

# PROCOLOPHONIDS FROM THE EARLY TRIASSIC OF POLAND

MAGDALENA BORSUK-BIAŁYNICKA and MARIUSZ LUBKA

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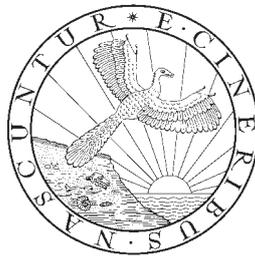
Early Triassic disarticulated bones from karst deposits at Czatkowice 1, southern Poland, are assigned to a procolophonine species *Procolina teresae* gen. et sp. n. *Procolina teresae* is characterized by a small adult size, unicuspid tooth crowns, and a derived heterodont dentition. Unicuspid tooth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

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

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## INTRODUCTION

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

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

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

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

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

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

**Acknowledgements.** — We are indebted to Mariusz Paszkowski and Józef Wieczorek (Jagiellonian University, Kraków) who discovered the Czatkowice 1 breccia and, offered it for study, as well as to the late Halszka Osmólska (Institute of Paleobiology, Polish Academy of Sciences, Warsaw) and Teresa Maryńska (Museum of the Earth, Polish Academy of Sciences, Warsaw), who kindly transmitted the material to us. Teresa Maryńska, who was engaged in the procolophonid studies some years ago, supported us with her experience and gave comments on the manuscript. We are grateful for her help. Thanks are due to Susan Evans and to the referees, Robert Carroll (Redpath Museum, Montreal) and Hans-Dieter Sues (National Museum of Natural History, Washington), for their valuable criticism and helpful comments. Thanks are also due to the following staff members of the Institute of Paleobiology, Polish Academy of Sciences in Warsaw: Ewa Hara for preparation of the material, Cyprian Kulicki for SEM microphotographs, and Aleksandra Hołda-Michalska for preparing computer illustrations.

## GEOLOGICAL SETTING

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

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

## MATERIALS AND METHODS

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

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

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

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

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

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

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

\* based on Lubka (1999).

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

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

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

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

## SYSTEMATIC BACKGROUND

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

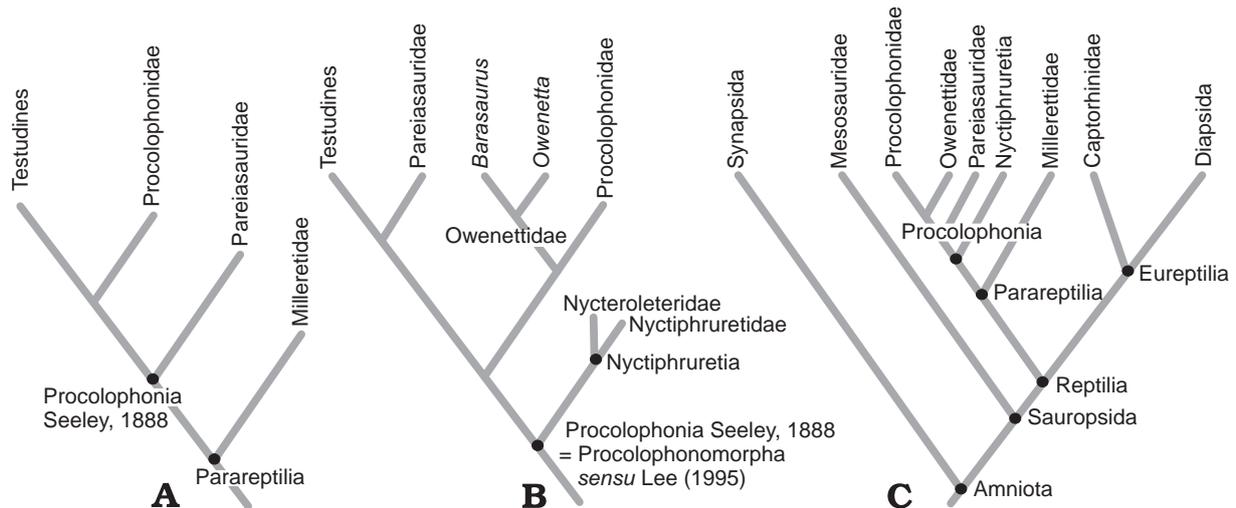


Fig. 1. **A. B.** Relationships within the Parareptilia. **A.** Simplified cladogram by Laurin and Reisz (1995). **B.** According to Lee (1995). **C.** Position of the Procolophonidae within the Amniota according to Laurin and Reisz (1995).

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

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

## SYSTEMATIC PALEONTOLOGY

Subclass **Parareptilia** Olson, 1947

Order **Procolophonia** Seeley, 1888

Family **Procolophonidae** Seeley, 1888

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

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

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

Derivation of the name: From abbreviated family name.

**Diagnosis.** — As for the species.

*Procolina teresae* sp. n.

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

Type horizon: Early Late Olenekian.

Type locality: Czatkowice 1, southern Poland.

