

# EARLY TRIASSIC TEMNOSPONDYLS OF THE CZATKOWICE 1 TETRAPOD ASSEMBLAGE

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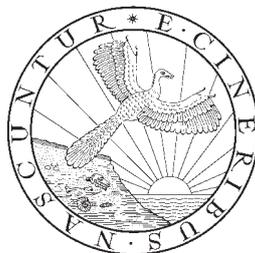
Examination of dissociated Early Triassic vertebrate microfossils from the fissure infillings of the Czatkowice quarry in southern Poland (locality Czatkowice 1) allowed recognition of the two taxa of temnospondyl amphibians, the capitosaurid *Parotosuchus* (*Parotosuchus speleus* sp. n.) and brachyopid *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 trematosauroids, is typical for the areas adjacent to brackish water or lagoonal environments. The absence or negligible role of trematosauroids 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 *Capitosauroida* is accepted to unite the bulk of the Triassic taxa placed by most authors in the *Capitosauroida* or *Mastodonsauroida* (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 *Trematosauroida* 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 *spelaiōn*, 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.

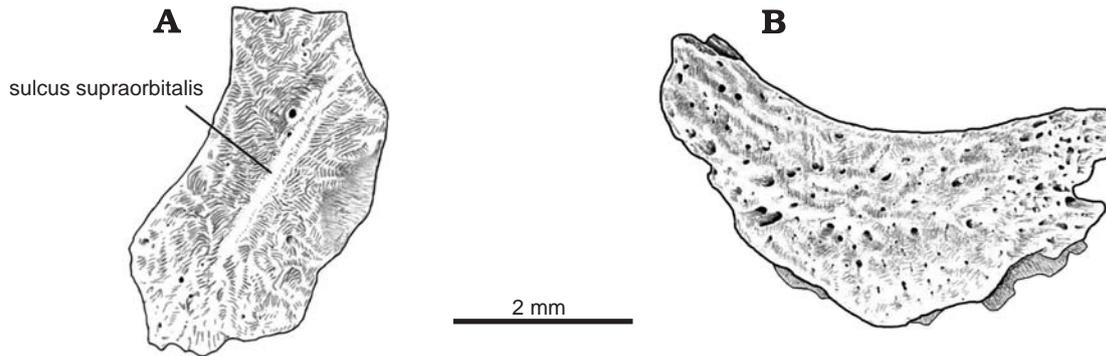


Fig. 1. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Bones of skull roof in dorsal view. **A.** Left postfrontal ZPAL AbIV/43. **B.** Right postorbital ZPAL AbIV/151.

**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 Capitosauroida (*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

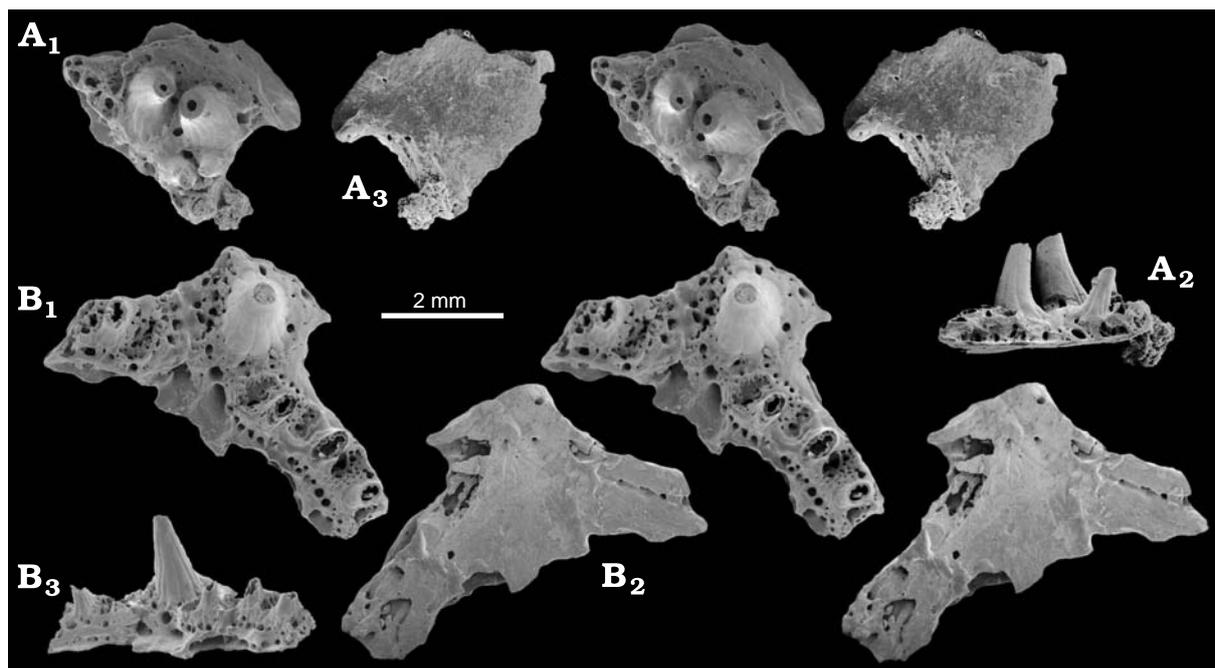


Fig. 2. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Vomers: ZPAL AbIV/65 (A) and ZPAL AbIV/105 (B, holotype), in ventral (A<sub>1</sub>, B<sub>1</sub>), dorsal (A<sub>2</sub>, B<sub>2</sub>), and medial (A<sub>3</sub>, B<sub>3</sub>) views. SEM micrographs; all but A<sub>3</sub>, B<sub>3</sub> stereo-pairs.

exoccipital and surangular, the Czatkowice 1 brachyopid conforms to *Batrachosuchooides* 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 *Batrachosuchooides*. 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<sub>1</sub>) 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<sub>2</sub>) 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<sub>1</sub>) bears smoothed ornament and faint indications of the postorbital sensory groove bending around the orbital rim.

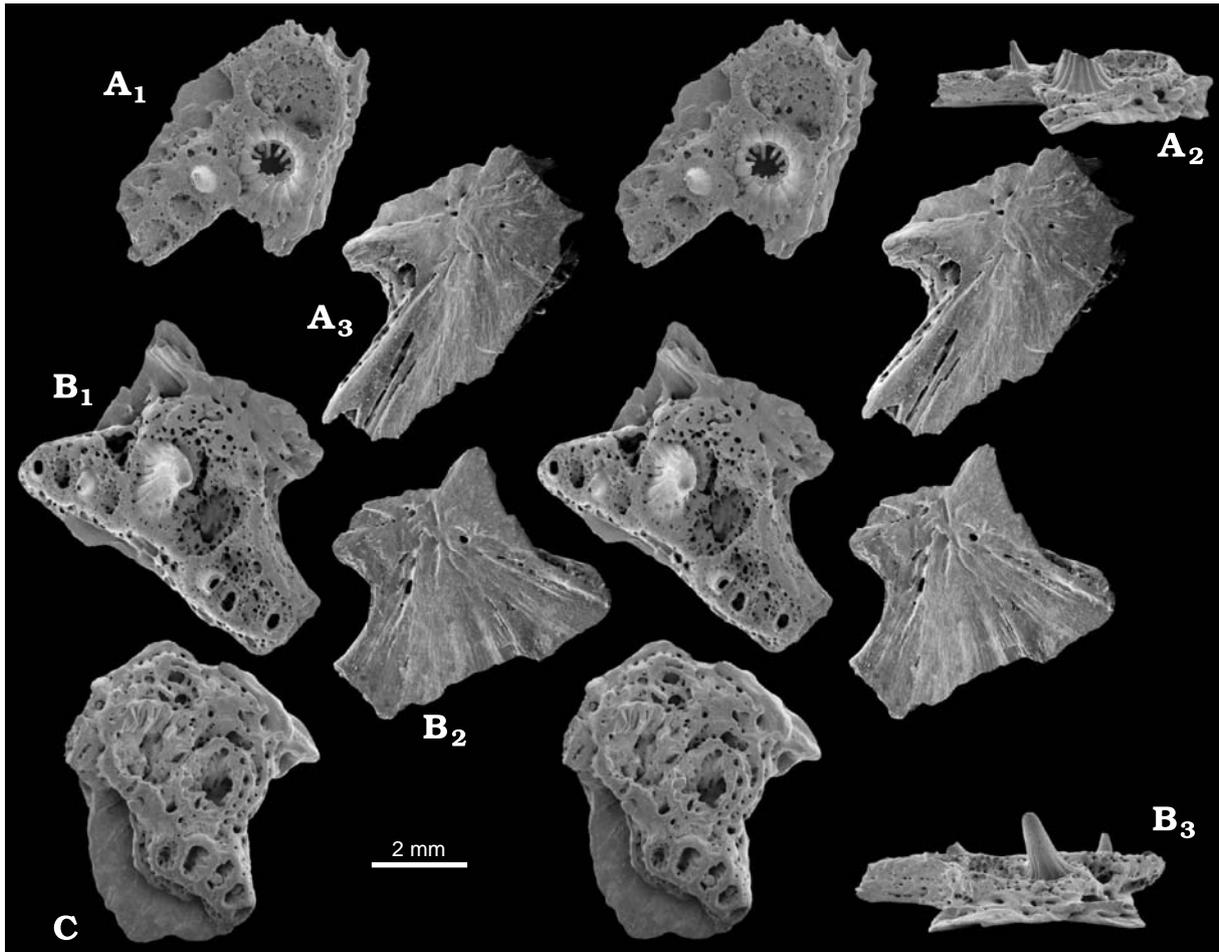


Fig. 3. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Vomers: ZPAL AbIV/38 (A), ZPAL AbIV/37 (B), and ZPAL AbIV/66 (C), in ventral (A<sub>1</sub>, B<sub>1</sub>, C), dorsal (A<sub>2</sub>, B<sub>2</sub>), and medial (A<sub>3</sub>, B<sub>3</sub>) views. SEM micrographs; all but A<sub>3</sub>, B<sub>3</sub> 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<sub>1</sub>, A<sub>3</sub>, B<sub>1</sub>, B<sub>3</sub>, 3A<sub>1</sub>, A<sub>3</sub>, B<sub>1</sub>, B<sub>3</sub>, 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).

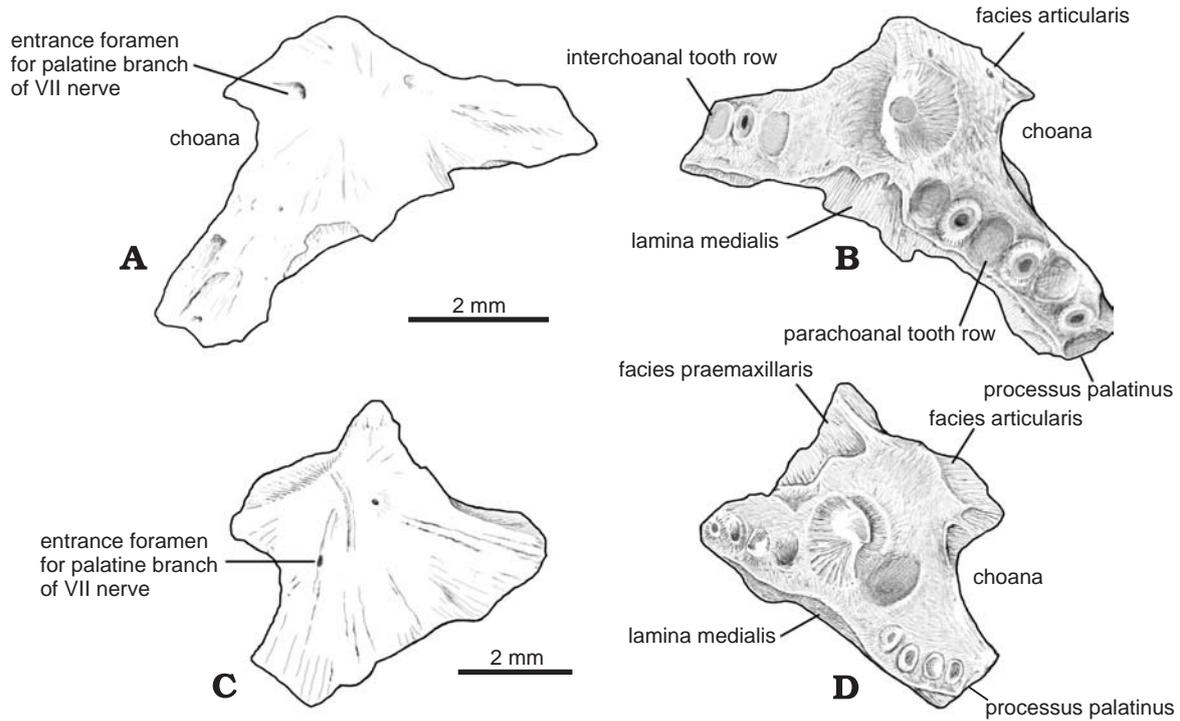


Fig. 4. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Vomers: ZPAL AbIV/105, holotype (A, B) and ZPAL AbIV/37 (C, D), in dorsal (A, C) and ventral (B, D) views.

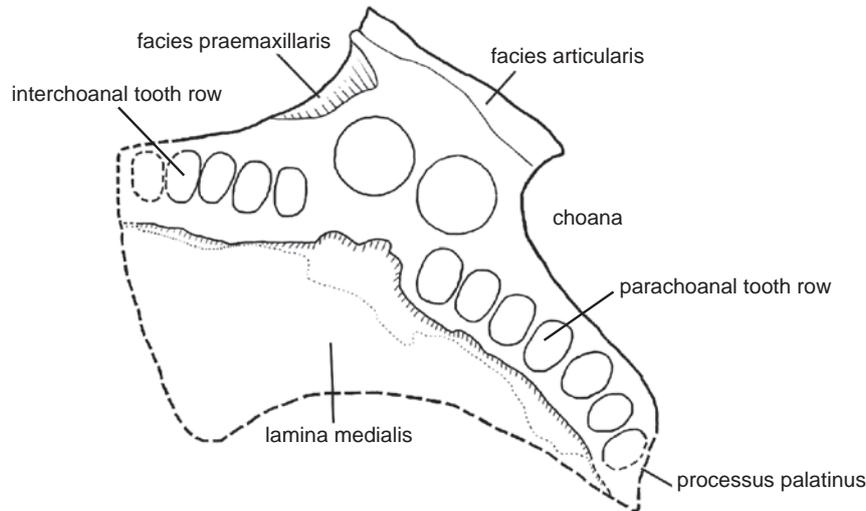


Fig. 5. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Left vomer of juvenile individual in ventral view (diagram): attempted reconstruction based on ZPAL AbIV/37 and ZPAL AbIV/105. Not to scale.

