Measurements. — Appendix 1, Supplement 1.

Diagnosis. — A small archosauriform. Cervical centra 12–13 mm in adult length, smaller than in any other known archosauriforms except euparkeriids. From known euparkeriids it differs in having more elongate and cylindrical cervical centra, and costal articulations barely protruding from the body of the centrum, while resembling the East European rauisuchids *Tsylmosaurus*, *Vytshegdosuchus*, and *Dongusuchus* except in smaller size. Weak development of ventral crests makes the vertebrae most similar to those of *Tsylmosuchus*, but posteroventral obliquity of the centrum is less. In cervicals the centrum length to posterior depth index is about 2.07 except at the transition between cervical and dorsal series where it drops to 1.8. In caudals it ranges from 1.9 to 3.7 and increases down the tail.

Range. — Olenekian.

VERTEBRAL COLUMN

The atlas/axis complex. — The atlas/axis complex has not been identified except for an isolated axis spine ZPAL RV/587 (Fig. 5A) that is lower and more elongate than that of *Osmolskina*.

Postaxial cervicals. — The postaxial cervical centra are elongate cylinder-shaped and slightly amphiceolous (Fig. 20A, B, D, E, Supplement 1A). The ventral sagittal crest is absent. Cervical centra are not beveled. They slope at an angle of about 4–9° to an axis perpendicular to the articular surfaces, and there is no obvious gradation of this feature. The articular ends of the centra protrude ventrad. The diapophysis and parapophysis protrude only slightly from the body of the centrum and are quite close to its anterior border. The diapophysis is supported by a posteriorly extending crest (posterior diapophyseal lamina of Wilson 1999) that is much less ventrally concave than in *Osmolskina*. Below the crest, the lateral wall is not excavated. The posterior centroparapophyseal crest (Wilson 1999) is developed in anterior cerviacals.

The neural canal is subquadrangular in outline. The subhorizontal prezygapophyseal facets are more elongate than those of *Osmolskina* and converge slightly ventro-medially. Their lateral borders pass into sharp crests that converge posteriad to fuse at the base of the spine. Between them is a triangular, non-articular shelf with a concavity for the interspinal ligament at the base of the spine. Extending from the postzygapophyses, the crests, analogous to the anterior ones, produce a high, narrow, triangular concavity. The spine is always damaged, but specimen ZPAL RV/579 (Fig. 20A) shows it to be almost as high as the vertebra itself, with a straight anterior margin. It is supported by the posterior half of the arch. One problematic specimen, ZPAL RV/893 (Fig. 20M), that exceeds the size range of *Osmolskina* but is shorter than most *Collilongus* cervicals (ratio 1.8) might be a transition vertebra between the elongate cervical and much shorter dorsal vertebrae. Some morphological features, such as the more protuberant diapophyses, more ventrally concave posterocentrodiapophyseal lamina, and excavated ventrolateral centrum wall, might be, at least partly, centrum length dependent.

Dorsals. — The assignment of dorsal vertebrae to *Collilongus rarus* is based on large size, and is only tentative. ZPAL RV/584, 585, 588, and 663, exceed the observed size range of *O. czatkowicensis* (Supplement 1B). The dorsal centra are slightly more bilaterally flattened than the cervical centra. They have a faint

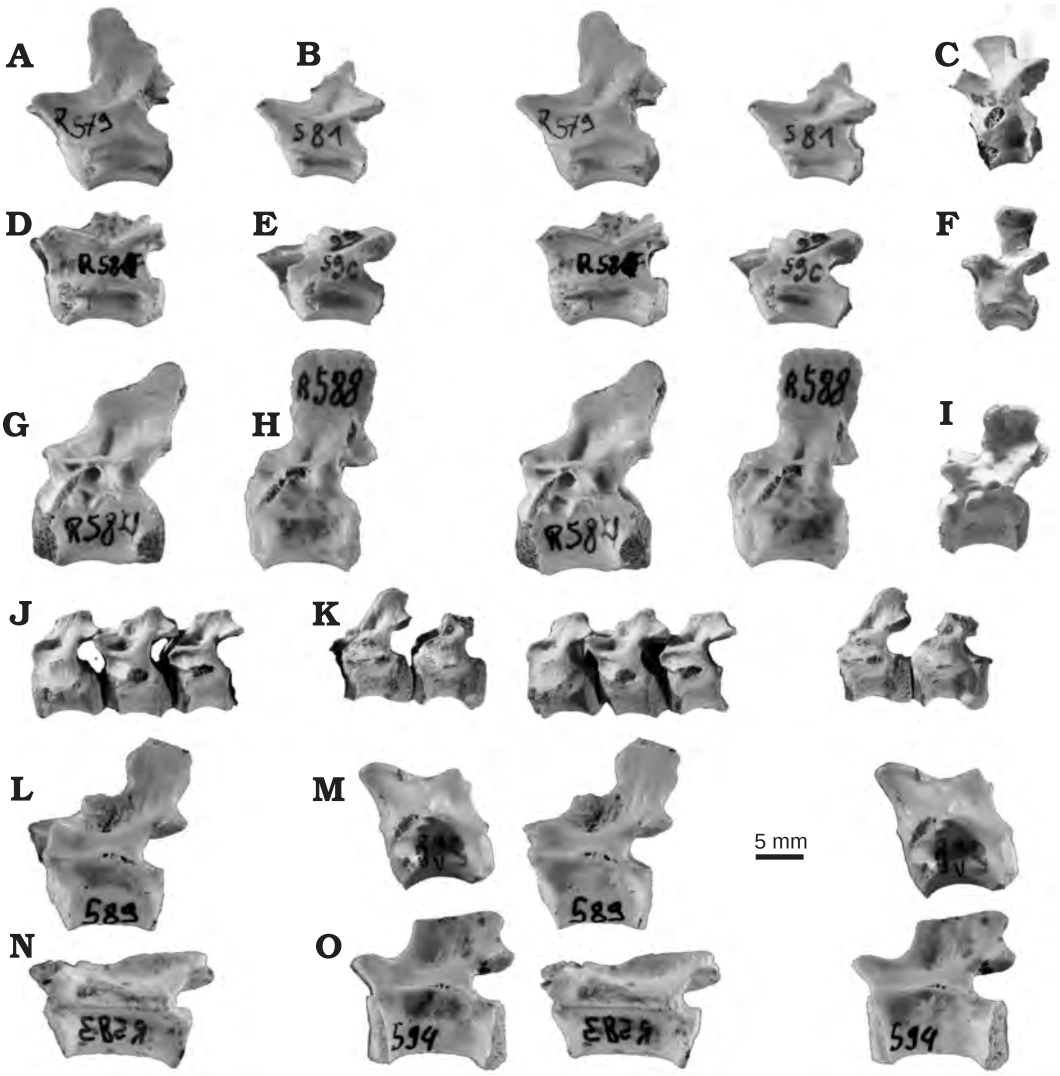

Fig. 20. **A**, **B**, **D**, **E**, **G**, **H**, **L**–**O**. *Collilongus rarus* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Cervical vertebrae: ZPAL RV/579 (**A**), ZPAL RV/581 (**B**), ZPAL RV/580 (**D**), and ZPAL RV/596 (**E**). Dorsal vertebrae: ZPAL RV/584 (**G**) and ZPAL RV/588 (**H**). **L**. Anterior caudal vertebra ZPAL RV/589. **M**. Posterior cervical vertebra ZPAL RV/893. **N**. Midcaudal vertebra ZPAL RV/583. **O**. Anterior caudal vertebra vertebra ZPAL RV/594. **C**, **F**, **I**–**K**. *Osmolskina czatkowicensis* Borsuk-Białynicka and Evans, 2003, Early Triassic of Czatkowice 1, Poland. **C**. Posterior cervical vertebra ZPAL RV/607. **F**. Midcervical vertebra ZPAL RV/571. **I**. Posterior dorsal vertebra ZPALRV/572. **J**. Anterior caudals in possible natural sequence ZPAL RV/659, 657, 658. **K**. Slightly more posterior caudals in a possible natural sequence ZPAL RV/576, 660. Left side view. All but C, F, I stereo-pairs.