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

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

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

**Range.** — Early Late Olenekian.

## SKULL BONES

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

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

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

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

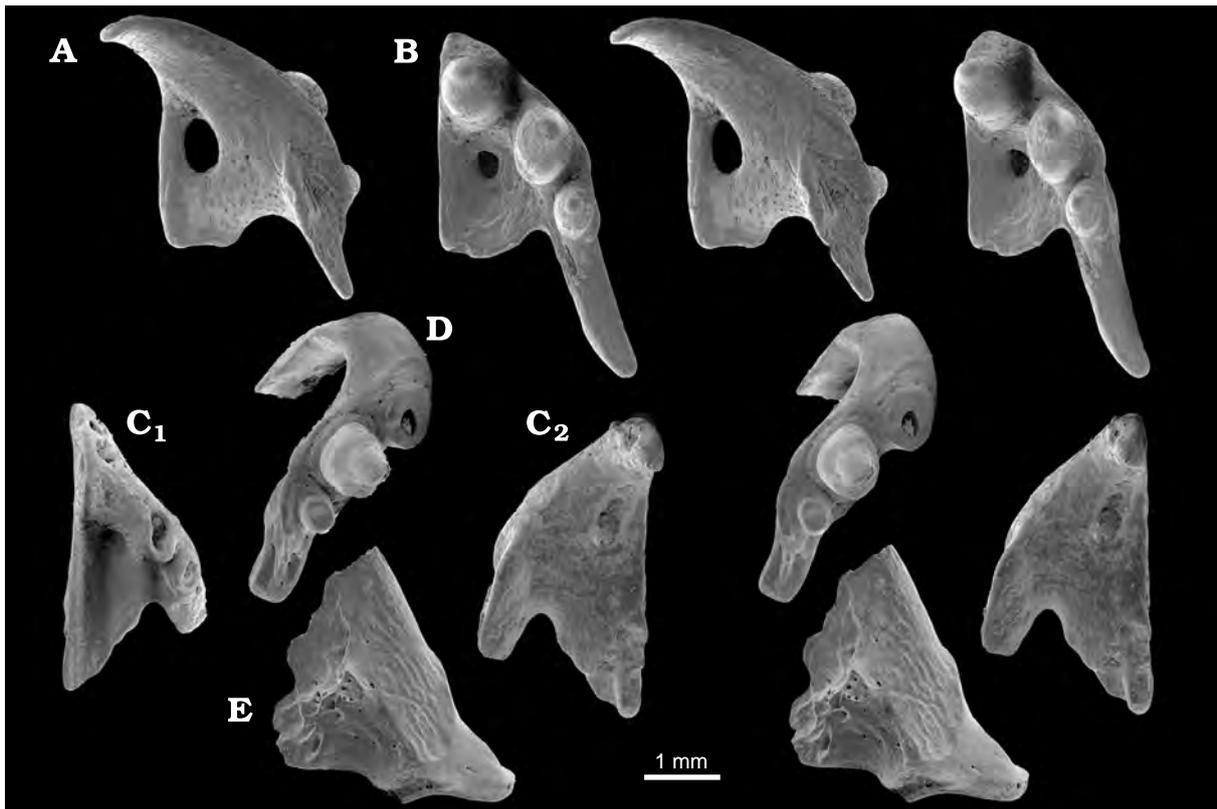


Fig. 2. *Procolina teresae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. A–D. Premaxillae. A. Right bone ZPAL RV/794, in dorsolateral view. B. Left bone ZPAL RV/797, in ventral view. C. Left bone ZPAL RV/795, in anteroventral (C<sub>1</sub>) and dorsal (C<sub>2</sub>) views. D. Right bone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

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

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

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

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

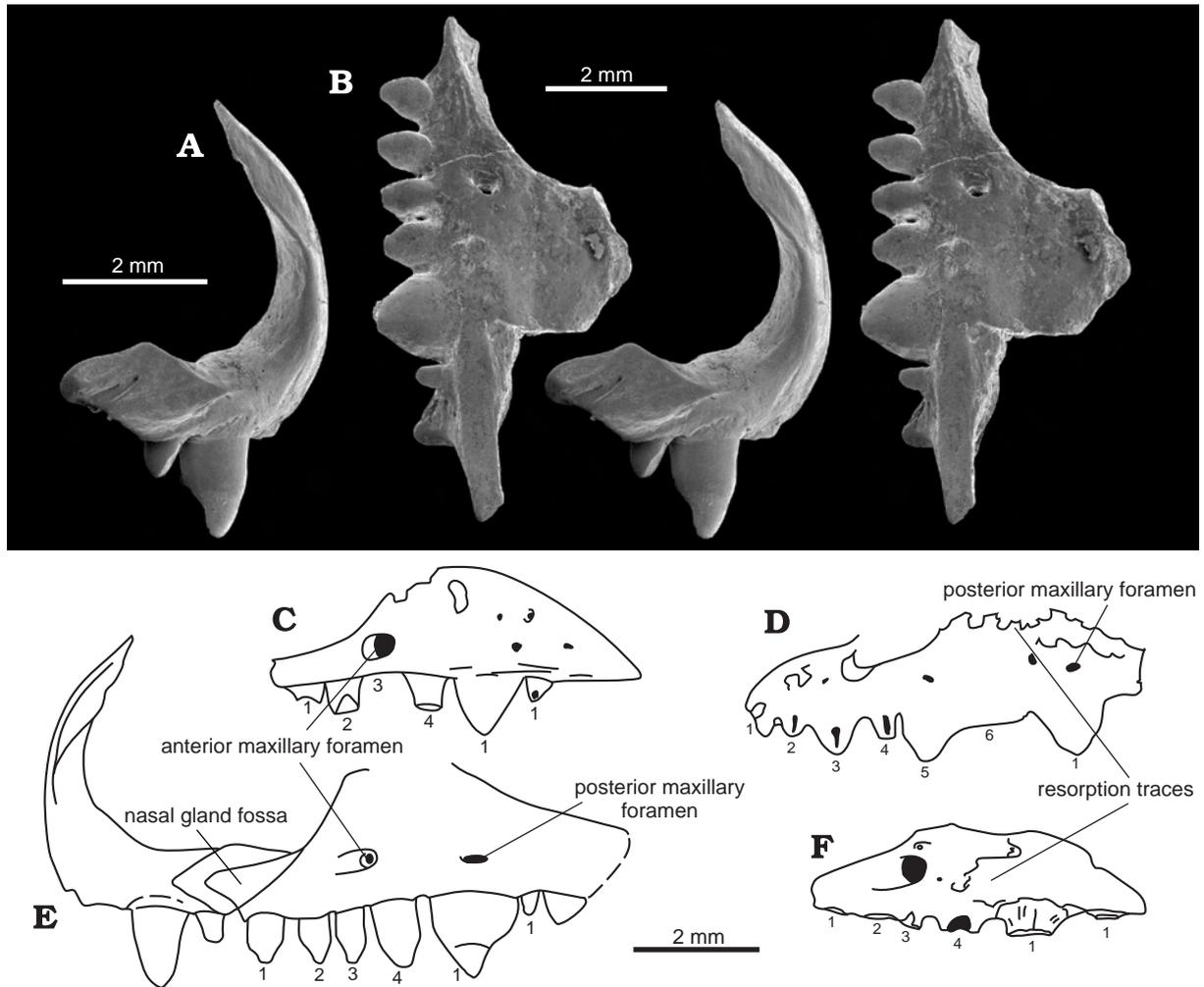


Fig. 3. **A–C, E, F.** *Procolina teresae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A.** Right premaxilla ZPAL RV/796. **B.** Right maxilla ZPAL RV/711. **C.** Juvenile right maxilla ZPAL RV/735 (reversed). **E.** Left maxilla ZPAL RV/711 combined with the premaxilla ZPAL RV/796. **F.**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