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<sub>1</sub>, 3A<sub>1</sub>, B<sub>1</sub>, 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<sub>1</sub>, 4B).

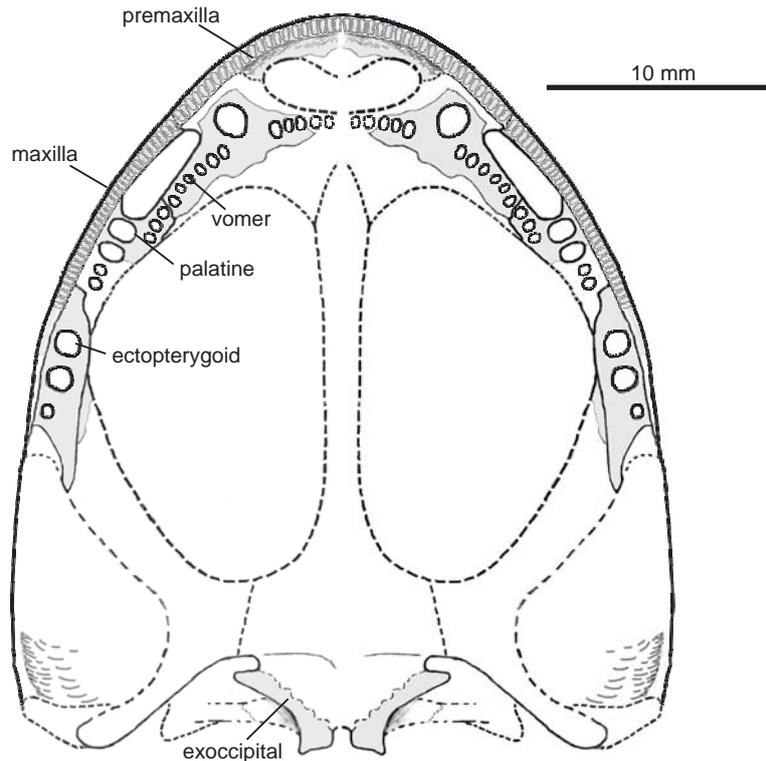


Fig. 6. Skull of early juvenile of *Parotosuchus speleus*, Early Triassic of Czatkowice 1, Poland. Reconstruction of palate showing the pattern of palatal dentition. Based mainly on the vomer ZPAL AbIV/105, palatine ZPAL AbIV/97, ectopterygoid ZPAL AbIV/50, exoccipital ZPAL AbIV/33, and premaxilla ZPAL 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<sub>1</sub>, 3A<sub>1</sub>, B<sub>1</sub>, 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<sub>1</sub>, B<sub>2</sub>, 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 unambiguous conclusion about the shape of the choana.

A tooth-bearing area forming the main body of the vomerine ossification shows a standard capitosaurid dentition, *i.e.*, a pair of prechoanal tusks combined with the interchoanal and parchoanal 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<sub>1</sub>), 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-

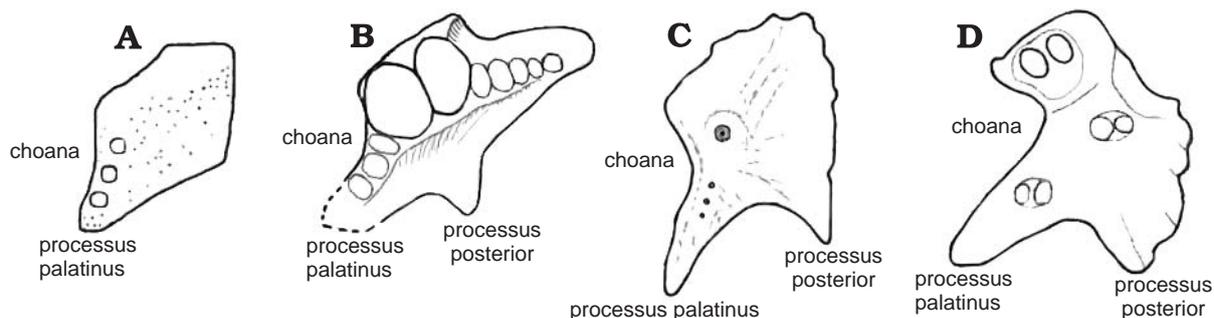


Fig. 7. Patterns of vomer in paedomorphic temnospondyls as exemplified by some dissorophoids (A, C, D) and trimerorhachoids (B). A. *Apateon* (“*Branchiosaurus*”). B. *Dvinosaurus*. C. *Branchierpeton*. D. *Micropholis*. After Boy (1972), Shishkin (1973), Wernerburg (1988), and Schoch and Rubidge (2005). 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<sub>1</sub>, 3B<sub>1</sub>, 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

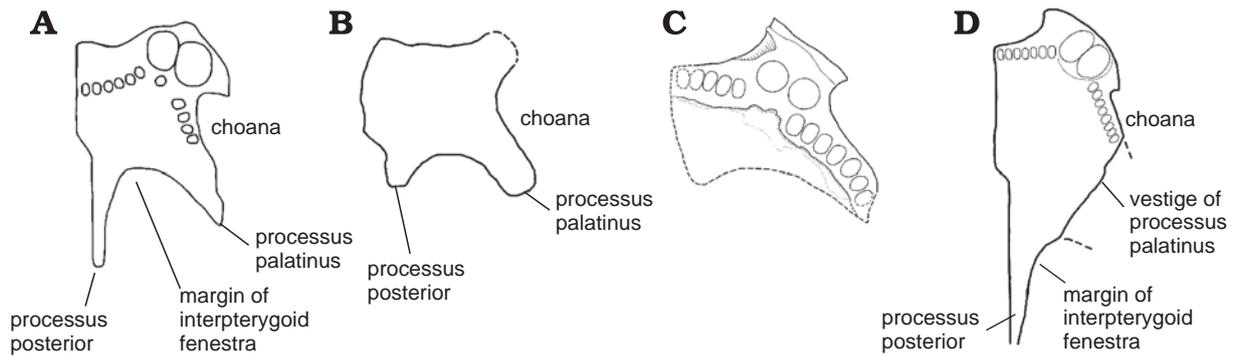


Fig. 8. Modifications of vomerine processes in capitosauroids. **A.** Rhinesuchid *Muchocephalus* (*M. muchos*). **B.** Juvenile of early capitosaurid *Rewanobatrachus* (*R. aliciae*). **C.** Juvenile of capitosaurid *Parotosuchus* (*P. speleus*). **D.** Adult *Parotosuchus* (*P. orenburgensis*). A after 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 pedomorphic 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 posterior* and *p. palatinus*, the examined specimens, as preserved, show only the *p. palatinus*, extending towards the palatine. As in many pedomorphic 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<sub>2</sub>, 3A<sub>2</sub>, B<sub>2</sub>, 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.

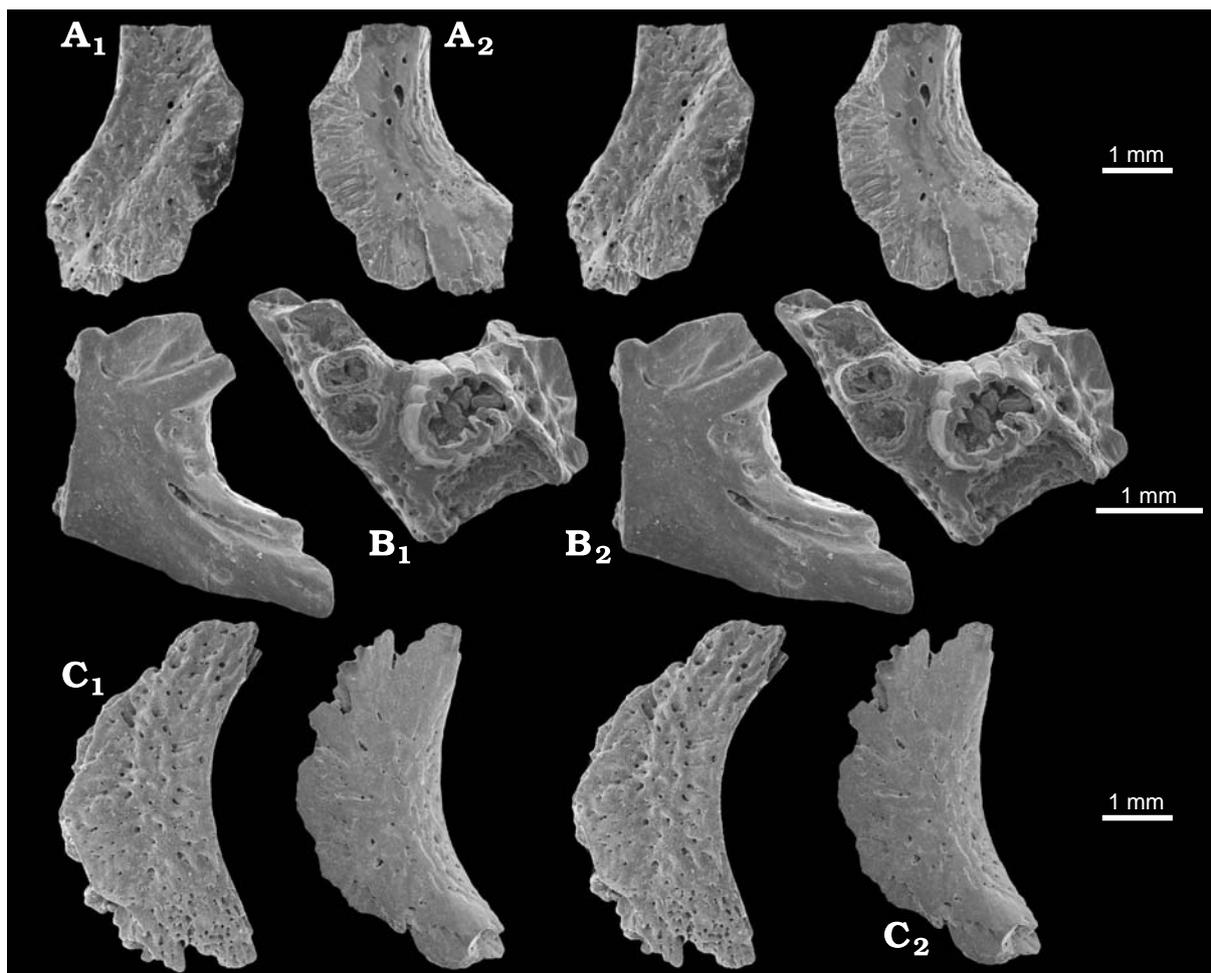


Fig. 9. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Cranial bones: left postfrontal ZPAL AbIV/43 (A), fragment of left palatine ZPAL AbIV/97 (B), and right postorbital ZPAL AbIV/151 (C), in dorsal (A<sub>1</sub>, B<sub>2</sub>, C<sub>1</sub>) and ventral (A<sub>2</sub>, B<sub>1</sub>, C<sub>2</sub>) views. SEM stereo-pairs.

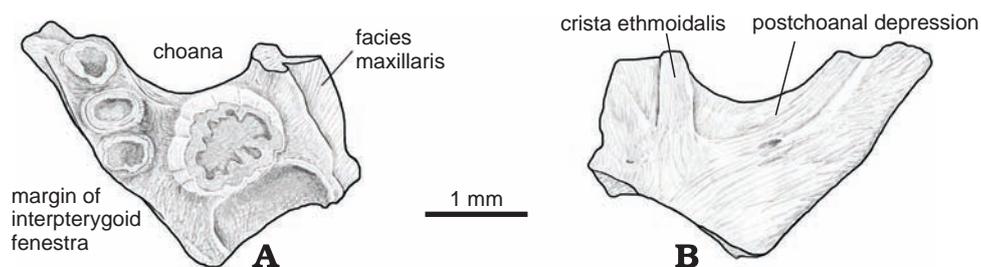


Fig. 10. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Anterior portion of left palatine ZPAL AbIV/97, in ventral (A) and dorsal (B) views.