sagittal crest and are not beveled. As preserved in ZPAL RV/588 (Fig. 20H), the neural spine is as high as the vertebra itself and 2/3 as long at the base. It is subrectangular with a narrow top.

Caudals. — Large sized sacrals such as *e.g.*, and 1369 are tentatively considered to belong to *Collilongus rarus*. In ZPAL RV/1369 the large oval scars left by the diapophyses are situated at the level of the neural arch base and cover almost the whole length of the arch. The specimen corresponds in size to caudals attributed to *Collilongus rarus* and may be a posterior sacral vertebra. With a ratio 1.39 the specimen is much shorter than the caudals that increase in length down the tail. There is no finished bone on the articular surfaces.

In anterior caudals, the spines are large (Fig. 20L, O), tall blades sloping posteriad, supported by the whole length of the neural arch, but further caudally, the spines become low crests supported by narrow postzygapophyses (Fig. 20M). With increasing length and slenderness of the centra, the diapophyses are gradually reduced to crests. Ventral crests appear at some distance from the sacrum, and are doubled for chevron attachment. The borders of the articular surfaces protrude ventrally. Otherwise, the centra are straight ventrally along the sagittal axis. The articular facets of the centra are U-shaped and deeper than wide, the centra being more bilaterally flattened than they are in *Osmolskina*. As usual, the neural canal is relatively smaller than in dorsals.

Comments. — The vertebrae of *Collilongus rarus* approximate prolacertiform type vertebrae in the proportions of the cervical centra (Appendices 2 and 3), but their short, tall neural spines contrast with the elongated crest-like prolacertiform type cervical neural spines. Prolacertiform vertebrae in the Czatkowice 1 material (Borsuk-Białynicka *et al.* 1999) belong to animals of much smaller size (about 6 mm cervical centrum length and a length-to-height proportion of about 4.0). The other archosauriform type dorsal, sacral, and caudal vertebrae are tentatively associated with the cervicals. Their conspecificity is highly likely. All the vertebrae in this series are mature as shown by the completely closed neurocentral sutures.

In their elongate shape, the cervical vertebrae of *Collilongus* most closely resemble those of Olenekian rauisuchids from Russia, and particularly those of the group including *Tsylmosuchus*, *Vytshegdosuchus*, *Dongusuchus*, and *Energosuchus*. Sennikov (1999) considered six species: *T. samariensis*, *T. jakovlevi*, *T. donensis*, *V. zheshartensis*, *D. efremov*, and *E. garjanovi*, to be consecutive members of the same phylogenetic line, ranging from Early Olenekian to Ladinian (Supplement 4). This hypothesis is based on the common possession of elongate cervical vertebrae with a central axis sloping posteroventrally at 6–20° (Supplement 4); a concave ventral centrum profile; and diapophyses and parapophyses that hardly protrude from the centrum. As these taxa are represented by isolated bones, no other feature can be used to unite them. Just two species, *T. jacovlevi* and *V. zheshartensis*, include fragmentary ilia with a supra-acetabular buttress that approximates the rauisuchid condition (Sennikov 1995; Gower and Sennikov 2000), and this forms the basis for the rauisuchid attribution of the whole group. *Collilongus* cervical vertebrae are much smaller and less sloping (1 to 9°), less waisted, and slightly less ventrally concave, but otherwise quite similar to those of any of these apparent rauisuchids. However, no synapomorphy can be named to support their relationships.

Family, gen. et sp. indet.

Osteoderms. — Heavy, compound osteoderms (Fig. 5B, H, K, L, N) are provisionally excluded from *Osmolskina czatkowicensis*.

FORELIMB

Humerus. — The almost complete specimen ZPAL RV/877 (Fig. 8E) is the longer and more slender of the two morphotypes recognized in Czatkowice 1 material. Detached proximal ends (ZPAL RV/1174, 1276) and detached distal ends (ZPAL RV/1161–1163, 1170, 1173) (Fig. 8B, F) probably belong to the same morphotype. All these specimens are less extended transversely than are the corresponding parts in *Osmolskina*, and are better ossified even in relatively small specimens (*e.g.*, Fig. 8B). The less deeply excavated olecranon fossa and the less protruding entepicondyle, also suggest these specimens belong with the longer morphotype (ZPAL RV/877; Fig. 8D). For a detailed discussion see p. 298).

Radius. — A distal radius end, ZPAL RV/1232 (Fig. 9B), 11 mm in distal width and much more waisted than that of *Osmolskina* is considered phylogenetically distinct.

HINDLIMB

Femur. — Specimens ZPAL RV/1132, 1174 (Fig. 12A, G), and the distal femoral end, ZPAL RV/1254, may not be conspecific with *Osmolskina czatkowicensis,* because they exceed it in size. However, their fragmentary preservation precludes their morphological distinction from those assigned to *Osmolskina*, and they remain *incertae sedis* among the Czatkowice 1 archosauriform assemblage.

Tibia. — In both length and width, the tibia ZPAL RV/1175 (Fig. 15A) is about 50% larger than comparable elements of *Osmolskina* (Fig. 15B, C). It differs also in being less waisted, with a more flattened shaft. Furthermore, the puboischiotibialis scar on the proximal end is situated in the middle of the larger surface in contrast to *Osmolskina* where it lies on the narrower side. The size difference thus combines with morphological differences.

Fibula. — As reconstructed herein (Fig. 16) on the basis of specimens ZPAL RV/1180–1182, this fibula type corresponds to *Osmolskina* in size, but is distinctive in the strong protrusion of the anterior trochanter. This makes it appear crooked, a feature tentatively considered to be characteristic of basal crurotarsians (Sereno 1991). Despite the striking slenderness, this element may suggest the presence of a basal crurotarsian in the Czatkowice 1 assemblage.

Calcaneum. — ZPAL RV/1281 is a calcaneum that exceeds the expected upper size limit for *O. czatkowicensis* by 50%.

Comments. — These aberrant bones excluded from the *O. czatkowicensis* hypodigm might belong to *Collilongus rarus*, as suggested by their size and number, but this attribution is tentative.

DISCUSSION

HETEROGENEITY OF CZATKOWICE 1 ARCHOSAURIFORM FAUNA

Archosauriform postcranial bones are the largest and most frequent within the bulk of Czatkowice 1 material. Most of them were assigned to *Osmolskina czatkowicensis* (Borsuk-Białynicka and Evans 2003), but some elements (*e.g.*, vertebrae, humeri, femora, tibiae and a calcaneum) that exceed the typical size range of *O. czatkowicensis*, and are separated from it by a hiatus (Appendices 1 and 2, Figs 14 and 21–24), are considered to represent a second distinct, morphotype.