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

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

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

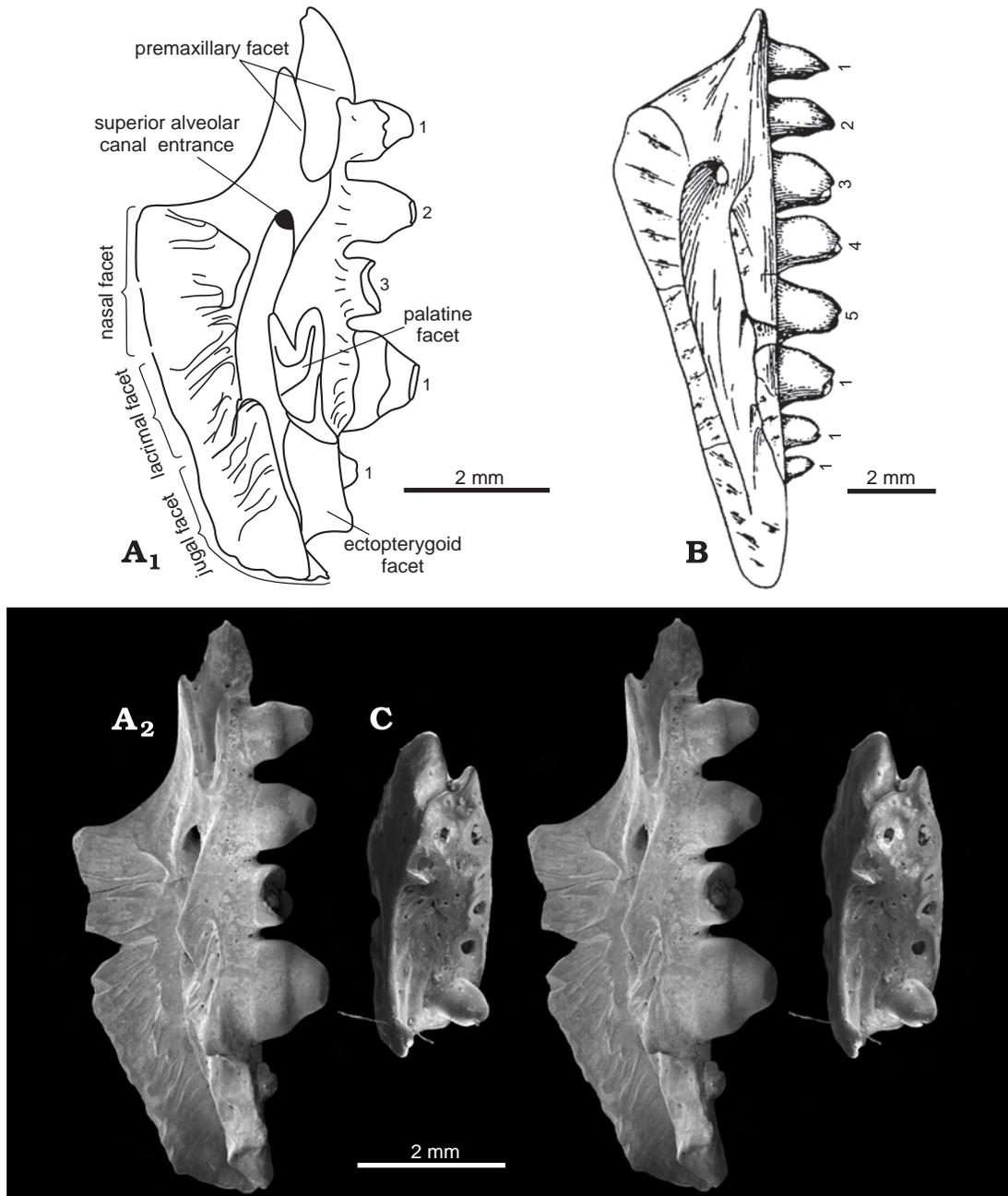


Fig. 4. **A, C.** *Procolina teresae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A.** Left maxilla ZPAL RV/710, in medial view. **C.** Juvenile left vomer ZPAL RV/986, in ventral view. **B.** *Tichvinskia vjatkensis* Tchudinov et Vjushkov, 1956, right maxilla, reversed (after Ivakhnenko 1979, fig. 10B). A<sub>2</sub>, C, SEM stereo-pairs.

transversely set pair, and the remaining three follow the lateral tooth (Fig. 5A<sub>2</sub>). Surrounded by the teeth, the ventral surface of the bone is concave and bears some neurovascular foramina. The premaxillary process is pyramidal and has an anteriorly ascending position (Fig. 5A<sub>1</sub>). Ventrally, it bears an elongated concave premaxillary facet that slopes ventro-laterally (Fig. 5A<sub>2</sub>, A<sub>3</sub>, arrows) and matches the longitudinal step of vomerine facet of the premaxilla (see above). The posteromedial border of the bone is rarely preserved (Fig. 4C), but the posterolateral process seems to extend further posterior than the body of the bone itself, in which case it would match a deep subquadrangular medial incision on the palatine (Fig. 6B). The dorsal surface of the bone is concave (Fig. 5A<sub>1</sub>), and bears complicated palatine facets. When articulated the paired vomers produce an elongated posterior incision to receive the medial processes of the pterygoids (Fig. 8). The symphyseal surface of the bone is heavily sculptured (Fig. 5B) with oblique posteroventral furrows, and penetrated by vascular canals. In the posterior one third it bears a distinct facet, probably for the pterygoid.

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

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

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

The ventral surface of the bone (Fig. 6A) is strongly concave with the axis oriented parasagittally, towards the choana. A tongue-like process protrudes anterodorsally and slightly above the choanal border. It is accompanied by several smaller tubercles situated medial and posterior to it, that together make up a complicated facet facing anterodorsally that may have received the prefrontal (Fig. 6B<sub>1</sub>). Lateral to it, a sinuous facet was destined for the maxilla (ventrally) and most probably for the lacrimal (dorsally). It consists of two tubera separated by a U-shaped infraorbital incision situated directly at the lateral exit of the transversal furrow on the dorsal surface. Posteriorly, the maxillary facet passes into the ectopterygoid one, which probably merged with the ectopterygoid facet of the pterygoid. The posteromedial border was overlapped ventrally by the pterygoid, as demonstrated by a partly preserved shelf-like facet (Fig. 6A<sub>2</sub>). A deep excavation of the anteromedial border must have accommodated the posterior process of the vomer (Fig. 6B<sub>1</sub>).