**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<sub>1</sub>, 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<sub>2</sub>, 10B) somewhat departs from the typical pattern of adult Late Permian and Triassic temnospondyls. Peculiar to the latter is the presence of a cres-

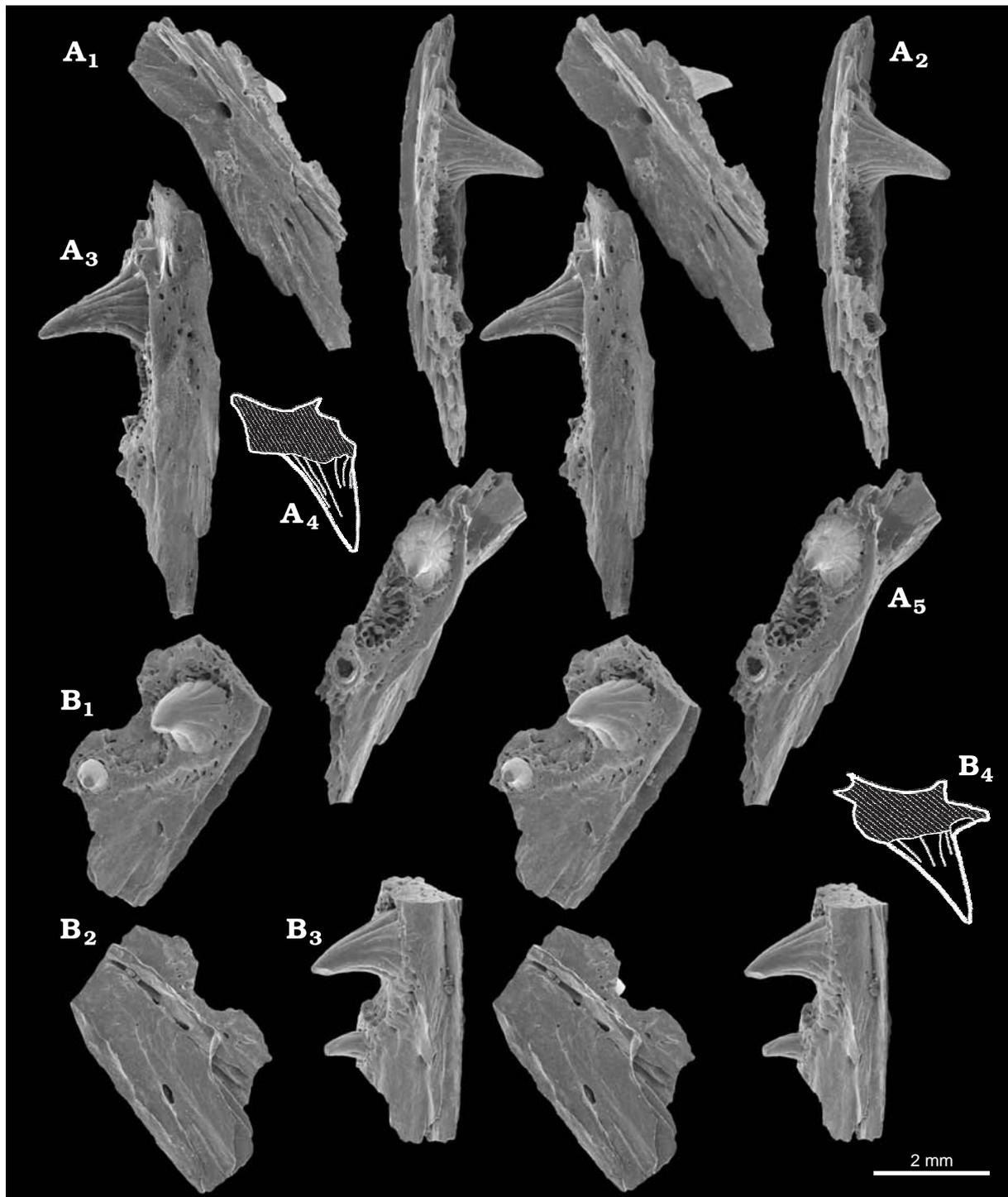


Fig. 11. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Right ectopterygoids: ZPAL AbIV/50 (A) and ZPAL AbIV/46 (B), in dorsal (A<sub>1</sub>, B<sub>2</sub>), lateral (A<sub>2</sub>), medial (A<sub>3</sub>, B<sub>3</sub>), ventral (A<sub>5</sub>, B<sub>1</sub>) views, and cross sections (A<sub>4</sub>, B<sub>4</sub>). All but A<sub>4</sub> and B<sub>4</sub> 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 pedomorphic dissorhophoids (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<sub>5</sub>, 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 ectopterygoid 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<sub>1</sub>).

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<sub>3</sub>, A<sub>4</sub>, 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<sub>4</sub>, 12D, H, 13).

The dorsal surface of the juvenile ectopterygoid (Figs 11A<sub>1</sub>, B<sub>2</sub>, 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

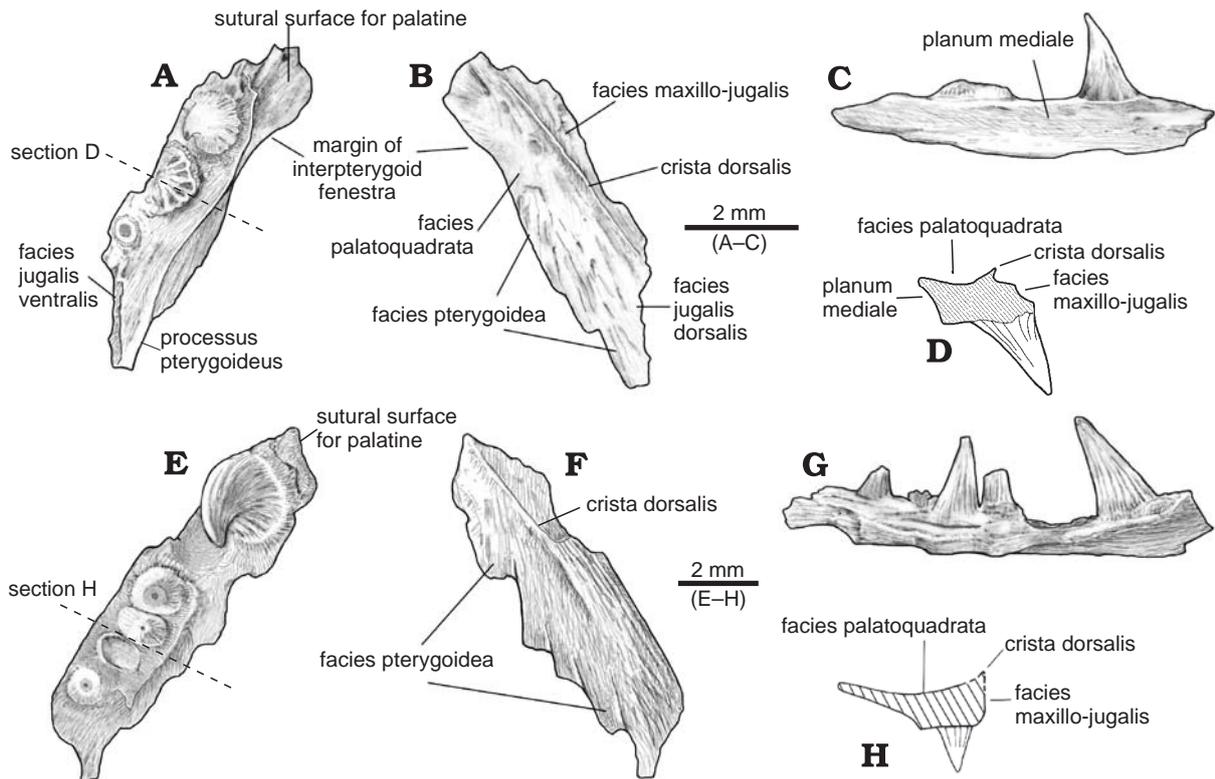


Fig. 12. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Right ectopterygoids ZPAL AbIV/50 (A–D) and ZPAL AbIV/107 (E–H), in ventral (A, E), dorsal (B, F), medial (C, G) views, and cross sections (D, H). Note the growth changes: increase in number of regular teeth, spreading forward 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<sub>1</sub>, 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

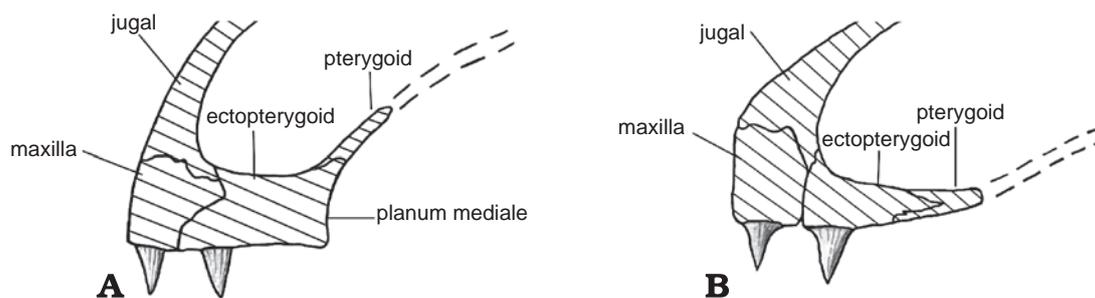


Fig. 13. Ontogenetic flattening of palatal vault in *Parotosuchus* as evidenced by three-dimensional growth changes of the ectopterygoid. Cross sections of cheek region of skull reconstructed for two generalised growth stages (diagram). **A.** Based on juvenile *Parotosuchus speleus* ZPAL AbIV/50. **B.** 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;

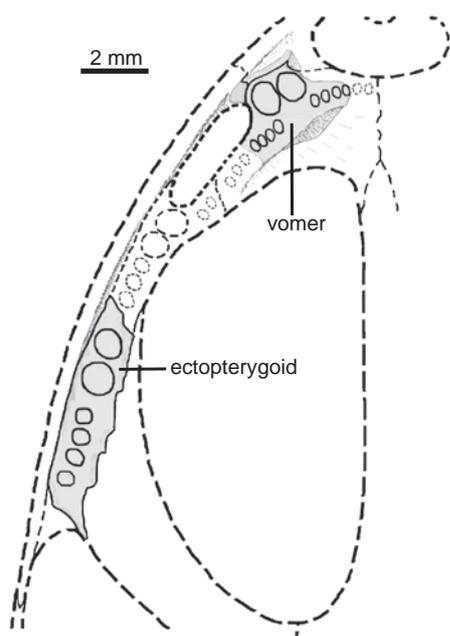


Fig. 14. Reconstruction of tooth-bearing portion of palate in advanced juvenile of *Parotosuchus speleus*. Based on the vomer ZPAL AbIV/37 and ectopterygoid ZPAL AbIV/107. In comparison with the earlier growth stage (Fig. 6), notable are the changes in design and dentition of the ectopterygoid combined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

(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-

ceeds the value known for the juvenile *Benthosuchus sushkini* PIN 2252/4 (less than 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

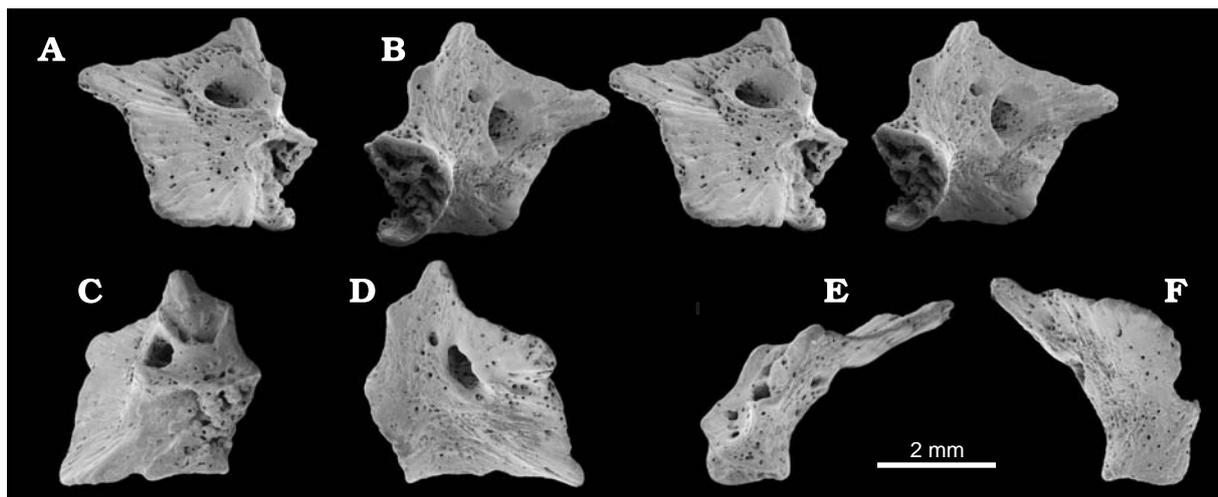


Fig. 15. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Right exoccipital ZPAL AbIV/33, in anteromedial (A), posterolateral (B), medial (C), lateral (D), dorsal (E), and ventral (F) views. SEM micrographs; A, B, stereo-pairs.

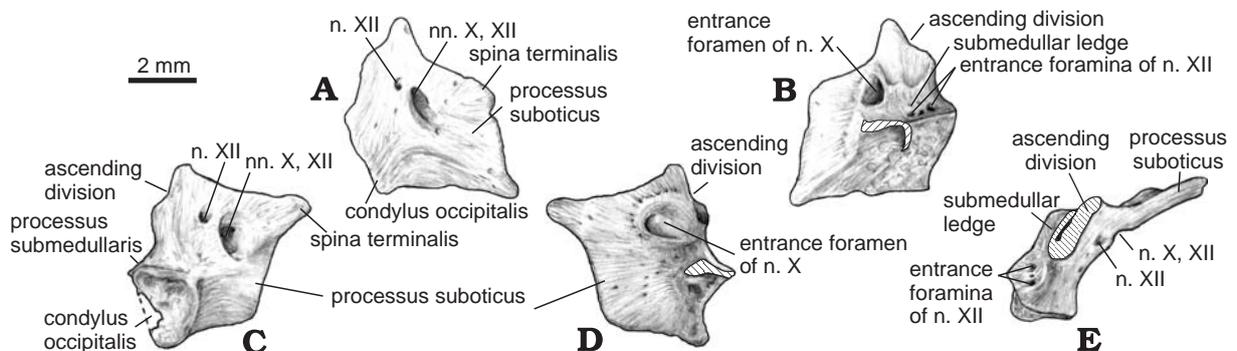


Fig. 16. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Right exoccipital ZPAL AbIV/33, in lateral (A), medial (B), posterolateral (C), anteromedial (D), and dorsal (E) views.