The heterogeneity of the material is best documented by morphometric analysis of vertebral centra. A frequency distribution of centrum length, and of the length to posterior depth index suggests bimodality of the samples. This is most obvious in the case of cervicals (Appendix 2, Supplement 2A, B). The main group, displaying a more or less normal distribution, considered to belong to *Osmolskina czatkowicensis,* is separated by a hiatus from rarer specimens of much larger size (Fig. 21) and elongate proportions (Fig. 22) that are assigned to *Collilongus rarus* gen. et sp. n. The heterogeneity is also expressed by the caudals. In the mixed sample, the anterior caudal centra display a more or less normal distribution, while revealing a slight bimodality (Fig. 23) or a large variance along the tail.

Among long bones, only the tibia definitely combines differences in size and morphology. The largest tibia (ZPAL RV/117; Fig. 15A_1) is distinguished by both the shape of its transverse section (Fig. 15B_1) and the position of the puboischiotibialis muscle scar (p. 305), and is thus considered distinct from *Osmolskina czatkowicensis*.

There are thus at least two archosauriform taxa in the Czatkowice 1 assemblage.

PHYLOGENETIC VALUE OF CENTRUM PROPORTIONS

Centrum proportion is often the most noticeable feature in damaged disarticulated vertebrae, and the one most readily defined precisely. Appendix 2 includes frequency distributions of the centrum length to posterior depth index across the available archosauriform material (mostly Russian Triassic material, PIN RAS, Supplements 3, 4) and from the literature (Krebs 1965; Gebauer 2004; Sennikov 1995 and references therein; Gower and Sennikov 2000; Young 1964).

The cervical vertebrae (Fig. 24) show a roughly bimodal distribution, the main peak occurring about a length/depth index value of 1.4–1.6, the second above 2.0. *Osmolskina* contributes to the main peak of the curve along with the proterosuchids, but this means simply that it shares centrum proportions common to many Early Triassic archosauriforms. With its length/depth index in the range 1.4–1.6, *Osmolskina* has slightly longer cervical centra, and *Collilongus* has them still more elongate than *Euparkeria* (Appendix 2).

The erythrosuchid sample is included in the left slope of the curve (Fig. 24) with a modal value about 0.8 for cervicals and slightly more than this (about 0.9) for dorsals. Interestingly, some Middle Triassic rauisuchids (*Batrachotomus* and *Stagonosuchus*), and the putative proterosuchid *Sarmatosuchus*, display almost erythrosuchid proportions of cervicals (Appendix 2). This suggests centrum proportions reflect function more than affinity, although monophyletic groups do usually have some general adaptations in common.

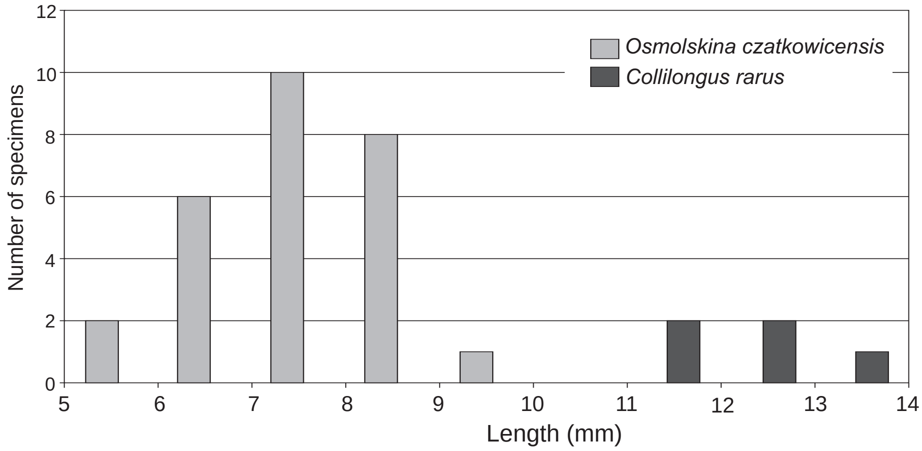

Fig. 21. Frequency distribution of cervical centrum length in Archosauriformes from the Early Triassic of Czatkowice 1, Poland.

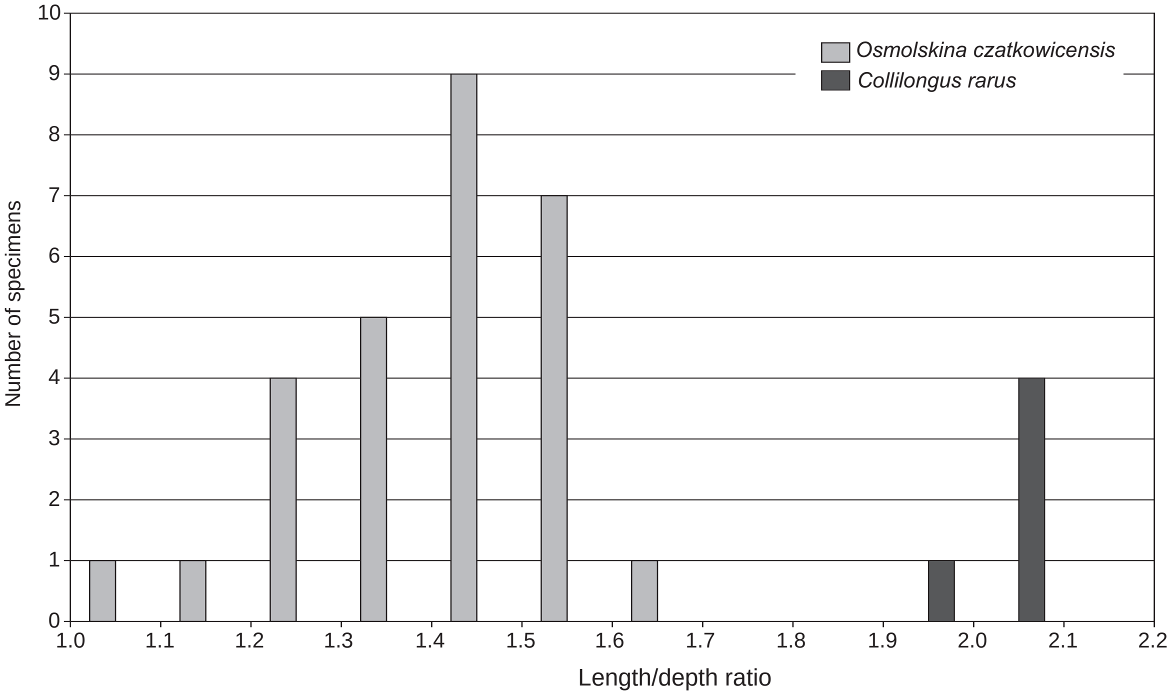

Fig. 22. Frequency distribution of vertebral index (cervical centrum length to posterior depth) in Archosauriformes from the Early Triassic of Czatkowice 1, Poland.