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

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

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

**Pterygoid.** — The pterygoid of *Procolina* displays broad proportions with largely expanded palatal wing and large quadrate process. The ventral surface of the palatal wing (Fig. 7B<sub>2</sub>, C) is strongly concave between a medial margin that is thick and truncate, and a lateral one that is sharp. The concavity passes gently through the neck onto the medial side of the quadrate process. The palatal wing is not separated from the neck by any crest. The dorsal surface of the palatal wing is convex transversely (Fig. 6A), and concave longitudinally. It is very smooth and bears no vascular traces. The quadrate process bears a deep excavation bordered by protruding ridges (possible sites of insertions of the protractor pterygoidei and levator pterygoidei muscles). The medial border of the palatal wing is never completely preserved to demonstrate either the kind of articulation with the

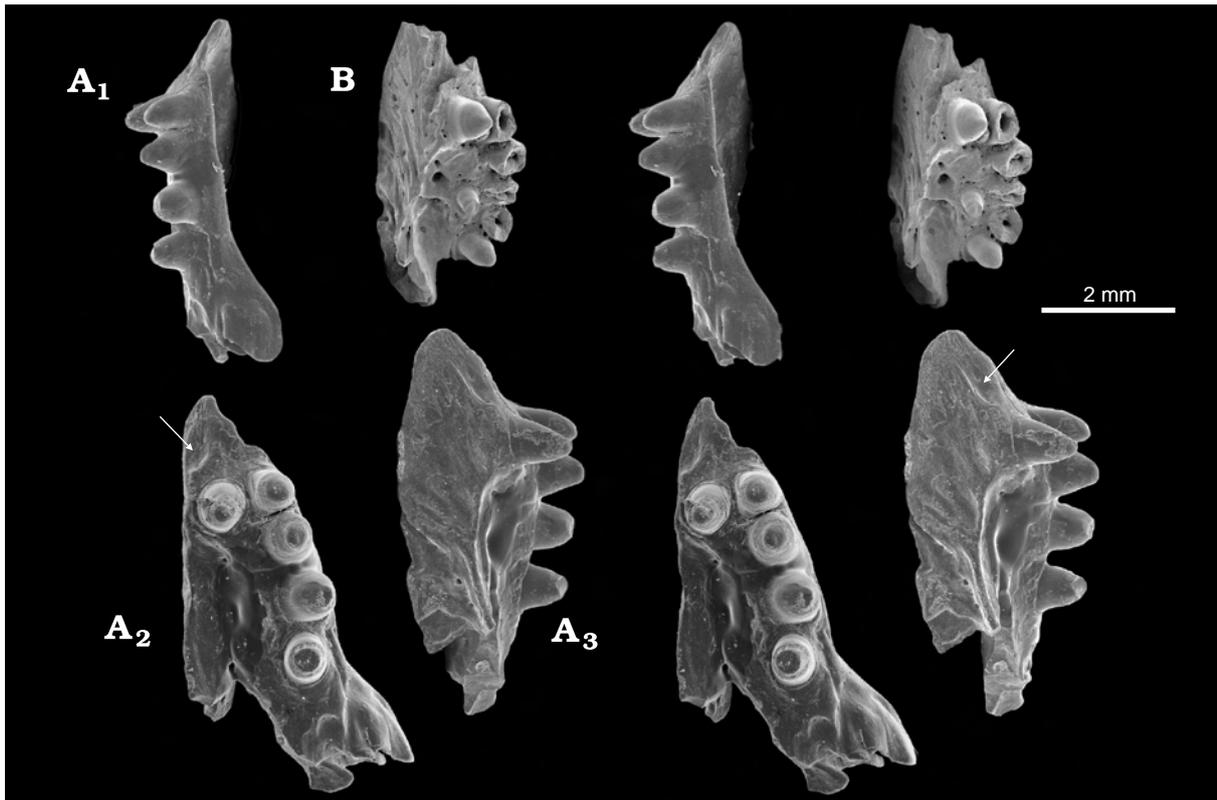


Fig. 5. *Procolina teresae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A.** Left vomer ZPAL RV/714, in lateral (A<sub>1</sub>), medial (A<sub>2</sub>), and ventral (A<sub>3</sub>) views. **B.** Left vomer ZPAL RV/729, in medio-ventral view. The arrows indicates premaxillary facet. SEM stereo-pairs.

vomer or any possible articulation with the contralateral pterygoid. The preserved fragment of the medial border bears one row of denticles (Fig. 7B<sub>2</sub>, E), but there are no teeth on the ectopterygoid process (Fig. 7B<sub>2</sub>, C).

In a number of specimens, the thick ectopterygoid process is present intact. On this process, the palatine facet (Fig. 7B<sub>2</sub>, C) presents a shelf-like offset almost half as large as the entire palatal wing and is medially delimited by an incision. The ectopterygoid facet extends on both ventral and dorsal surface of the thick lateral end of the process. The medial side of the neck is deeply excavated for the basipterygoid articulation, which lacks a bordering knob and is notable in being widely open ventrally (Fig. 7C). In life, the basipterygoid fossa must have faced more or less medially to articulate with the basipterygoid processes, and this implies a medioventral orientation of the excavated surface of the quadrate process.