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<sub>1</sub>, 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<sub>2</sub>, 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

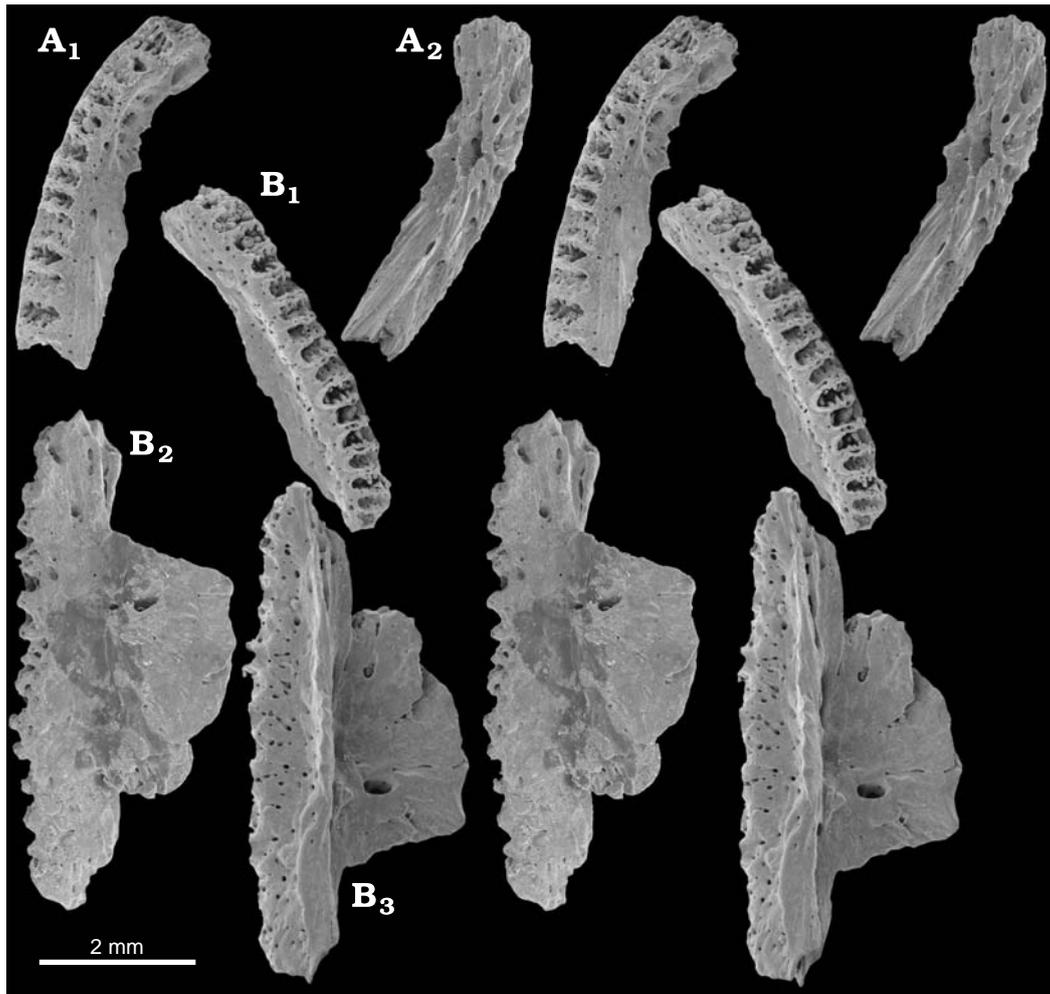


Fig. 17. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Upper jaw bones. **A.** Right premaxilla ZPAL AbIV/92, in ventral ( $A_1$ ) and dorsal ( $A_2$ ) views. **B.** Left maxilla ZPAL AbIV/106, in ventral ( $B_1$ ), labial ( $B_2$ ), and medial ( $B_3$ ) views. SEM stereo-pairs.

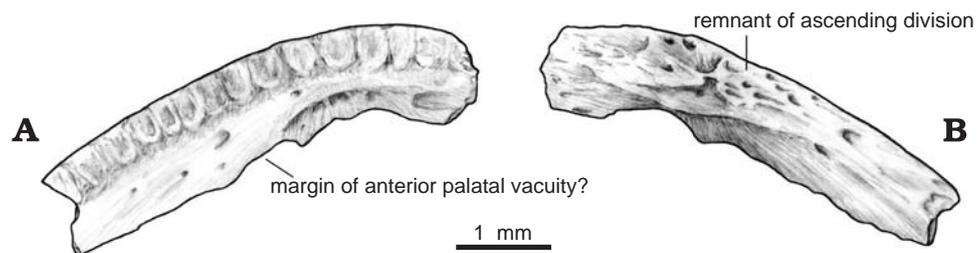


Fig. 18. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Right premaxilla ZPAL AbIV/92, in ventral (A) and dorsal (B) views.

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

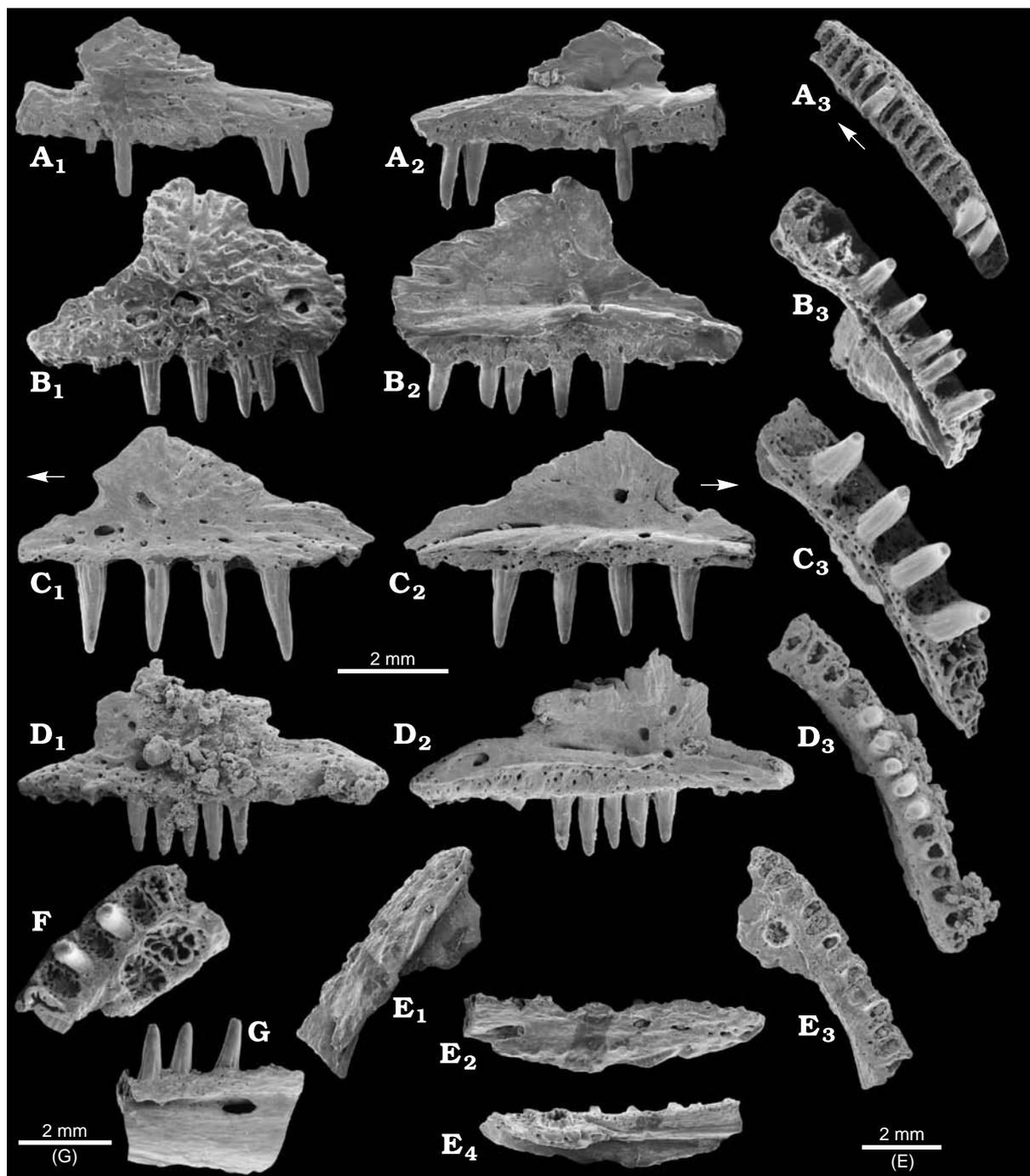


Fig. 19. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Jaw bones: left maxillae ZPAL AbIV/118 (A), ZPAL AbIV/31(B), ZPAL AbIV/116 (C), ZPAL AbIV/153 (D); symphyseal portions of dentaries ZPAL AbIV/119 (E), ZPAL AbIV/32 (F), and fragment of dentary ZPAL AbIV/34 (G), in labial (A<sub>1</sub>, B<sub>1</sub>, C<sub>1</sub>, D<sub>1</sub>, E<sub>2</sub>, G), medial (A<sub>2</sub>, B<sub>2</sub>, C<sub>2</sub>, D<sub>2</sub>, E<sub>4</sub>), ventral (A<sub>3</sub>, B<sub>3</sub>, C<sub>3</sub>, D<sub>3</sub>, E<sub>1</sub>), and dorsal (E<sub>3</sub>, 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<sub>1</sub>, 19A<sub>3</sub>–D<sub>3</sub>). 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<sub>1</sub>, B<sub>3</sub>, 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

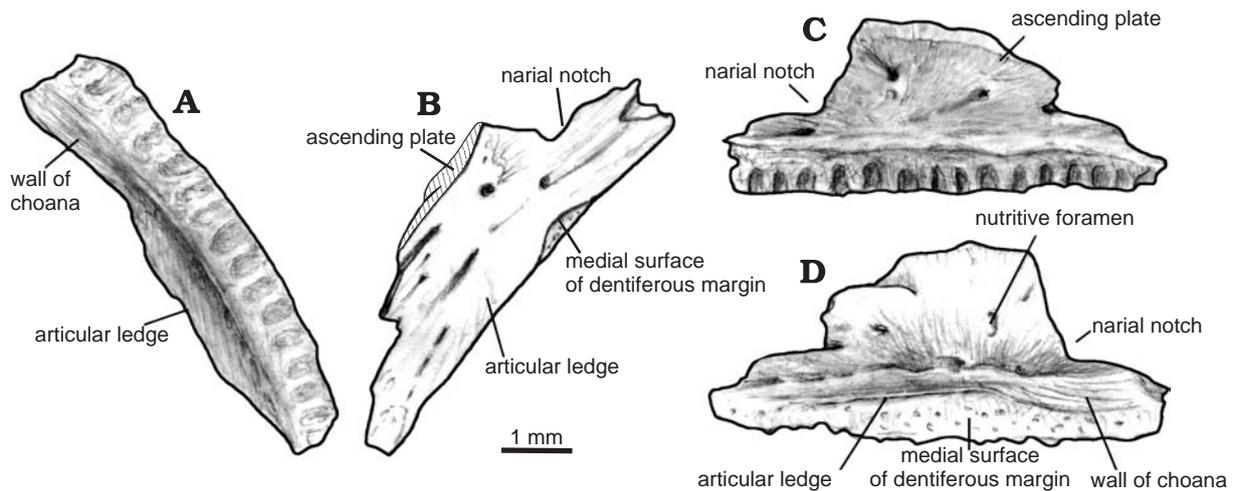


Fig. 20. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Left maxilla ZPAL AbIV/106, in ventral (A), dorsal and slightly medial (B), ventrolabial (C), and medial (D) views.

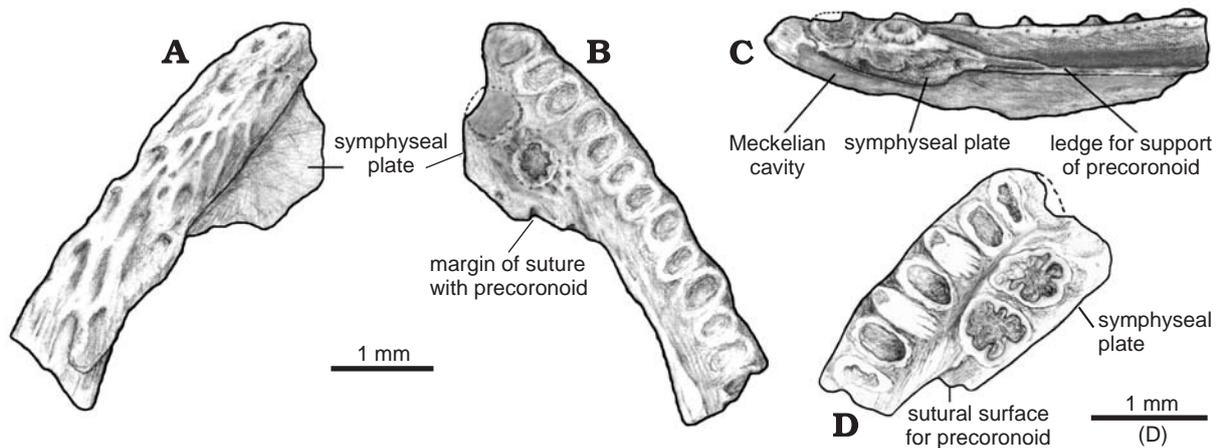


Fig. 21. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Symphyseal portions of right dentary ZPAL AbIV/119 (A–C) and left dentary ZPAL AbIV/32 (D), in ventral (A), dorsal (B, D), and lingual (C) views.

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<sub>2</sub>, B<sub>3</sub>, 19A<sub>1</sub>–D<sub>1</sub>, 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 capitosauroids. 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<sub>1</sub>, B<sub>1</sub>).

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<sub>2</sub>, B<sub>3</sub>, 19A<sub>1</sub>–D<sub>1</sub>, A<sub>2</sub>–D<sub>2</sub>, 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<sub>3</sub>, 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<sub>1</sub>, E<sub>3</sub>, 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 symphyseal plate abruptly terminates as a free horizontal flange instead of being gradually included into the lingual side of the dentary (Figs 19E<sub>1</sub>, E<sub>3</sub>, 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<sub>4</sub>, 21C). Hence, at this developmental stage the precoronoid formed a posterior continuation of the symphyseal plate rather than a portion of lingual mandibular wall. Accordingly, like the plate itself, the precoronoid surface faced dorsally rather than 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 of 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-

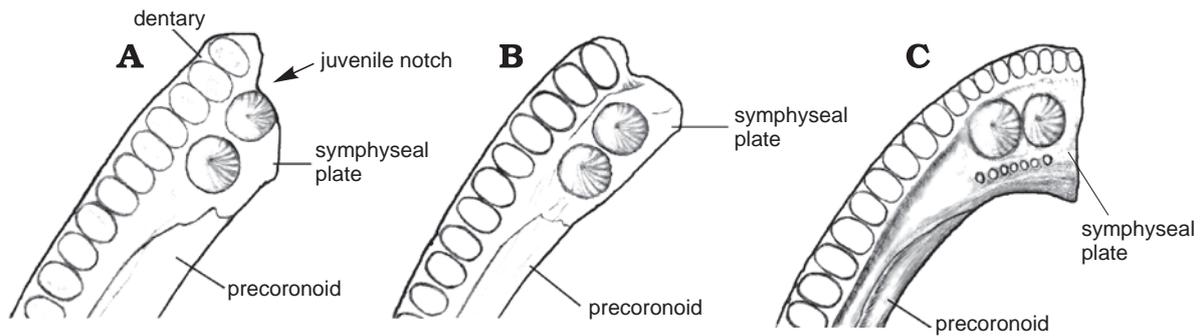


Fig. 22. Ontogenetic changes in the mandible of *Parotosuchus* showing development of the precoronoid into a subvertical position and loss of contact between the precoronoid and symphyseal plate of the dentary. **A, B.** Juvenile stages. **C.** Adult stage. **A, B** reconstructions based on the dentaries 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.