Collilongus matches the variability range of four Russian "rauisuchid" (*sensu* Gower and Sennikov 2000) genera, *Tsylmosuchus*, *Vytshegdosuchus*, *Dongusuchus*, and *Energosuchus*, that have been considered to form a clade (Sennikov 1990). Although not representative in statistical terms, these five genera (including *Collilongus*) correspond to the right side of the frequency curve (2.1–2.2; Fig. 25, Appendix 2). They are unique among Triassic archosauriforms in their elongate neck, which might be indicative of relationship. Other possible Eastern European "rauisuchids", *Jaikosuchus*, *Vjushkovisaurus*, and *Scythosuchus* (Sennikov 1995, 1999), have centrum proportions that differ less from those of Early to early Middle Triassic archosauriforms (Supplement 4). Their centra are more elongate than those of the earliest proterosuchids *Archosaurus* and *Vonhuenia*, but resemble Olenekian proterosuchids like *Chasmatosuchus* and *Gamosaurus*.

The relative lengths of the postaxial cervical centra have been discussed in a slightly different context by Sereno (1991, p. 34 and table 1), and were subsequently included into Juul's (1994) data matrix. According to these authors, the elongation of the anterior neck vertebrae is a synapomorphy of the Ornithodira. The Russian material (Supplements 3, 4) shows that the same has occurred, obviously independently, in some

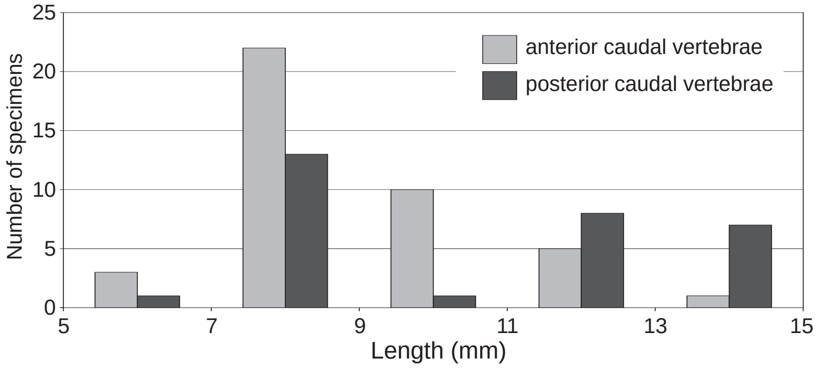

Fig. 23. Frequency distribution of caudal centrum length in Archosauriformes from the Early Triassic of Czatkowice 1, Poland.

"rauisuchids". This does not undermine Sereno's synapomorphy (according to Gower and Wilkinson 1996: "a derived character should not be unique to a clade to provide evidence for that clade"). Sereno (1991) also claimed that, in most basal archosauriforms, cervical centra were subequal or shorter than the average middorsal centrum. Our material is not sufficient to comment definitively on the relative lengths of cervical and dorsal vertebrae, but we support the relative shortening of the neck vertebrae at the origin of Archosauriformes. Strongly elongate cervical vertebrae prevail (Appendix 3) in the consecutive outgroups of the Archosauriformes (Evans 1988), as represented by "prolacertiforms" (recently considered paraphyletic; Dilkes 1998; Müller 2004; Borsuk-Białynicka and Evans 2009b) such as *Prolacerta*, *Macrocnemus*, *Tanystropheus*, and *Megalancosaurus*, but also in the most primitive diapsids, Araeoscelidia. In those taxa, the cervical centrum length/depth index oscillates between 2 and 3.7 (reaching the value 11.3 in *Tanystropheus*), while being much less in the proterosuchids. According to limited data on the proterosuchids, mainly of the Tatarian–Induan age (Supplements 3, 4), the initial cervical centrum index ranged between 1.2–1.5, up to 1.8 at most. At the same time, skull length that reaches only 40% to 55% of the trunk length in "prolacertiforms" (exceptionally only 31% in *Tanystropheus*), rises as high as 66% to 85% in those basal archosauriforms for which data are available (Appendix 3).

FUNCTIONAL CONSIDERATIONS

A negative correspondence between head size and neck length is known in vertebrate anatomy. The interference of various functional, biomechanical, and phylogenetic factors tends to obscure this association which is most evident in extreme cases, such as the disproportionately heavy skull and correspondingly short cervical region of erythrosuchids (see also elephants). Scarce as they are, the data available (Appendix 3) suggest that an allometric increase in skull size could have been a selective agent driving neck length reduction as a possible novelty at the origin of archosauriforms. Once head to body proportions had reached equilibrium and stabilized, there was a further radiation in neck length and mobility, as shown by the variability of Triassic archosauriforms.

A possible scenario is as follows: in the earliest diapsids, a trend to neck elongation might have been advantageous for sensory monitoring of the environment. This trend was sometimes reversed in heavy-skulled animals (Appendix 3, column 4), such as rhynchosaurs (Benton 1983) and trilophosaurs (Carroll 1988). In the same way, in archosauriforms, the allometric growth of skull (Appendix 3, columns 6–12) could have been recompensed by shortening of the neck, the requirements for better environmental monitoring having been satisfied mainly by a facultative bipedality which itself have been substantially enhanced by the improvement of biomechanical parameters of the ilio-sacral joint (Borsuk-Białynicka 2008).

The advantages of erect posture for fast locomotion have been stressed many times in the literature (Bakker 1971; Bonaparte 1971; Charig 1972; Parrish 1986), but extant tetrapod studies demonstrate that a sprawling gait might be equally efficient in tetrapod manoeuvrability and speed of locomotion (Sereno 1991 and references therein). The choice between gait types in diapsid phylogeny could have been haphazard from the point of view of locomotion, the primary adaptive agent being orientation. According to the scenario we propose, bipedality was first selected to improve environmental control, whereas an erect posture followed it