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

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

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

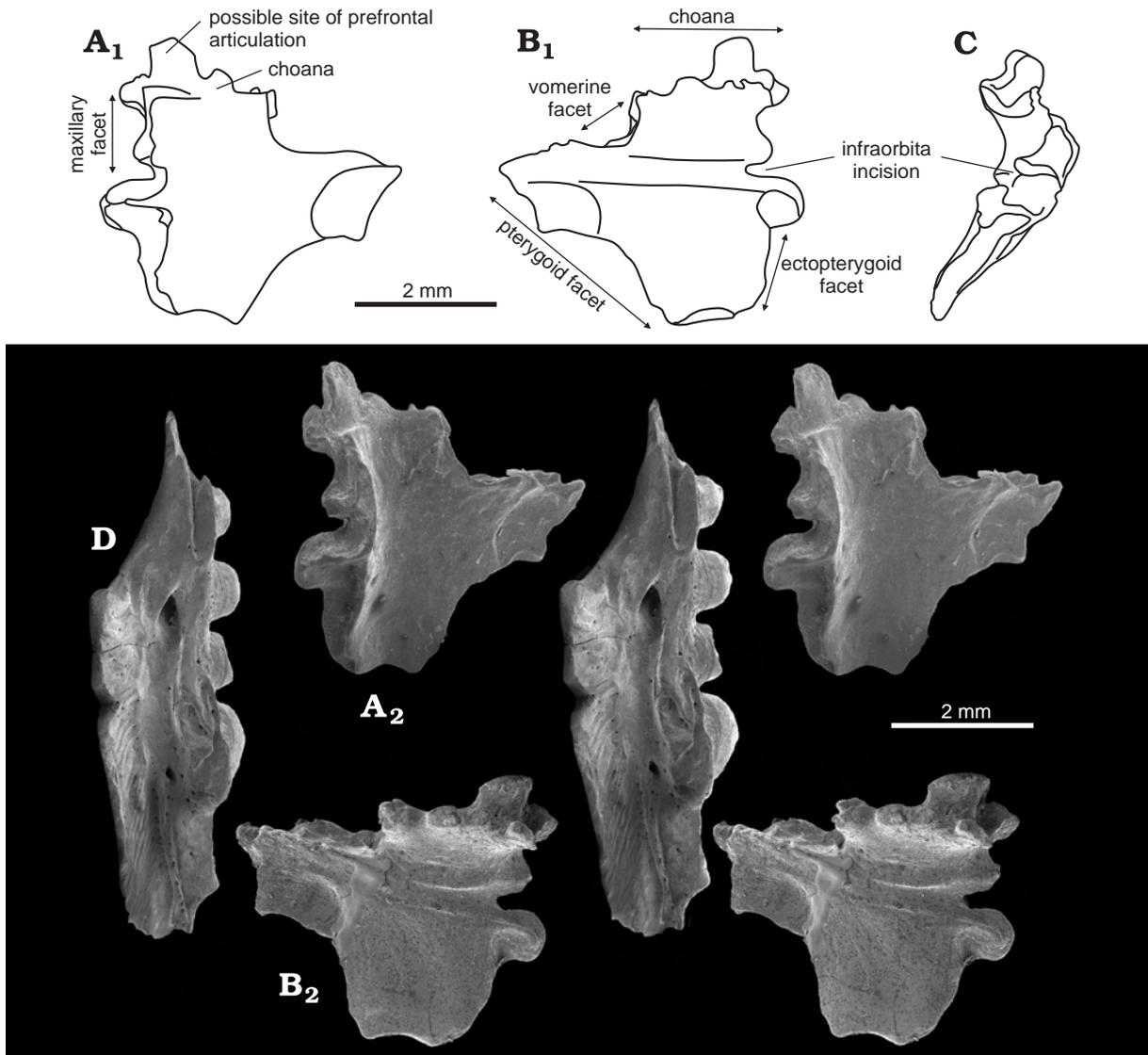


Fig. 6. *Procolina teresae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. A–C. Right palatine ZPAL RV/526, in ventral (A<sub>1</sub>, A<sub>2</sub>), dorsal (B<sub>1</sub>, B<sub>2</sub> reversed), and lateral (C) views. D. Left maxilla ZPAL RV/710, in dorso-lingual view. A<sub>2</sub>, B<sub>2</sub>, D, SEM stereo-pairs.

On the lingual side of the dentary, the irregularly U-shaped symphysis faces anteromedially (Figs 9, 11D<sub>1</sub>). Its position determines the angle between the mandibular rami as about 60°. The tooth-bearing margin is large and turns medially in the symphyseal region. Below the tooth row, a deep dental shelf is slightly flattened for the splenial contact, and bears an elongated coronoid facet posterodorsally (Figs 9, 10A<sub>2</sub>). As a rule, the posterior rudimentary teeth, referred to herein as accessory teeth, are located above this facet. The dental shelf overhangs the Meckelian fossa. Separated from the fossa by an osseous wall, a dorsal canal carried the inferior alveolar nerve. Its entrance (Fig. 9, indicated by an arrow), situated below the posterior one third of the tooth row, serves as a reference point for the dental formula (see below). The concavity of the Meckelian fossa is ventrally bordered by the thick edge of the dentary, which is lingually flattened for the ventral contact with the splenial. As measured on 13 specimens (Appendix 1), the approximate dimensions show variability range in tooth row length from 6 mm (juvenile) to about 10 mm, with a mean value of about 8 mm and a mean ratio of dentary depth (dd) to the tooth row length of about 1:4.7. These numbers give only a rough indication, because of the small sample on which the measurements can be taken, and the difficulties in taking them exactly. The mandibular proportions given by Ivakhnenko (1979) for procolophonid jaws, and those for mandible to skull length in *Procolophon* (Carroll and Lindsay 1985), allow estimates of mandible length in *Procolina* as about 15 to 25 mm, and hence a total skull length of