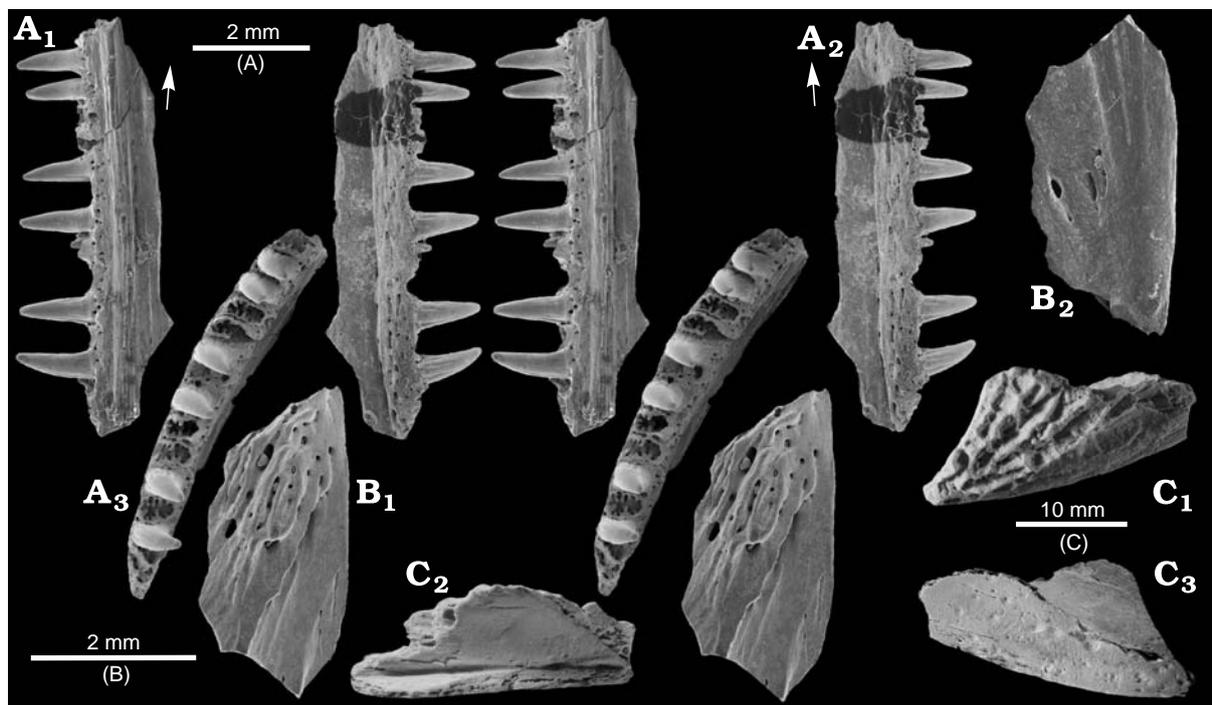


Fig. 23. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Fragments of lower jaw bones: left dentary ZPAL AbIV/35 (**A**), right surangular ZPAL AbIV/68 (**B**), and left angular ZPAL AbIV/63 (**C**), in lingual (**A**<sub>1</sub>, **B**<sub>2</sub>, **C**<sub>3</sub>), labial (**A**<sub>2</sub>, **B**<sub>1</sub>, **C**<sub>1</sub>), and dorsal (**A**<sub>3</sub>, **C**<sub>2</sub>) views. SEM micrographs; **A** and **B**<sub>1</sub>, stereo-pairs.

ing its dorsal, labial, ventral, and partially lingual sides (Fig. 19E<sub>1</sub>, E<sub>4</sub>, 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<sub>2</sub>, 24A). The lingual division is not developed and is reduced to a massive longitudinal ridge bordering the tooth-bearing surface (Figs 23A<sub>1</sub>, 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<sub>3</sub>, 24C), which bears 14–15 compressed teeth and tooth pits and

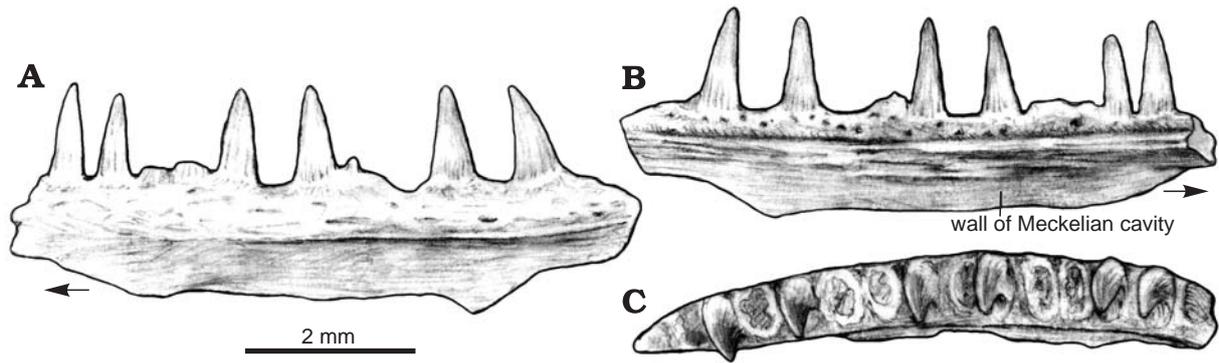


Fig. 24. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Left dentary (posterior portion) ZPAL AbIV/35, in labial (A), lingual (B), and dorsal (C) views.

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

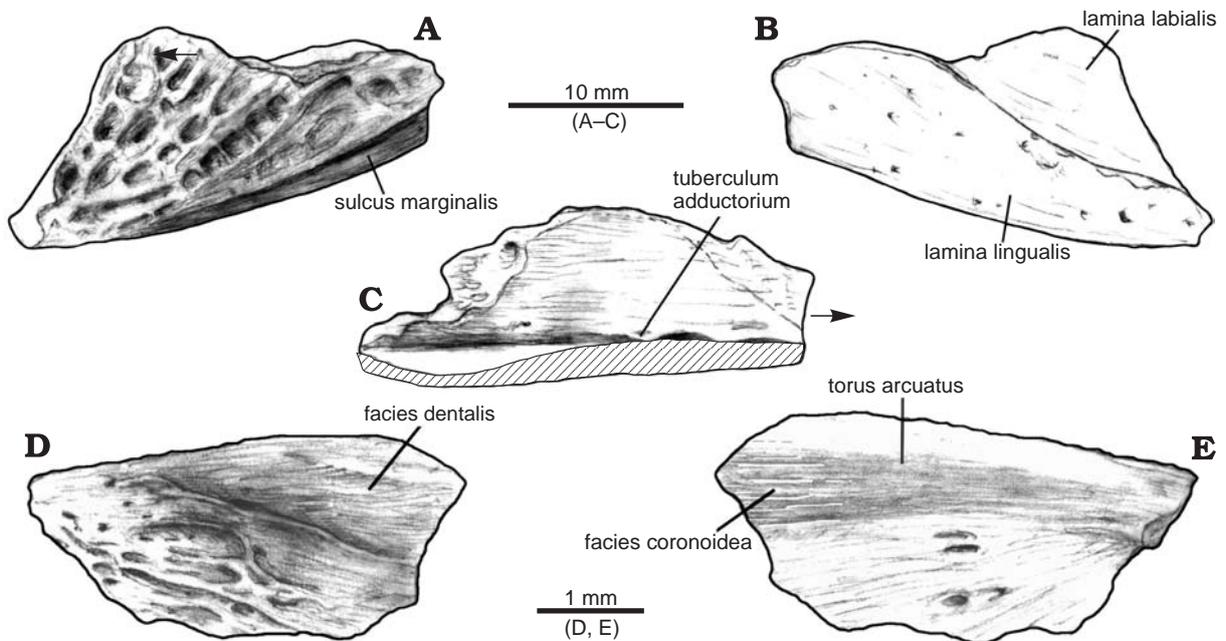


Fig. 25. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Fragments of left angular ZPAL AbIV/63 (A–C) and of right surangular ZPAL AbIV/68 (D, E), in labial (A, D), lingual (medial) (B, E), and dorsolateral (C) views.

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<sub>1</sub>, 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<sub>3</sub>, 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<sub>2</sub>, 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<sub>2</sub>, 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<sub>1</sub>, 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<sub>2</sub>, 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

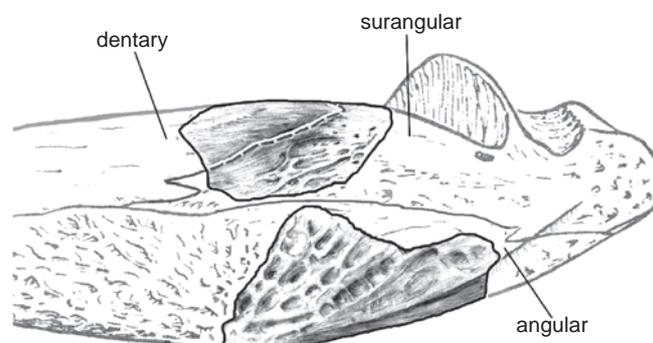


Fig. 26. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Conjectural reconstruction of adductor division of the mandible showing position of preserved fragments of the angular (ZPAL AbIV/63) and surangular (ZPAL AbIV/68, mirror image). Not to scale.

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-

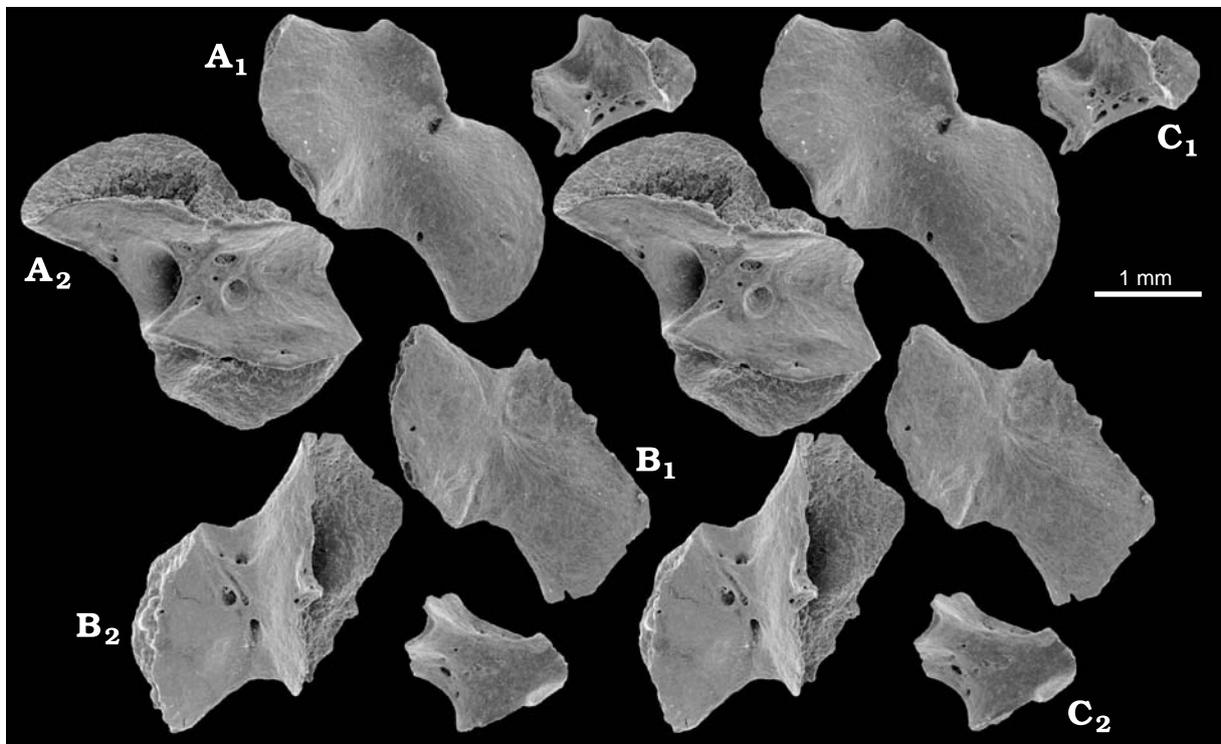


Fig. 27. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Neural arches: ZPAL AbIV/159 (A), ZPAL AbIV/158 (B), and ZPAL AbIV/160 (C), in lateral (A<sub>1</sub>, B<sub>1</sub>, C<sub>2</sub>) and medial (A<sub>2</sub>, B<sub>2</sub>, C<sub>1</sub>) views. SEM stereo-pairs.

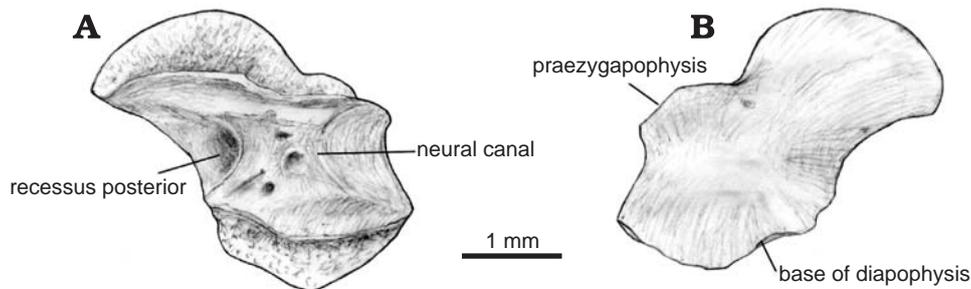


Fig. 28. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Neural arch (left antimeres) ZPAL AbIV/159, in medial (A) and lateral (B) views.