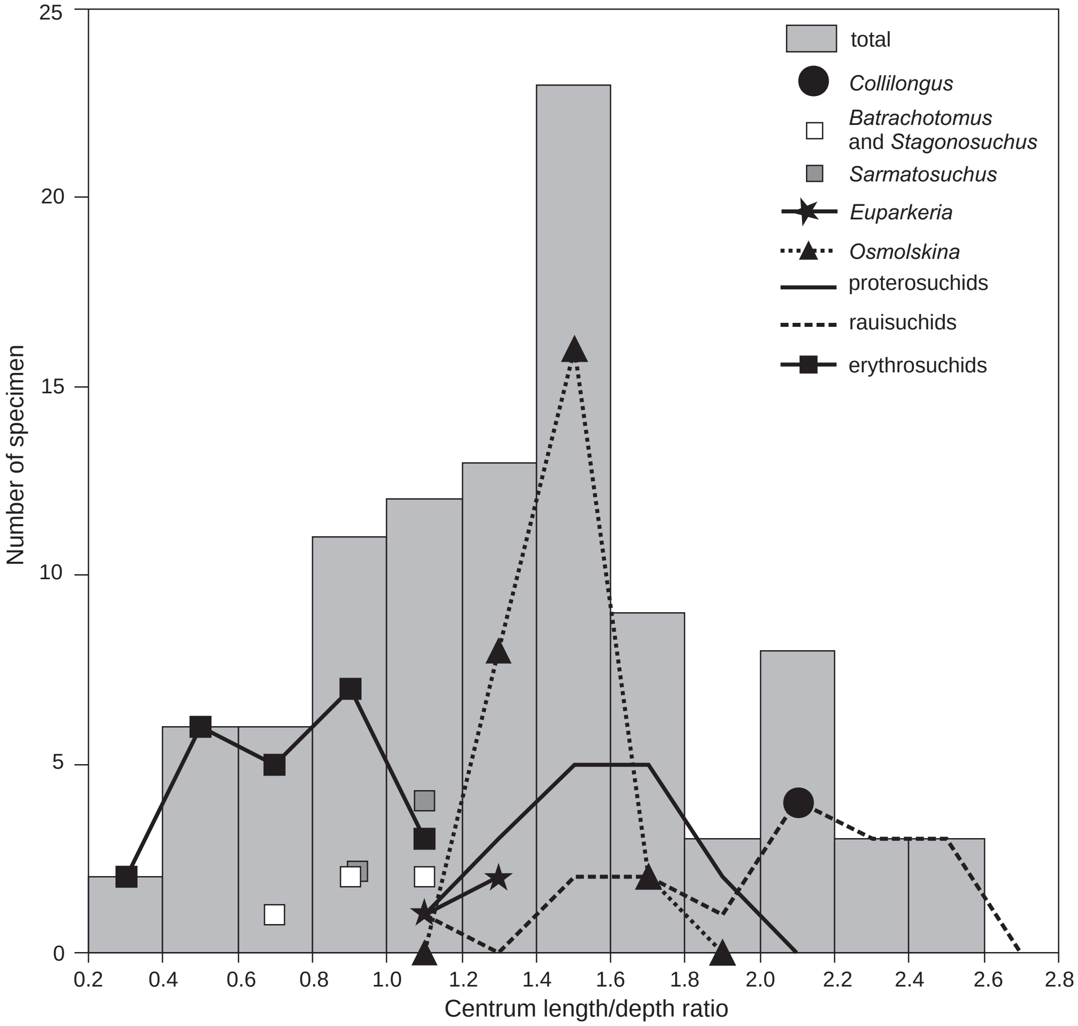

Fig. 24. Frequency distribution of cervical centrum length to posterior depth index in basal archosauriforms and rauisuchids.

in some groups. Sereno's (1991) statement that "erect posture may be a prerequisite for bipedalism" clearly concerns obligate bipedalism only.

OSMOLSKINA RECONSTRUCTION PROBLEMS

Given the close similarity between *Euparkeria capensis*, a species known from several partly preserved but articulated skeletons, and *Osmolskina czatkowicensis*, based on disarticulated material, any detailed reconstruction of the latter should be referred to the former.

Ewer (1965) estimated there were 22 presacral in *Euparkeria*, 7 cervicals, 15 dorsals, 2 sacrals, and 30–40 caudal vertebrae. The numbers were probably similar in *Osmolskina* but its cervical centra were slightly longer than those of *Euparkeria* (Appendix 2). In spite of poor preservation and approximate measurements, the humerus of *Osmolskina* may be estimated as roughly 70% of femur length, similar to that in *Euparkeria* (68%, Ewer 1965, table 3). In *Euparkeria*, the tibia length is 82–83 % of femur length (Ewer 1965), which probably holds for *Osmolskina.* Other proportions cannot be estimated even roughly. The trunk to hind leg length proportion, indicative of locomotor type, remains unknown.

In *Euparkeria* spine tables are developed in the posterior cervical and anterior dorsal regions. These also occur (Fig. 4H) in some better preserved anterior dorsal vertebrae of *Osmolskina*, but they were probably absent from more posterior dorsal vertebrae (Fig. 4B, C). According to Ewer (1965), the spine tables provide attachment sites for tendons of the transversospinalis system, and their localization relates to relative mobility of particular vertebral regions rather than to the overlying scutes. They occur more posteriorly when the tail is heavy and active (*e.g.*, as a weapon: *Stagonolepis*, Walker 1961), and in more anterior vertebrae when neck mobility is important (Ewer 1965). The importance of raising the anterior end of the column in facultative bipeds may explain the localization of spine tables in *Euparkeria* (Ewer 1965). This relation probably hold in *Osmolskina*.

Osmolskina (Fig. 7A_4) and *Euparkeria* (Fig. 7E_2) appear to differ in the angulation of the coracoid with respect to the scapula (as presented by Ewer's 1965, fig. 9). If it is correct, the rib-cage would be narrower in *Osmolskina* and might correspond to more elevated position of the thorax. However, the reconstruction (Ewer 1965) of *Euparkeria* as a facultatively bipedal animal (based on persuasive arguments *e.g.*, ratio of a hindlimb to thorax length and depth of the acetabulum) fits better with the narrow rib-cage we suggest for *Osmolskina*. The *Euparkeria capensis* specimen SAM 5867 illustrated by Ewer (1965, fig. 20) is distorted and Ewer's (1965, fig. 9) interpretation seems wrong.

The ilium of *Osmolskina* is exactly like that of *Euparkeria* (Ewer 1965; personal observation of GPIT 1681/1 by MBB), including the position of the sacral rib facets, the apparently subparallel (instead of dorsally divergent) iliac blades, and traces of sacroiliac ligaments. The ilia of both genera have a morphology that is typical of Triassic archosauriforms. The anterior sacral rib facet is situated directly on the medial wall of the acetabulum. According to Borsuk-Białynicka (2008) this is a prerequisite for bipedality. Given a proximal rather than directly medial orientation of the femoral head in both *Osmolskina* and *Euparkeria*, the resting position of the leg was sprawling rather than erect, and the bipedality could have been only facultative. The well developed fourth trochanter of the femur in both genera supports the view that they raised the body when running fast. In addition, the slender humeral proportions and absence of epicondyles also point to the frequent adoption of a more erect stance.

As reconstructed, *Osmolskina* has the tarsus essentially transversally aligned with the calcaneal tuber laterally directed, but the astragalocalcaneal canal has been lost. The ventromedial pyramid of the calcaneum was probably received into the notch on the calcaneal facet of the astragalus (Fig. 19B–D). The same was probably true of *Euparkeria.* Some amount of mobilty was possible in this joint, but its range was rather limited. In both genera, the tarsus was mesotarsal in type as defined by Gower (1996) or MPM type in Cruickshank and Benton's terminology (1985). In *Osmolskina*, the distal facet of the astragalus extends dorsally (Fig. 18C), and the same is true of the distal facet of the tarsal IV, which indicates an essentially horizontal resting position of the pes.

THE PHYLOGENETIC POSITION OF *OSMOLSKINA*

The placement of *Osmolskina czatkowicensis* at the euparkeriid level of archosauriform phylogeny was based on a combination of derived and primitive braincase characters (Borsuk-Białynicka and Evans 2003, 2009a).