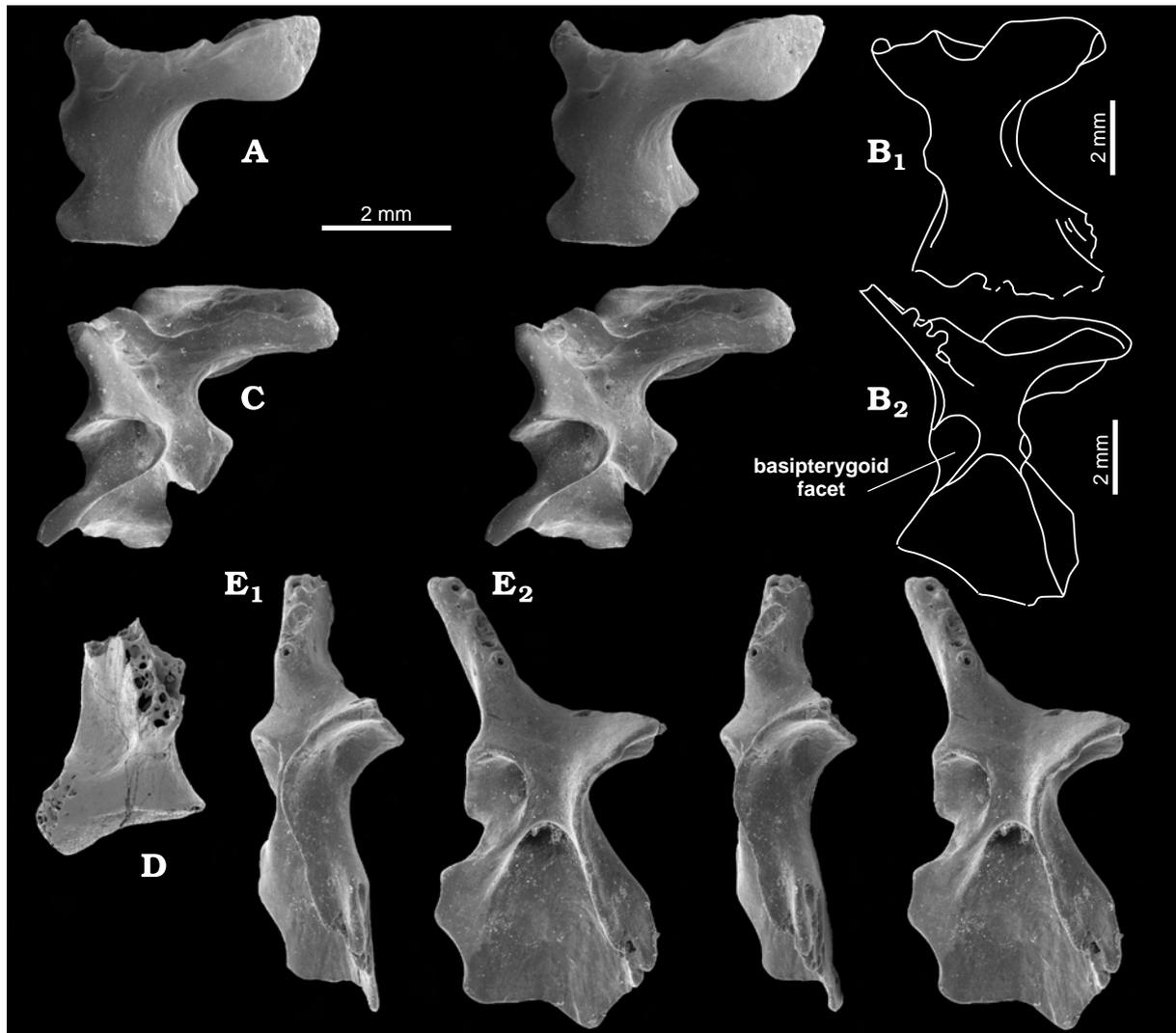


Fig. 7. *Procolina teresae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. A. Right pterygoid ZPAL RV/63, in dorsal view. B. Reconstruction of the right pterygoid, in dorsal view (B<sub>1</sub>) and the left pterygoid, in ventral view (B<sub>2</sub>). C. Left pterygoid ZPAL RV/521, in ventral view. D. Right quadrate ZPAL RV/756, in anterior view. E. Left pterygoid ZPAL RV/505, in lateral (E<sub>1</sub>) and medioventral (E<sub>2</sub>) views. All but B SEM micrographs; all but B, D stereo-pairs.

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

#### DENTITION

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

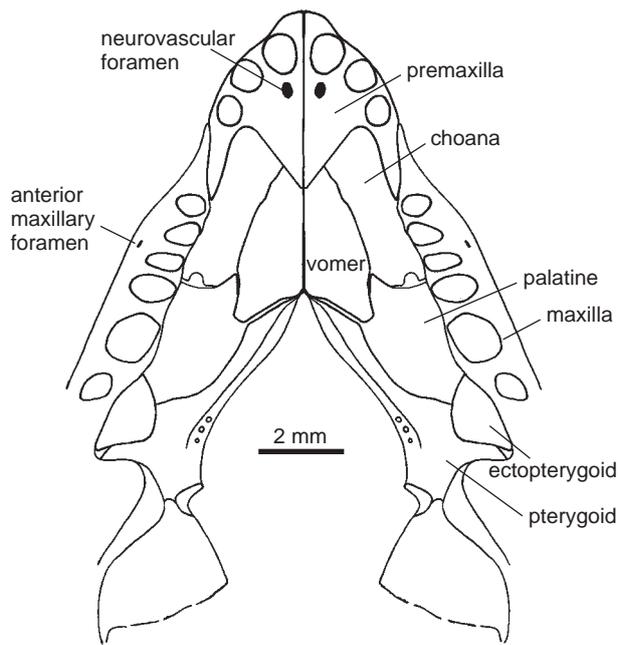


Fig. 8. *Procolina teresae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Reconstruction of palate and jaws, in ventral view.

anterior to the molariform tooth. Significantly, a maxilla specimen ZPAL R/735 (Fig. 12A), smaller than the average and showing traces of tooth replacement already displays the modal tooth formula 4.1.1. Specimen ZPAL RV/721 bears traces of fusion of tooth buds II and III into one tooth, and probably the same in the case of buds V and VI (Fig. 12B).

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

Some anterior shift of the posterior teeth (Appendix 1, Fig. 9E) is evidenced by the differences in relations of the dominant tooth to the posterior alveolar foramen, and to the coronoid facet (see p. 109). There is considerable variability in the size and position of accessory teeth, which may be quite small (Fig. 9C) or equal in size to the molariform tooth (Fig. 10D). Their position varies from posterolabial (Figs 10A, 11D) to directly posterior to the molariform tooth (Fig. 10C). Only in one instance, is there a trace of tooth replacement in a form of small cavities posterolingual to the tooth sites (Fig. 10A<sub>3</sub>).

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

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

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

**Tooth shape.** — Most specimens display a consistent tooth shape (Figs 10–12) with no trace of bicuspid condition. Incisiform teeth are roughly chisel-like (Fig. 10C<sub>1</sub>). The outline of their bases, are more or less transversely flattened. Beginning with the premolariform teeth, the crown bases become increasingly more robust toward the rear. They are bulbous, but cylindrical rather than spherical, and are capped with cone-shaped apices of blackish enamel. Wear facets generally face posteromedial on the premaxilla, medial or apical on the maxilla, and apical or posteromedial on the dentary.

**Dental formula.** — As a whole, the upper (premaxillary + maxillary) tooth row includes 8 or 9 teeth. The premaxilla bears 3 slender and more acute incisor-like teeth referred to as incisiforms. The maxillary tooth row includes 5 or 6 teeth of which the last one is tiny (Fig. 12B, C). The penultimate, usually the biggest, is the molariform. The number of premolariform teeth is subject to a small amount of intraspecific and/or ontogenetic variability. There are either 3 (Figs 4A, 12B) or 4 teeth (Fig. 3E) distributed within the same jaw section