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<sub>1</sub>, 28B), the base of the arch bears a barely detectable rudiment of the diapophysis. The prezygapophysis is well differentiated, 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<sub>2</sub>, 28A) shows a hollowed lateral wall of the wide neural

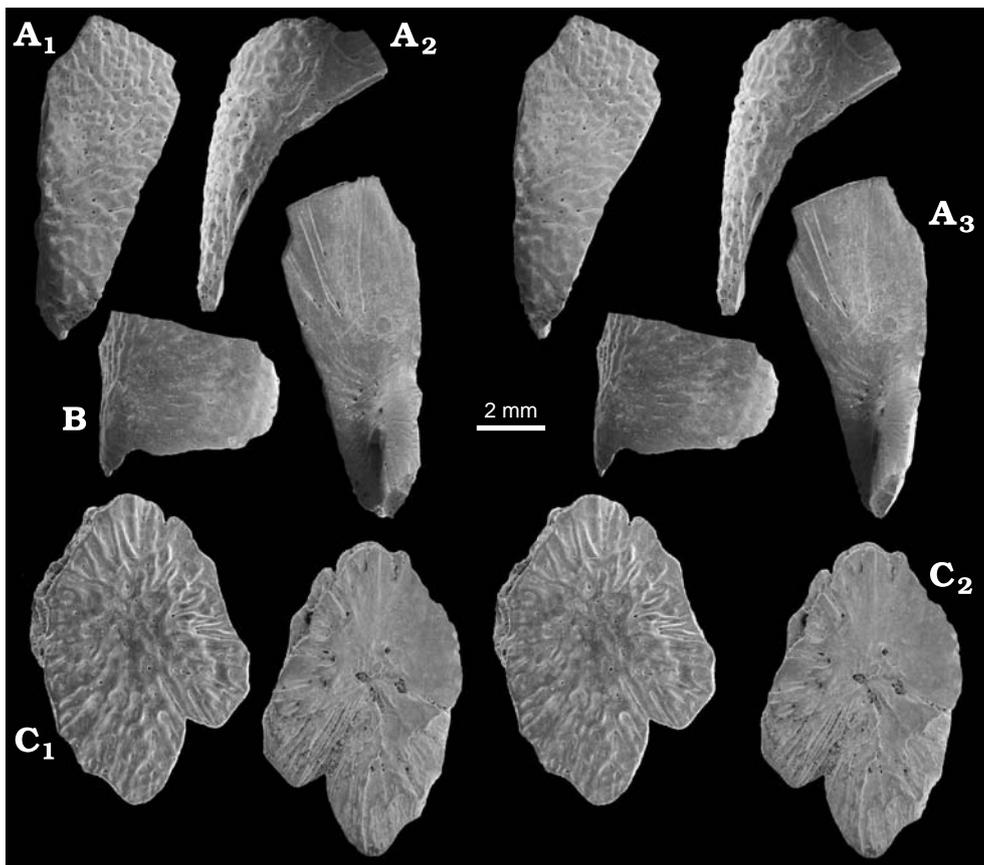


Fig. 29. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Elements of dermal shoulder girdle: right clavicles ZPAL AbIV/87 (A), ZPAL AbIV/75 (B), and interclavicle ZPAL AbIV/102 (C), in ventral (A<sub>1</sub>, B, C<sub>1</sub>), lateral (A<sub>2</sub>), and dorsal (A<sub>3</sub>, C<sub>2</sub>) views. SEM stereo-pairs.

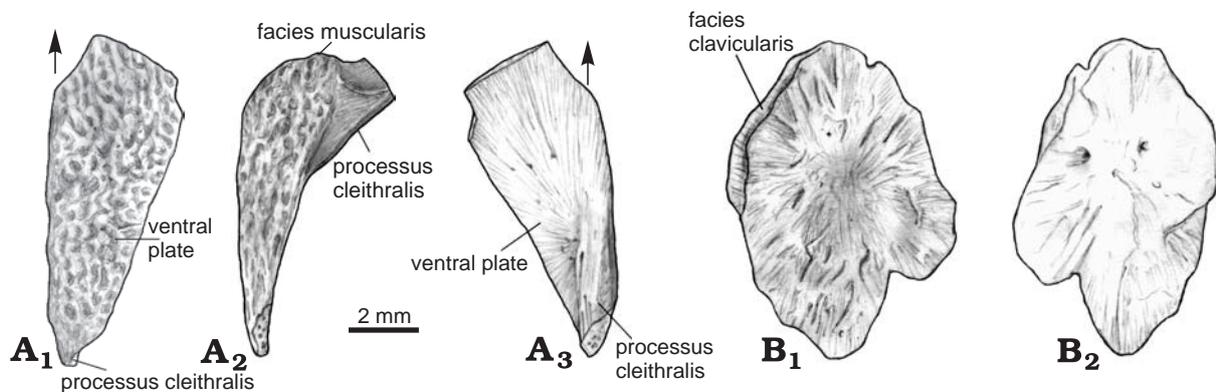


Fig. 30. *Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Right clavicle ZPAL AbIV/87 (A) and interclavicle ZPAL AbIV/102 (B), in lateral (A<sub>2</sub>), dorsal (A<sub>3</sub>, B<sub>2</sub>), and ventral (A<sub>1</sub>, B<sub>1</sub>) views.

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<sub>1</sub>, 30A<sub>1</sub>), and the basal portion of the dorsal (cleithral) process (Figs 29A<sub>2</sub>, 30A<sub>2</sub>). 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).

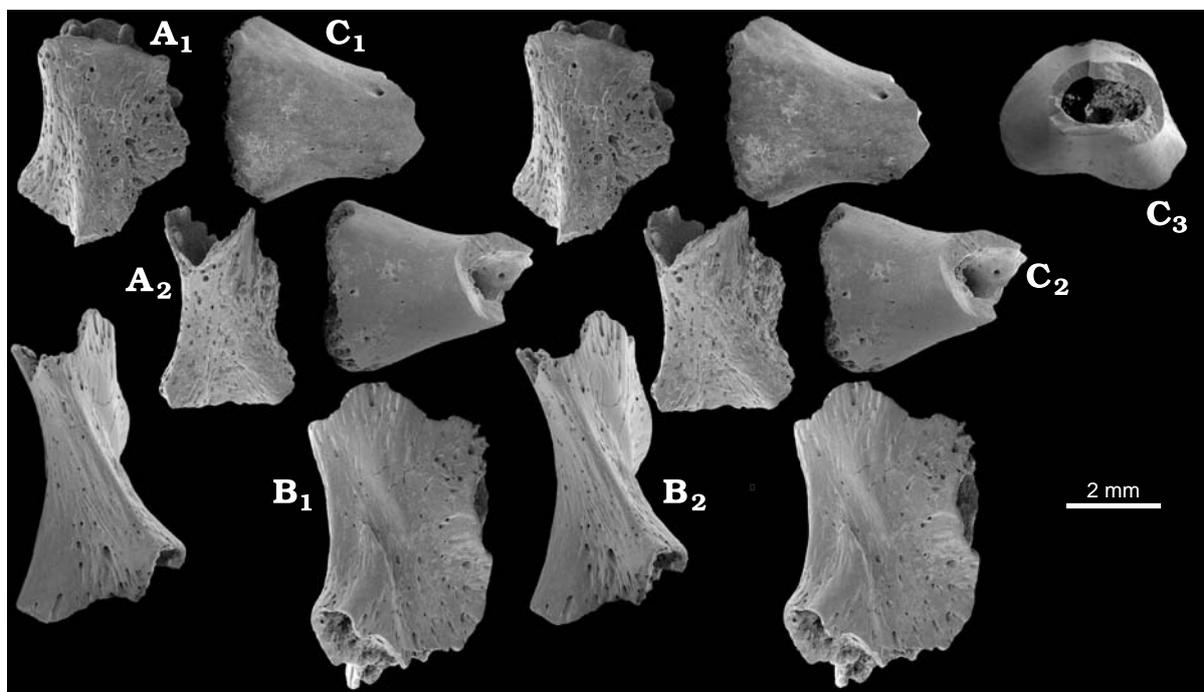


Fig. 31. (?)*Parotosuchus speleus* sp. n., Early Triassic of Czatkowice 1, Poland. Fragments of limb bones: scapulae ZPAL AbIV/88 (A), ZPAL AbIV/103 (B), and radius(?) ZPAL AbIV/96 (C). SEM micrographs; all but C<sub>3</sub> stereo-pairs.

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 sub-vertical 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 commissure) 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

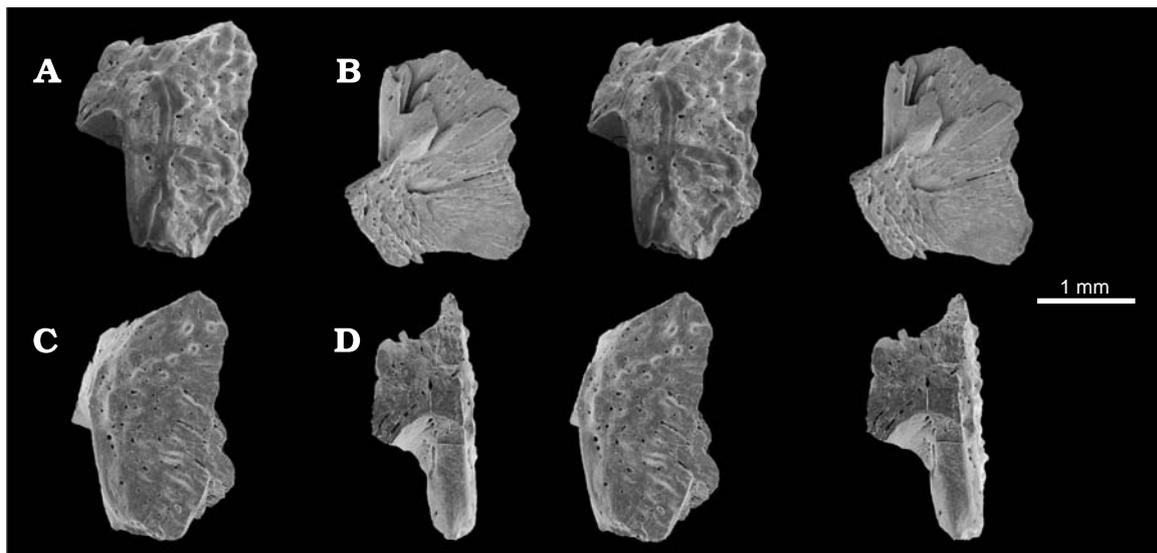


Fig. 32. *Batrachosuchoides* sp., Early Triassic of Czatkowice 1, Poland. Right postparietal ZPAL AbIV/101, in posterodorsal (A), anteroventral (B), anterodorsal (C), and posterior (D) views. SEM stereo-pairs.

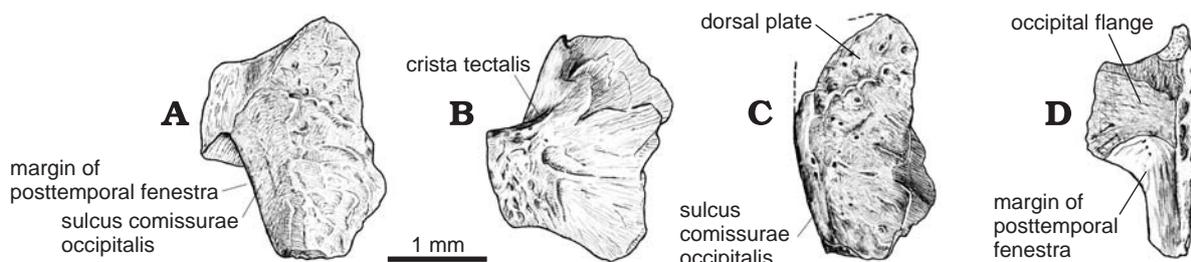


Fig. 33. *Batrachosuchoides* sp., Early Triassic of Czatkowice 1, Poland. Right postparietal ZPAL AbIV/101, in posterodorsal (A), anteroventral (B), anterodorsal (C), and posterior (D) views.

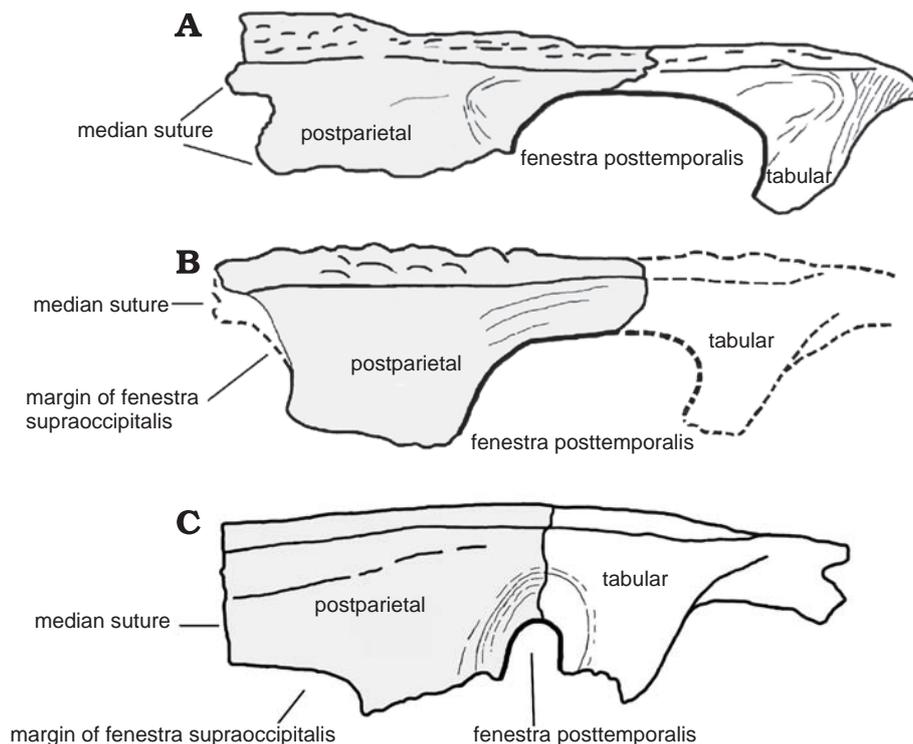


Fig. 34. Recapitulation of ancestral shape of the post-temporal fenestra in ontogeny of brachyopid occiput (**B, C**) as demonstrated by comparison with the trimerorhachoid (*dvinosaurid*) condition (**A**). The postparietal and tabular in occipital view. **A**. Adult *Dvinosaurus*. **B**. Juvenile *Batrachosuchoides*. **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<sub>2</sub>, 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 than 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 brachyopid-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<sub>1</sub>, A<sub>2</sub>, 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