The Archosauriformes (*sensu* Gauthier 1986 equal to Archosauria *sensu* Romer 1956) have been diagnosed mainly on skull characters by consecutive authors (Benton 1985, Benton and Clark 1988, Gauthier *et al.* 1988, Juul 1994). From the extensive description of the archosauriform postcranium given by Romer (1956), most characters were shown to be valid for the less inclusive groups. Only two characters, the absence of the humeral ectepicondylar foramen that relates to reduction of ectepicondyle (or distal end of humerus reduced in width — as worded by Benton 1985, p.126), and the presence of the fourth trochanter on the femur, were included in the archosauriform diagnosis by Gauthier *et al.* (1988) and Benton and Clark (1988) respectively. Of these characters, only the second is uniquely derived, and only for the clade Archosauriformes less Proterosuchidae (Juul 1994, character 4). Both characters are locomotion dependent. Two further postcranial characters: the presence of an anterior iliac process (Juul 1994, character 8), and the presence of dorsal osteoderms (Juul 1994, character 14) have been considered synapomorphic for the same less inclusive clade (Archosauriformes less Proterosuchidae). The ventral pelvic elements (Charig 1972) and tarsus (*e.g.*, Krebs 1965; Cruickshank 1979; Cruickshank and Benton 1985; Sereno 1991; Gower 1996) have been widely discussed in relation to archosauriform evolution. The pubis and ischium have become increasingly elongate (ischium longer than iliac blade — character 10 of Juul 1994, p. 38) and directed more or less ventrad (character 33 of Benton and Clark 1988), but again the initial stages of these morphological changes have not been defined as discrete novelties that could be included into the archosauriform diagnosis.

Juul (1994) discussed character distribution within the Archosauriformes, and summarized the results of previous cladistic analyses (Benton and Clark 1988; Gauthier *et al.* 1988; Sereno and Arcucci 1990; Sereno 1991; Parrish 1993), including them in his own data matrix. The latter forms the basis for our discussion. From Juul's list we have chosen only postcranial characters, and only those preserved in *Osmolskina* (Appendix 4). The numbering of characters is after Juul (1994) except for a new character, numbered 0, introduced to the maxtrix in the present study.

Character 0. — Iliosacral joint above the level of the supraacetabular ridge (0), overlapping the dorsal half of medial wall of the acetabulum (1), overlapping the whole medial wall of the acetabulum (2).

The position of the sacral rib facet relative to that of the acetabulum, the former lying on the medial, the latter on the reverse side of the ilium, is difficult to study, and has been rarely described. Some recent dinosaur papers (Novas 1996, fig. 7; Langer and Benton 2006, fig. 7) include the respective illustrations. Rare data on prolacertiform-grade reptiles (*Prolacerta broomi*, Gow 1975, *Macrocnemus bassani*, Rieppel 1989, as well as MBB's personal observations on *Macrocnemus bassani*, specimens PIMUZ T2472, T4822, and T4355) show the iliosacral joint lying above the acetabulum level. In contrast, in both *Osmolskina* and *Euparkeria* (Ewer 1965, fig. 11, MBB personal observation on the GPTI specimen), the anterior sacral rib overlaps the dorsal half of the medial wall of the acetabulum, and the same is true of *Dorosuchus neoetus* (Sennikov 1995, fig. 19L). Cruickshank's illustration (1972, fig. 8) suggests the same position of the joint in *Proterosuchus vanhoepeni*. If this is correct, then the character appeared within the proterosuchids or in the common archosauriform ancestor. This evolutionary shift in iliosacral morphology was probably a crucial event at the origin of archosauriforms, which enhanced a development of bipedality (Borsuk-Białynicka 2008).

Once developed, this character remained quite stable. As illustrated by Huene (1960) in *Vjushkovia*, by Young (1964, fig. 41A, B) in *Shansisuchus*, and by Gower (2003) in *Erythrosuchus*, the erythrosuchid ilium has the iliosacral joint in exactly the same position. It was retained in basal archosaurs, as exemplified by *Turfanosuchus dabanensis*, a crurotarsian from China (Wu and Russell 2001, fig. 11), in ornithosuchids (Walker 1964, fig. 11E), in phytosaurs (MBB personal observation of *Nicrosaurus kapffi* SMNS 52971), aetosaurs (Long and Murry 1995, fig. 80), and rauisuchids (Long and Murry 1995, fig. 134; Nesbitt 2005, fig. 23, MBB personal observation on *Batrachotomus kupferzellensis* SMNS 80273). In the extant crocodiles the sacral facet extends still further ventrad to overlap the entire medial wall of the acetabulum. In Dinosauromorpha (*sensu* Sereno 1991) the morphology of the iliosacral joint gets more complex (Langer and Benton 2006), but the biomechanics of this joint are poorly understood. This character obviously needs further study.

All 27 of Juul's (1994) characters, that could be scored for *Osmolskina* (Appendix 4) match the states of *Euparkeria.* Of them only seven show the derived condition, and these are shared by basal archosauriforms less proterosuchids. Of the remaining 20 plesiomorphic character states that exclude both genera from the crown-group, the following are particularly significant. The calcaneal tuber (character 24, Juul 1994) is lateral in orientation instead of posteriorly angulated, the facet for distal tarsal IV on the calcaneum (character 25) is oriented distally and is fully separated from the fibular facet, instead of touching it, and the relative transverse diameters of the calcaneum and astragalus (corresponding to DD character of Sereno 1991, p. 50, and character 57 of Juul 1994) are close to the proterosuchid ratio.

The following characters of Juul's (1994) matrix deserve some comments.

Character 12. — Intertrochanteric fossa present (0) or absent (1). The intertrochanteric fossa displays a continuous spectrum of states in archosauriforms, depending on the development of the posterior branch of the ventral ridge system (Romer 1956), and of the fourth trochanter. In our opinion this fossa is quite distinct in *Osmolskina* (Fig. 13E, F), and closely corresponds to the state in *Euparkeria* (Ewer 1965, fig. 31) *contra* Juul (1994, pp. 34, 38; the expression "intertrochanteric fossa on humerus" is evidently a mistake) who considers the fossa to be absent in *Euparkeria*.

Character 13. — Primitive mesotarsal joint ("PM" of Chatterjee 1982: the astragalus and calcaneum tightly adhering to each other) (0); Modified primitive mesotarsal joint ("MPM" of Cruickshank and Benton 1985 — perforating astragalocalcaneal canal between astragalus and calcaneum lost) (1). MPM type was considered synapomorphic for archosauriforms less proterosuchids and erythrosuchids (Sereno 1991, p. 6, supported by Juul 1994), but it has been shown to be shared by erythrosuchids (Gower 1996). This character is important in placing *Osmolskina* above the proterosuchid node.

Character 19. — The presence (0) or absence (1) of a non-articular space between the crural facets on the astragalus, was scored "0" in *Euparkeria* by Juul (1994), who followed Sereno and Arcucci (1990) and Sereno

(1991). We support this scoring, contra Gower's (1996) opinion that *Euparkeria* possessed the contiguous crural facets characteristic of archosaurs. The presence of a non-articular space between the astragalar crural facets in *Euparkeria* is suggested by stereophotographs of SAM 6049 (Ewer 1965) and Broom's (1913) unnumbered specimen (Ewer 1965, fig. 30 and Fig. 19C herein), and verified by MBB's personal observation of GPTI 1681/1 (Fig. 19A). This interpretation is also supported by the retention of the primitive condition in *Osmolskina* (Fig. 17A), a genus morphologically close to *Euparkeria* in other respects. However, the character may sometimes vary at a generic level as demonstrated by Gower (1996) in the erythrosuchids.