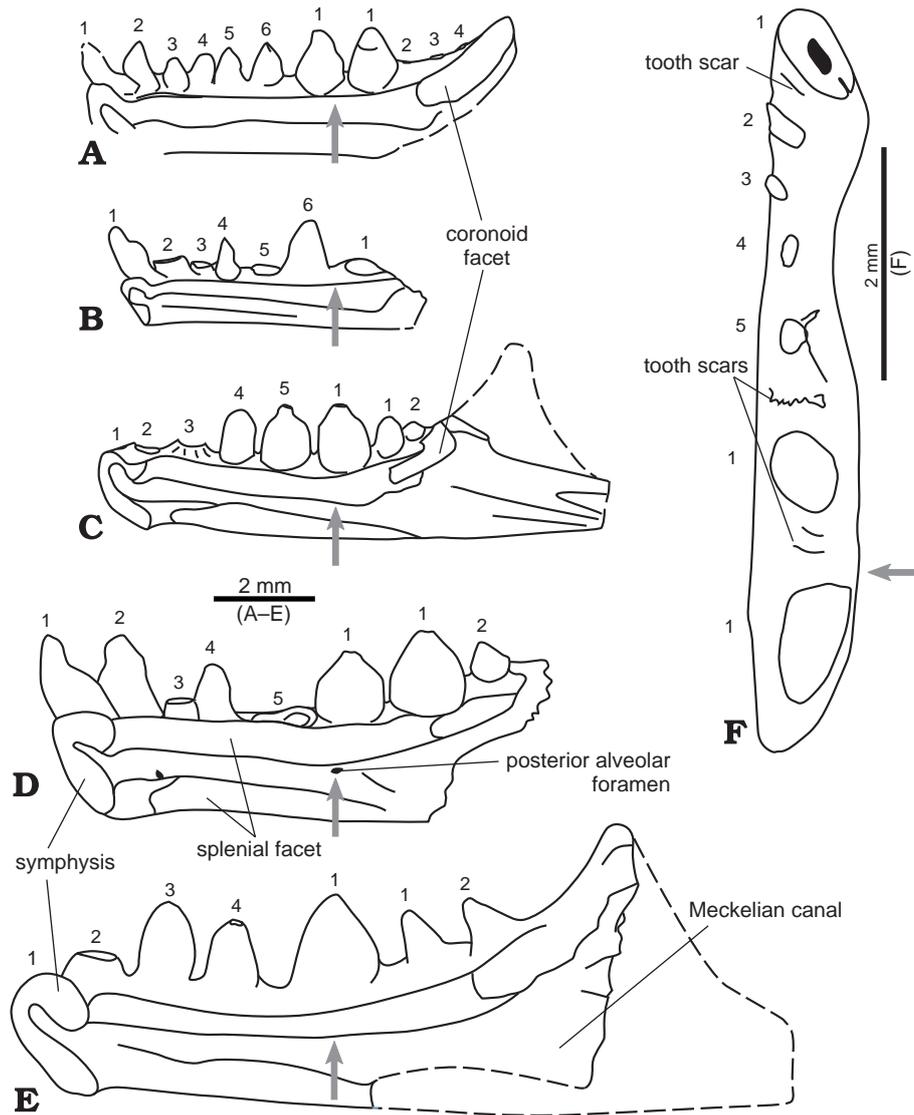


Fig. 9. Right dentaries from the Early Triassic of Czatkowice 1, Poland, in medial view. **A, F.** Procolophonidae gen. indet. I: ZPAL RV/733 (**A**) and ZPAL RV/989 (**F**). **B, C–E.** *Procolina teresae* gen. et sp. n.: ZPAL RV/516 (**B**), ZPAL RV/515 (**C**), ZPAL RV/524 (**D**), and ZPAL RV/683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

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

### VERTEBRAL COLUMN

The better ossified procolophonid vertebrae (Fig. 19A, H) of the Czatkowice 1 material are here associated with the better ossified skull material assigned to *Procolina teresae*. *Procolina teresae* seems to have the spines placed more anteriorly than do other Czatkowice 1 procolophonids, which results in the posterior fossa being more exposed (Fig. 19A<sub>2</sub>, B<sub>2</sub>), but these differences might be subjective. It also has less swollen bases of the neural spines. Vertebrae representing all regions of the vertebral column of *Procolina teresae* are known. However, the atlas-axis complex elements and well-preserved sacrals are very rare (respectively ZPAL RV/825, 826 and ZPAL RV/835–838). On the basis of overall morphology we were able to distinguish seven cervical verte-

brae (Fig. 16A, ZPAL RV/825–830 and Fig. 16C, the first from the left, ZPAL RV/831). The seventh and probably eighth vertebrae (ZPAL RV/831 and 832) seem to be transitional to the dorsal series. Dorsals (Fig. 16C three on the right, ZPAL RV/845, 833, 834) are proportionally slightly shorter than the cervicals and longer than the sacrals. Three sacrals (Fig. 18), each with distinctive sacral ribs have been tentatively assigned to *Procolina teresae*. Anterior caudals have well-developed pleurapophyses. All centra (pleurocentra) are amphicoelous and reach up to 7 mm in length (Table 1), but usually less than this.