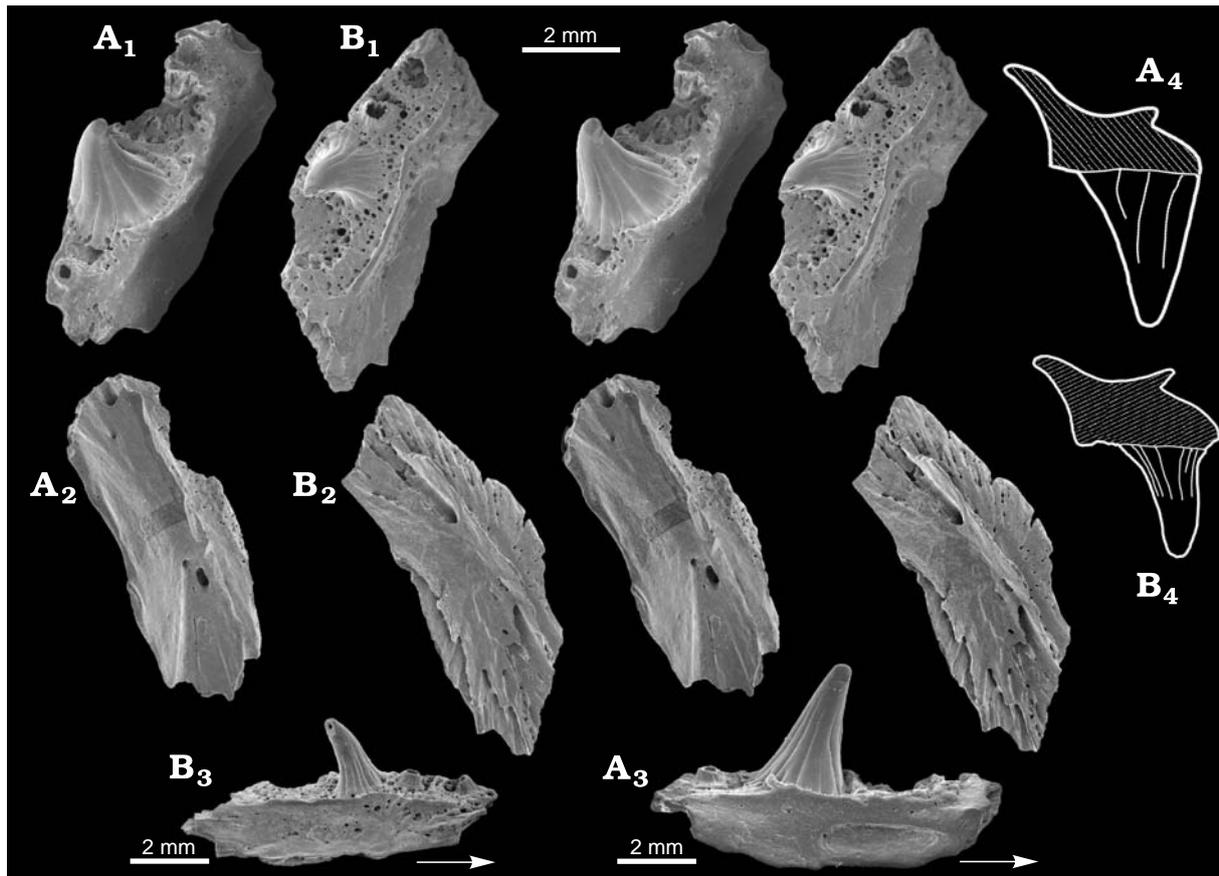


Fig. 35. *Batrachosuchoides* sp., Early Triassic of Czatkowice 1, Poland. Right ectopterygoids: ZPAL AbIV/53 (A) and ZPAL AbIV/36 (B), in ventral (A<sub>1</sub>, B<sub>1</sub>), dorsal (A<sub>2</sub>, B<sub>2</sub>), medial (A<sub>3</sub>, B<sub>3</sub>) views, and cross sections (A<sub>4</sub>, B<sub>4</sub>). All but A<sub>4</sub> and B<sub>4</sub> SEM micrographs; A<sub>1</sub>, A<sub>2</sub> and B<sub>1</sub>, B<sub>2</sub>, 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<sub>1</sub>, B<sub>3</sub>, B<sub>4</sub>, 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<sub>2</sub>, 36B) displays much the same basic pattern as in capitosaurid juveniles. Compared with them, the surface is shorter and more distinctly curved antero-posteriorly, 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 dorso-laterally, 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 surface, the zone of its natural exposure is notched by three well-marked sutural areas bearing faint ridges (Figs 35B<sub>2</sub>, 36B). The anterior of these, bordered medi-

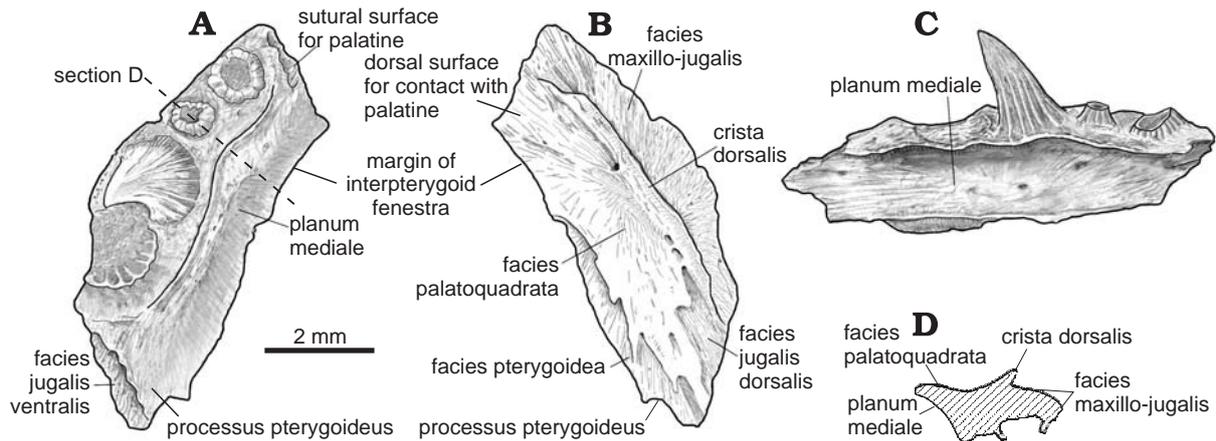


Fig. 36. *Batrachosuchoides* sp. from the Early Triassic of Czatkowice 1, Poland. Right ectopterygoid ZPAL AbIV/36, in ventral (A), dorsal (B), medial (C) views, and cross section (D).

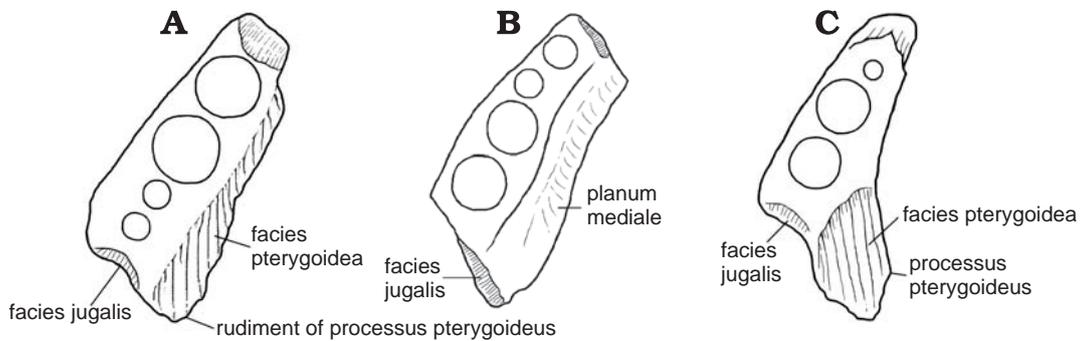


Fig. 37. Modifications of the palatal pterygoid-ectopterygoid suture in trimerhorhachoid and brachyopid temnospondyls as seen from patterns of their ectopterygoids. **A.** *Dvinosaurus primus* (palatal sutural surface for pterygoid narrow and very long; pterygoid process of ectopterygoid rudimentary). **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<sub>3</sub>, A<sub>4</sub>). 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<sub>2</sub>), 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.

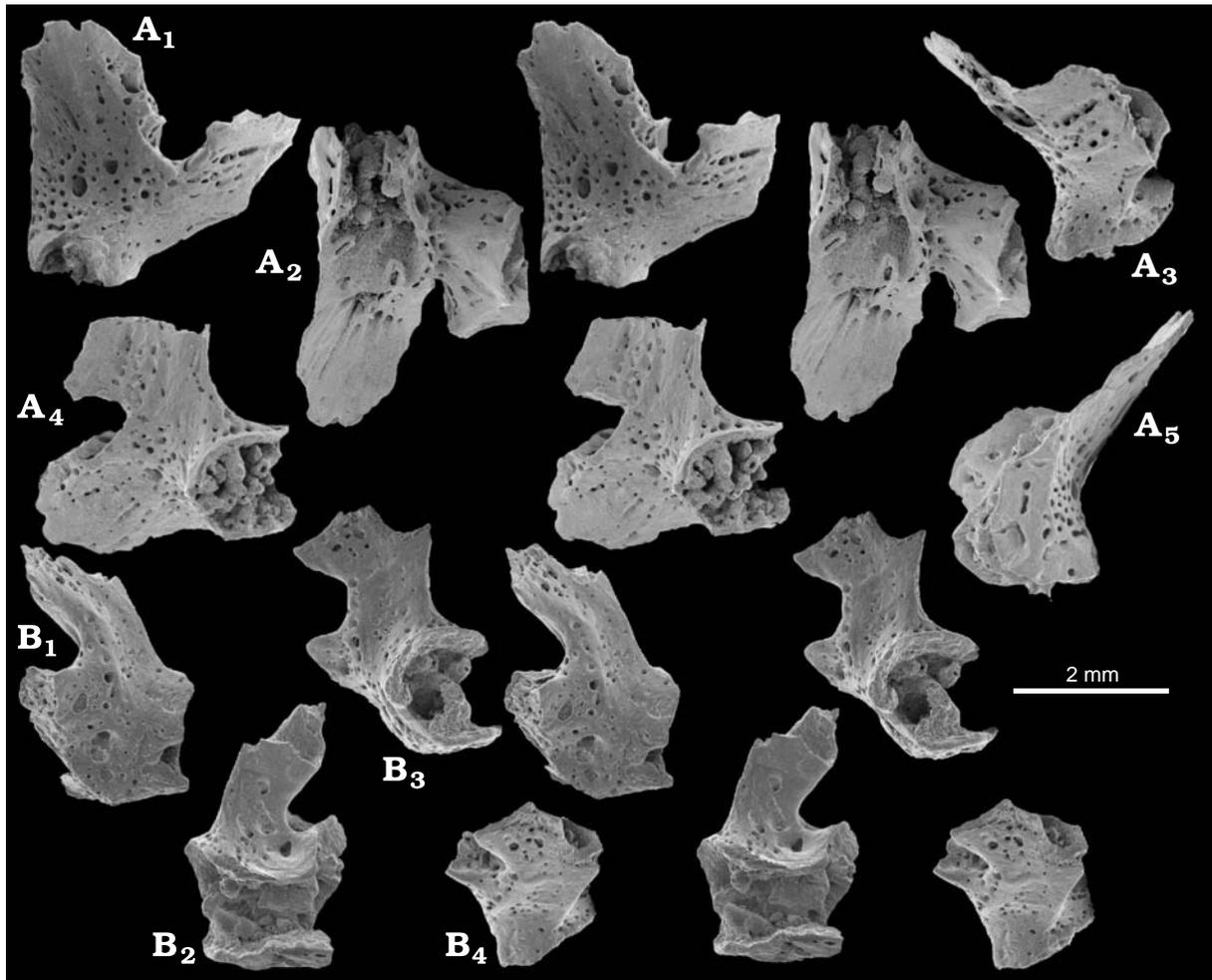


Fig. 38. *Batrachosuchoides* sp., Early Triassic of Czatkowice 1, Poland. Left exoccipitals: ZPAL AbIV/152 (A) and ZPAL AbIV/120 (B), in lateral (A<sub>1</sub>, B<sub>1</sub>), medial (A<sub>2</sub>, B<sub>2</sub>), dorsal (A<sub>3</sub>, B<sub>4</sub>), posterolateral (A<sub>4</sub>), ventral (A<sub>5</sub>), and posterior (B<sub>3</sub>) views. SEM micrographs; all but A<sub>3</sub> and A<sub>5</sub> 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<sub>4</sub>, B<sub>3</sub>, 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

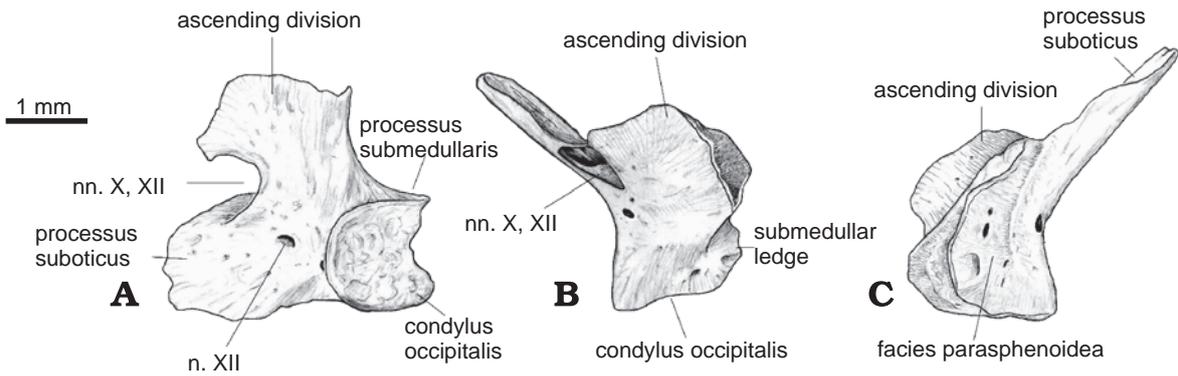


Fig. 39. *Batrachosuchoides* sp., Early Triassic of Czatkowice 1, Poland. Left exoccipital ZPAL AbIV/152, in posterolateral (A), dorsal (B), and ventral (C) views.