Character 28. — Fibular facet of the astragalus concave (0) flexed (1) — the facet in *Osmolskina* is slightly saddle-shaped, concave in its proximo-distal aspect, convex dorsoventrally. In biomechanical terms this suggests a slight mobility in this articulation, but not any specialized joint. The information on this facet in *Euparkeria* is too vague to be used for comparison.

Character 39. — Absence (0) or presence (1) of a supraacetabular crest. There is a lack of clarity as to what is meant by "supra-acetabular crest proper" (Juul 1994, p. 13). An anterodorsal crest, that makes the acetabulum more concave, occurs even in *Proterosuchus* (Cruickshank 1972, p. 108, fig. 8a) but in this genus, exactly as in *Prolacerta* (Gow 1975), it extends "along the front rim of the acetabulum" rather than dorsally. In both *Osmolskina* and *Euparkeria* the supraacetabular crest is mostly dorsal to the acetabulum and protrudes laterad. Certainly, the differences between *Euparkeria* grade archosauriforms and derived archosaurs is just quantitative.

Character 47. — Absence (0) or presence (1) of a brevis shelf. An elongate ventrally facing slightly excavated surface medially bordered by an acute crest probably received caudifemoralis brevis muscle in both *Osmolskina* and *Euparkeria* (Ewer's 1965 illustrations and MBB personal observations of GPIT 1681/1). It is here regarded as a homologue of the "brevis shelf". Similar to that of *Marasuchus* (Langer and Benton 2006) it differs from that of most basal dinosaurs, which faces ventrolaterally and extends further anteriad. *Osmolskina*, *Euparkeria,* and probably *Marasuchus* display an intermediate less derived state of the same character.

Characters 28, 39, 47. — Are considered questionable and have been omitted in the Appendix 4. The remaining characters of Juul's (1994) matrix, such as organization of the dermal armour, number of phalanges and most of the length ratios, percentages and details of the skeleton as a whole, as well as configurations of bones in the distal limb parts, are considered as unknown.

The close similarity between *Euparkeria* and *Osmolskina* poses the question of their generic distinction. To several discriminative skull characters of *Osmolskina* (main proportions, premaxilla overhanging, possible supplementary slit-like antorbital fenestra, poorly recessed main antorbital fenestra; Borsuk-Białynicka and Evans 2003, 2009a), considered significant at generic level, we may add only two postcranial features: the slightly longer cervical centra of *Osmolskina*, and the extremely anterior position of the coracoid foramen. Differences in size, stratigraphic age and geographic provenance, *Euparkeria* coming from the Anisian of the Gondwanan part of Pangea, *Osmolskina* from the Olenekian of the Laurasian part, tend to support a generic distinction, but we are aware of the arbitrary character of the decision.

Under a traditional classification, both genera *Osmolskina* and *Euparkeria* would be placed in the family Euparkeriidae Huene 1920, the Anisian *Dorosuchus* Sennikov, 1989, from Russia, about twice as large as *Osmolskina* and slightly more derived in femur structure, forming a third member (Sennikov 1995). Herein, we tentatively accept this formal solution However, it should be stressed that this family is not supported by any shared derived characters, unless an apparently unique combination of plesiomorphic and apomorphic character states may be considered as such.

CONCLUSIONS

The early Late Olenekian (Shishkin and Sulej 2009) Czatkowice 1 fauna includes two archosauriform genera and species, *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003 and *Collilongus rarus* gen. et sp. n.

Osmolskina czatkowicensis is the dominant animal in the Czatkowice 1 assemblage in terms of frequency, and exceeds all but *Collilongus* in size.

Osmolskina czatkowicensis shares a combination of plesiomorphic and apomorphic characters with the Anisian South African *Euparkeria capensis*, while differing in details of cranial and postcranial osteology, mostly reconstructed in probabilitic terms, which are considered significant at generic level. In this situation any computer cladistic analysis including *Osmolskina* seems redundant.

No unique derived character has been found in support of the monophyly of Euparkeriidae. However, the combination of primitive and derived character states *Euparkeria* and *Osmolskina* share with each other is tentatively considered as synapomorphic. Both genera share the absence of the astragalocalcaneal canal with all archosauriforms less proterosuchids, but lack archosaur synapomorphies (posteriorly deflected tuber calcanei, and continuous fibular and IV tarsal facets of calcaneum). They are both lightly built carnivores sharing no synapomorphies with the heavily built erythrosuchids.

The hypothesis that an overlap, or partial overlap, of the medial wall of the acetabulum by the sacral rib facet, is synapomorphic for the Archosauriformes (Borsuk-Białynicka 2008) is supported. By analogy with lizards, this archosauriform novelty is considered to have enhanced bipedality, initially facultative, in this clade.

The rare *Collilongus rarus* gen. et sp. n., based on cervical vertebrae, is the largest animal in the Czatkowice 1 fauna. It is most similar to long-necked rauisuchids from Russia, particularly *Tsylmosuchus* from the Early Triassic of the Russian Platform (Sennikov 1995), but is much smaller than any of these. However, its rauisuchid affinities, though possible, cannot be established with certainity on the basis of known elements.

The similarities of the Czatkowice 1 fauna to contemporaneous (Olenekian *Czatkobatrachus–Triadobatrachus*) or almost contemporaneaous (Olenekian *Osmolskina* – Anisian *Euparkeria*) Gondwanan faunas, may be a legacy of the uniformity of Permian teropod faunas throughout Pangea.

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APPENDIX 1

Postcranial size relations in *Euparkeria capensis* Broom, 1913, size estimations in mm for *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, and actual size ranges of *O. czatkowicensis* and *Collilongus rarus* gen. et sp. n. bones from Czatkowice 1. * roughly estimated values; N, observation number.

Character Taxon/ value	1. Skull length	2. Cervical centrum length	Ratio 1/2	3. Dorsal centrum length	Ratio 1/3	4. Scapula length	Ratio 1/4
E. capensis SAM5867 size range	87.0	8.5 8.5-9.0 N = 2	10.7	10.0 8.6–11.7 N = 27	8.7	37.4	2.3
O. czatkowicensis prediction	60.0	5.6		6.9		21	“
O. czatkowicensis actual size range		6.5-9.0 N = 22		6.8-10.0 N = 17		29–34 N = 7	–
C. rarus size range		6.5–13.0 N = 27	“	11.9 – 15.6 N = 4	“		

Character Taxon/ value	5. Humerus length	Ratio 1/5	6. Ilium length	Ratio 1/6	7. Femur length	Ratio 1/7	8. Tibia length	Ratio 7/8
E.capensis SAM5867 variability range	37.8 37.8–43.2 N = 2	2.1	33.1 29.5–37.8 N = 3	2.6	55.8 53.8–61.6 N = 3	1.54	47.8 44.1–51.0 N = 3	1.2
O. czatkowicensis prediction	29	“	23	“	39	“	28	“
O. czatkowicensis actual size range	25–36* N = 10				34–43* N = 4		28–36* N = 5	
C. rarus size range	45 N = 1	–	19.9–26.8 N = 15	–	70–76* N = 2	–	55* N = 1	–

Character Taxon/ value	9. Astragalus width	Ratio 8/9	10. Calcaneum width	Ratio 9/10	11. Mtt I, V	Ratio 8/11	12. Mtt II, III, IV	Ratio 8/12
E. capensis SAM6049	10	4.78	8.3	1.2	11.8–12.8 N = 3	3.7–3.9	17.7–21.7 N = 4	ca. 2.2–2.5
O. czatkowicensis prediction	6.9	“	5.7	“	7–7.5	“	11.2–13	“
archosauriform size estimations	7–10 N = 4		7–9 + 13.5 N = 7 + 1		10; 11.5; 15 N = 3		?16, ?18	

The predictions about the size of postcranial bones in *Osmolskina* are based on the skeletal proportions of *Euparkeria*, taking skull length as a reference point (Therrien and Henderson 2007). The skull length of *Osmolskina* was calculated from the most common skull bones (Borsuk-Białynicka and Evans 2009a) and is a rough approximation of the actual modal value. Data for *Euparkeria* are from the type specimen of *E. capensis* SAM 5867 (Ewer 1965, tables 2, 3, and illustrations). Ilium length, and tibia and tarsal widths calculated from information from the same paper.