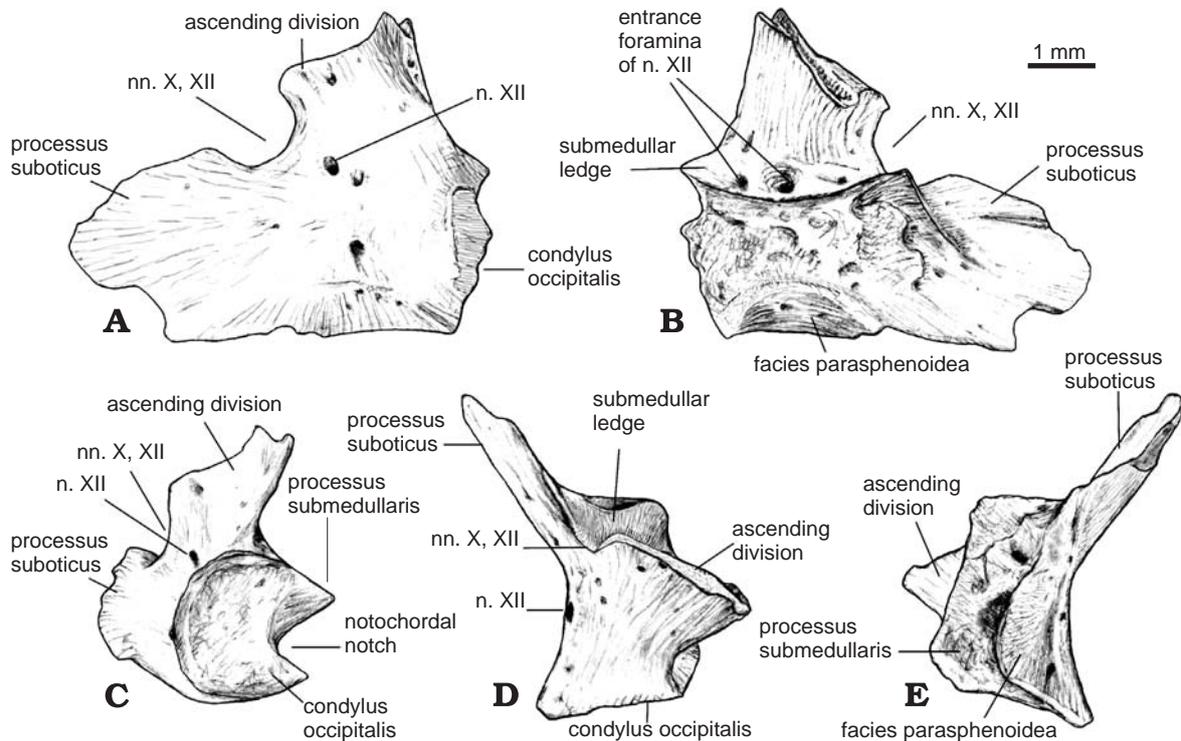


Fig. 40. *Batrachosuchoides* sp., Early Triassic of Czatkowice 1, Poland. Left exoccipital ZPAL AbIV/48, in lateral (A), medial (B), occipital (C), dorsal (D), and ventral (E) views.

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<sub>1</sub>, A<sub>4</sub>, B<sub>1</sub>, 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

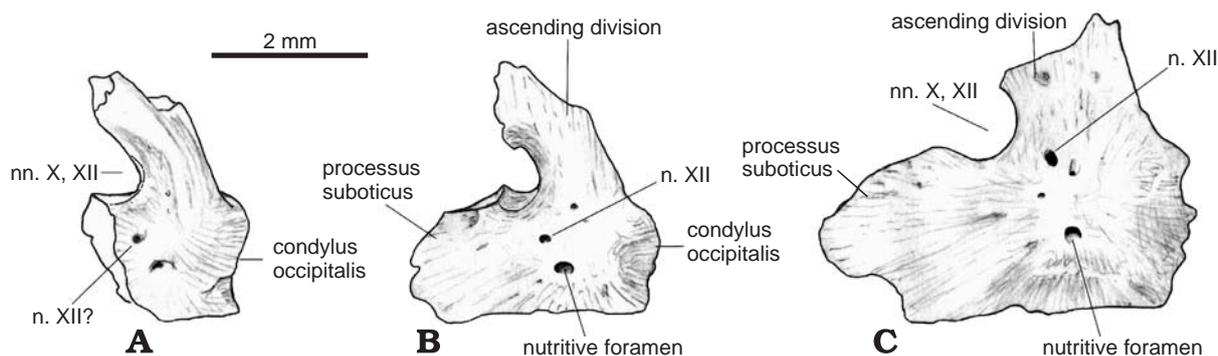


Fig. 41. *Batrachosuchoides* sp., Early Triassic of Czatkowice 1, Poland. Sequence of juvenile growth stages of the exoccipital as documented by specimens ZPAL AbIV/120 (A), ZPAL AbIV/152 (B), and ZPAL AbIV/48 (C), in lateral view.

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<sub>2</sub>, B<sub>2</sub>, 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<sub>3</sub>, A<sub>5</sub>, B<sub>4</sub>, 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<sub>5</sub>, 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-

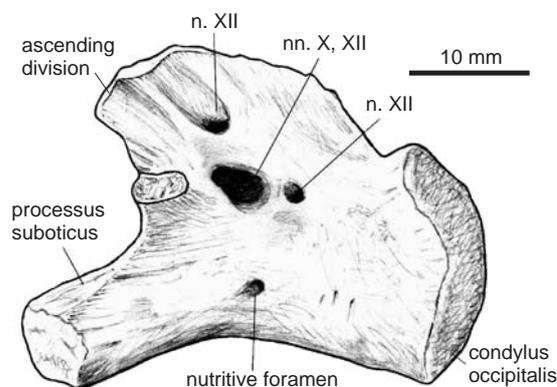


Fig. 42. *Batrachosuchoides* sp., Lower Triassic of Don River Basin, Russia. Adult left exoccipital PIN 1043/653 in lateral view.

imens ZPAL AbIV/120 and especially ZPAL AbIV/152 (Fig. 38A<sub>5</sub>, 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

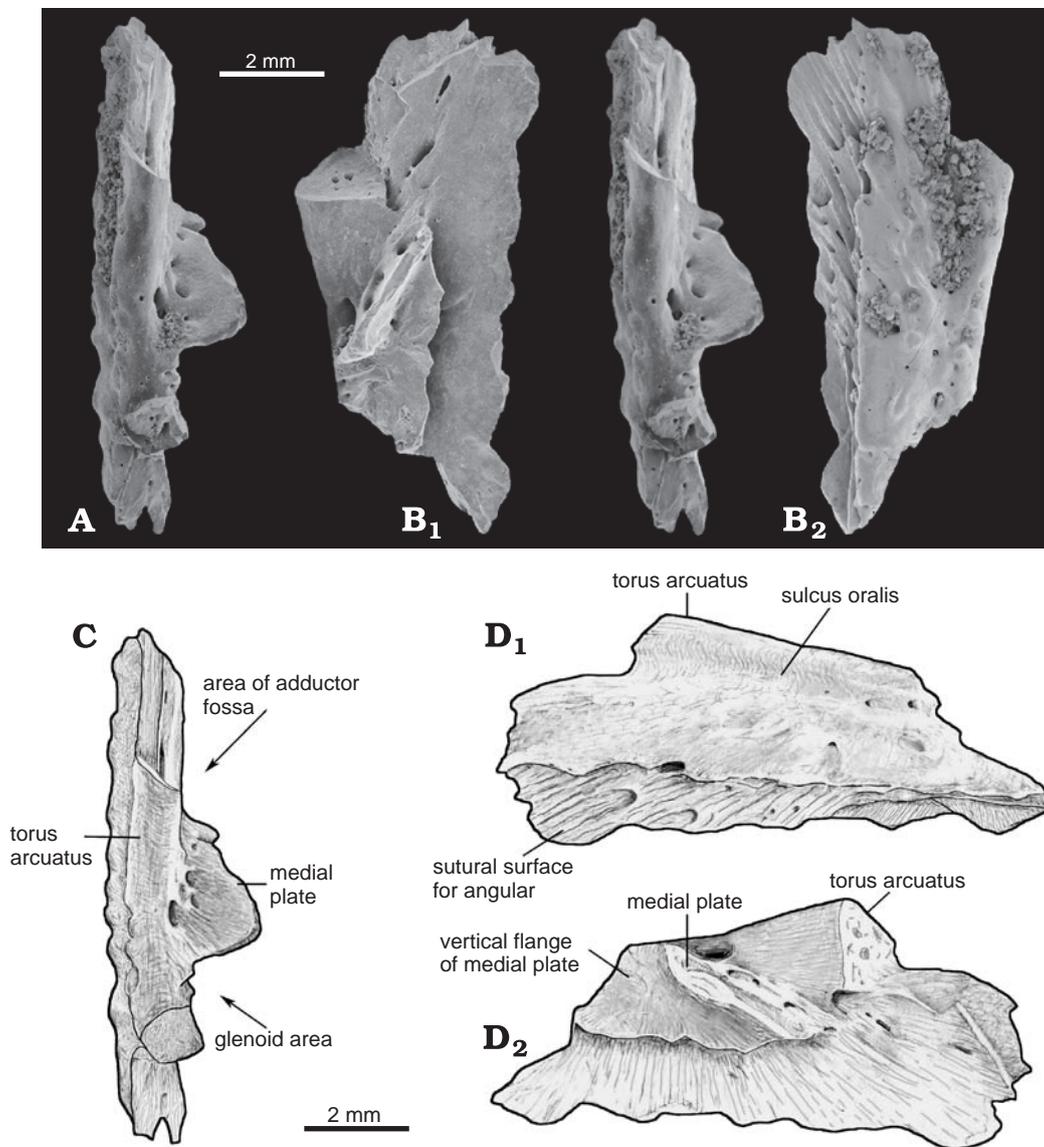


Fig. 43. *Batrachosuchoides* sp., Early Triassic of Czatkowice 1, Poland. Left surangular ZPAL AbIV/69, in lingual (B<sub>1</sub>, D<sub>2</sub>), labial (B<sub>2</sub>, D<sub>1</sub>), and dorsal (A, C) views. A, B, SEM stereo-pairs.

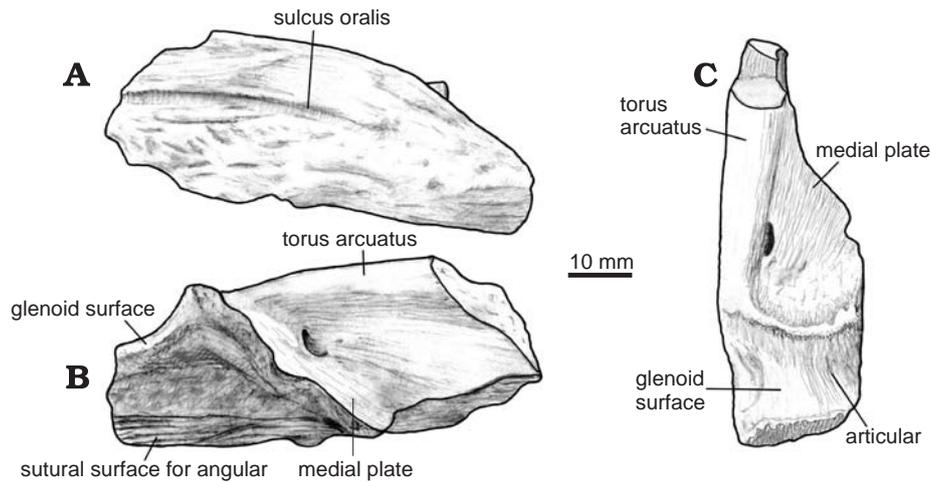


Fig. 44. *Batrachosuchoides lacer* Shishkin, 1966, Lower Triassic of Cis-Urals, Russia. Incomplete left surangular of adult individual PIN 2649/1, in labial (A), lingual (B), and dorsal (C) views.

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<sub>2</sub>, D<sub>1</sub>) 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 sideways. 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<sub>1</sub>, 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<sub>1</sub>, D<sub>2</sub>, 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. Maryńska 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<sub>1</sub>, D<sub>2</sub>). 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 *Batrachosuchooides* 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-described 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.

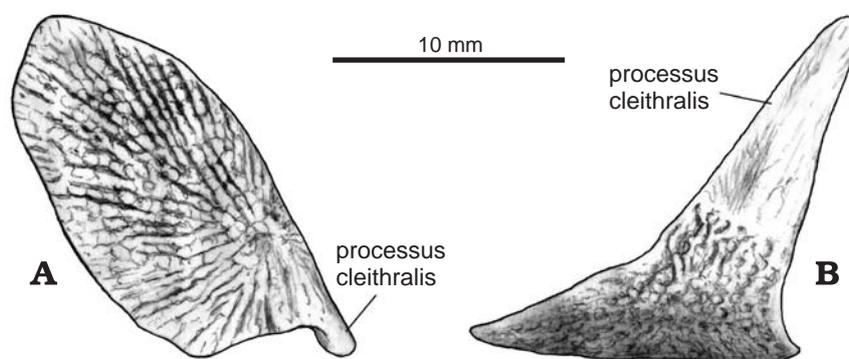


Fig. 45. (?)*Batrachosuchooides* sp., Early Triassic of Czatkowice 1, Poland. Left clavicle ZPAL AbIV/61, in ventral (A) and lateral (B) views.

## 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 pedomorphic 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<sub>2</sub>, A<sub>3</sub>, A<sub>5</sub>, B<sub>1</sub>, B<sub>3</sub>, 12A, C). With growth, this arrangement tends to grade into a more standard capitosaurid 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<sub>1</sub>, E<sub>3</sub>, 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<sub>1</sub>, B<sub>2</sub>, 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<sub>1</sub>, A<sub>3</sub>, B<sub>1</sub>, B<sub>3</sub>, 3A<sub>1</sub>, A<sub>3</sub>, B<sub>1</sub>, B<sub>3</sub>, 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.* Shishkin 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 exemplified by a number of very distantly related Paleozoic forms such as, for example, *Trimerorhachis* and *Dolesempeton* (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 dissorhoids (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<sub>3</sub>, A<sub>4</sub>, 12C, D, 13A, 35A<sub>1</sub>, A<sub>3</sub>, A<sub>4</sub>, B<sub>1</sub>, B<sub>3</sub>, B<sub>4</sub>, 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 unparalleled 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 paedomorphic 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<sub>3</sub>, 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<sub>1</sub>, 19A<sub>3</sub>, B<sub>3</sub>, C<sub>3</sub>, D<sub>3</sub>, 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<sub>1</sub>, 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<sub>1</sub>, A<sub>4</sub>, B<sub>2</sub>, B<sub>4</sub>, 12B, D, 35A<sub>2</sub>, A<sub>4</sub>, B<sub>2</sub>, B<sub>4</sub>, 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 paedomorph

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 extension 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 (Rybinkian-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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