APPENDIX 2

Frequency distribution of the index of vertebral centrum length (a) to posterior depth (d) in basal archosauriform and rauisuchid taxa. N = 99 postaxial cervicals.

Taxa a/d ratio classes	Protero-suchids	*Sarmato-suchus*	Erythro-suchids	*Eupar-keria*	*Osmols-kina*	*Colli-longus*	Raui-suchids	*Batra-chotomus Stagono-suchus*	Total
0.21–0.4			2						2
0.41–0.6			6						6
0.61–0.8			5					1	6
0.81–1.0		2	7					2	11
1.01–1.2	1	4	3	1	0		1	2	12
1.21–1.4	3			2	8		0		13
1.41–16	5				16		2		23
1.61–1.8	5				2		2		9
1.81–2.0	2				0	0	1		3
2.01–2.2	0				0	4	4		8
2.21–2.4	0					0	3		3
2.41–2.6	0						3		3
2.61–2.8							0		0

Proterosuchids including *Proterosuchus* (according to Cruickshank 1972, fig. 4) and *Archosaurus*, *Chasmatosuchus*, *Gamosaurus* (according to AGS).

Erythrosuchids including *Erythrosuchus* (after Gower 2003), *Garjainia*, *Vjushkovisaurus*, after AGS data (Supplement 4), *Shansisuchus* (after Young 1964, table 6).

Rauisuchids including *Ticinosuchus* (after Krebs 1965) and *Energosuchus*, *Jaikosuchus*, *Jushatyria*, *Vytshegdosuchus*, *Scythosuchus*, *Vjushkovisaurus* (according to AGS, Supplement 4).

APPENDIX 3

Skull to body proportion and centrum proportion indices in some diapsids.

	1	2	3	4	5	6
Genus Index	*Araeoscelis*	*Megalancosaurus*	Prolacertiformes	*Paradapedon*	*Trilophosaurus*	*Proterosuchus*
Acetabulum – glenoid distance/ Skull length	3.9	2.09	1.83–2.5 *Tanystropheus* 3.2	2.26 skull short but heavy	3.8	1.37
Cervical centrum proportion index ranges)	2.0 –3.33	aprox. over 4	2.0–3.2 *Tanystropheus* 3.69–11.3	0.67–0.86		1.27–1.3

	7	8	9	10	11	12
Genus Index	*Erythrosuchus*	*Vjushkovia*	*Garjainia*	*Euparkeria*	*Ornithosuchus*	*Silesaurus*
Acetabulum – glenoid distance/ Skull length	1.17	1.70	1.21	1.5	1.47	2
Centrum proportion index range (cervicals)	0.41–0.5	0.71–0.9	0.71–1.2	1.3–1.44	1.22–1.3	1.6–2.1

Rough measurements have been taken from illustrations by: 1, Reisz *et al.* (1984); 2, Renesto (2000); 3, Gow (1975), Chatterjee (1986), Rieppel (1989), Peyer (1937), Wild (1974); 4, Chatterjee (1974); 5, Gregory (1945); 6, Cruickshank (1972); 7, Charig and Sues (1976); 8, Huene (1960); 9, Ewer (1965); 11, Walker (1964); 12, Dzik (2003).

APPENDIX 4

List of character states mostly according to Juul (1994) scored for *Euparkeria capensis* (after Juul 1994; first place figure) and *Osmolskina czatkowicensis* (second place figure).

0. Character added: iliosacral joint above the level of the supraacetabular ridge (0), overlapping the dorsal half of medial wall of the acertabulum (1), overlapping the whole medial wall of the acetabulum (2): 1 1
4. Fourth trochanter absent (0), present (1): 1 1
8. Anterior process of iliac blade absent (0), present (1): 1 1
9. Pubic tuber anteroventrally directed (0), or strongly downturned in lateral aspect (1): 1 1
10. The ischium is not longer (0), or is longer than the iliac blade (1): 1 1
12. Intertrochanteric fossa present (0), or absent (1): 0 0
13. Ankle type PM (0), MPM (1), rotary crurotarsal (2), AM (3): 1 1
14. Dorsal body osteoderms absent (0) present (1): 1 1
19. Crural facets of the astragalus: separated by a non-articular surface (0), or continuous (1): 0 ?0
24. Orientation of calcaneal tuber lateral (0), or deflected more than 45° posterolaterally (1): 0 0
25. Articular surfaces for fibula and distal tarsal IV on calcaneum separated by a non-articular surface (0), continuous (1): 0 0
27. Hemicylindrical calcaneal condyle for articulation with fibula absent (0), present (1): 0 0 (the character corresponding to character 8 by Sereno 1991)
29. Calcaneal tuber shaft proportions taller than broad (0), broader than tall (1): 0 0
30. Calcaneal tuber distal end anteroposteriorly compressed (0), rounded (1), flared (2): 0 0
34. Accessory neural spine on mid caudal vertebrae absent (0), present (1): 0 0
36. Acetabulum laterally oriented (0), ventrally deflected (1), open ventrally (2): 0 0
42. Lesser trochanter on femur absent (0), weakly developed (1), or a spike or crest (2): 0 0
43. Prominent cnemial crest absent (0), present (1): 0 0
46. Number of sacral vertebrae two (0), two plus incipient third (1), three or more (2): 0 0
47. A brevis shelf absent (0), present (1): 0 0
48. Tibia femur length ratio 1.0 (0), more than 1.0 (1): 0 0
49. Fibula non-tapering and calcaneum unreduced (0), thin tapered fibula and reduced calcaneum (1): 0 0
51. Deltopectoral crest rounded (0), subrectangular (1): 0 0
56. Distal articular surface of the calcaneum: transverse width more (0), or less than 35% of that of astragalus: 0 0
57. Hooked proximal end of metatarsal V present (0), absent (1): 0 0
60. Acetabulum imperforate (0), semiperforate (1), largely perforate (2): 0 0
63. Proximal articular surface of the calcaneum convex or flat (0) or concave (1): 0 0
66. Hyposphene-hypantrum accessory intervertebral articulations in trunk vertebrae absent (0), present (1): 0 0
72. Dorsoventrally aligned median depression on distal end of tuber calcis absent (0) present (1): 0 0

INDEX OF GENERIC AND SPECIES NAMES

Explanation to index: * — text-fig., bold — description