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

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

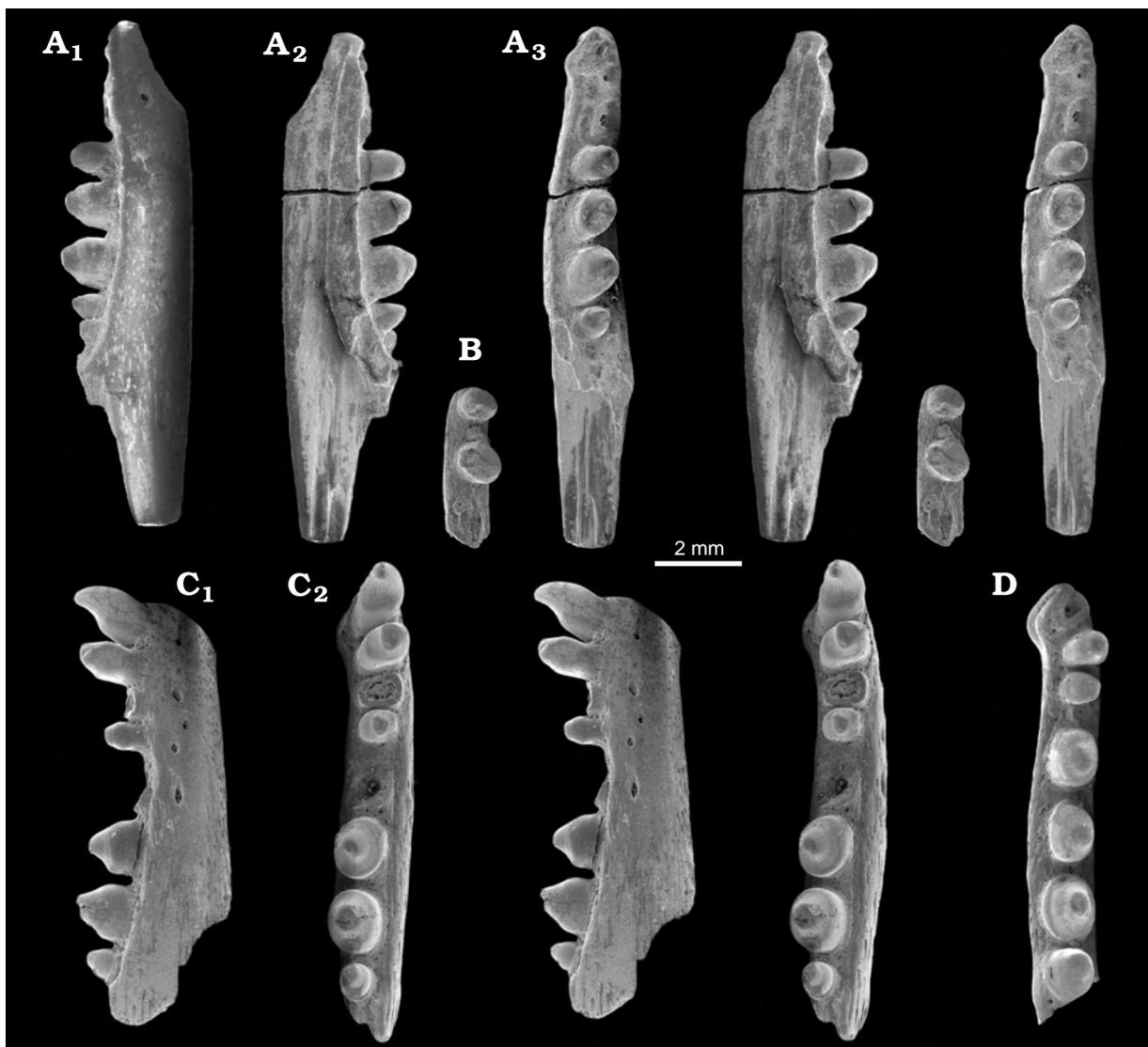


Fig. 10. A, C, D. *Procolina teresae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Right dentaries: ZPAL RV /515 (A), ZPAL RV/524 (C), and ZPAL RV /799 (D). B. *Procolophonidae* gen. indet. II, Early Triassic Czatkowice 1, Poland. The only fragment with bicuspid dentition ZPAL RV/507. Labial (A<sub>1</sub>, C<sub>1</sub>), lingual (A<sub>2</sub>), and occlusal (A<sub>3</sub>, B, C<sub>2</sub>, D) views. SEM micrographs; all but A<sub>1</sub>, D stereo-pairs.

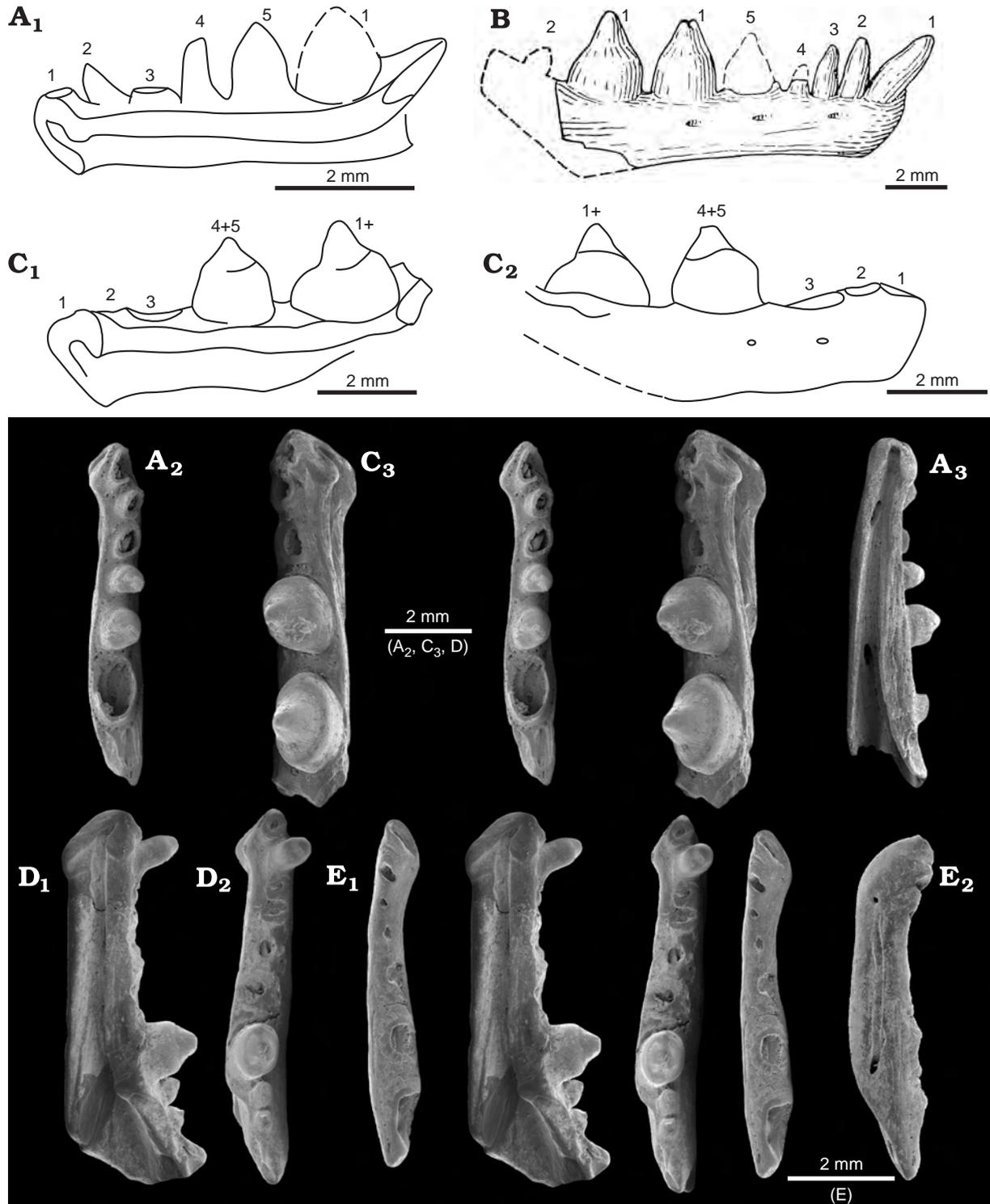


Fig. 11. Procolophonids from the Early Triassic of Czatkowice 1, Poland. **A, D.** *Procolina teresae* gen. et sp. n. Right dentaries: ZPAL RV /510 (**A**) and ZPAL RV/513 (**D**). **B.** *Burtensia burtensis* (Otschev, 1958), left dentary. **C.** Procolophoninae gen. indet. III ZPAL RV /716. **E.** Procolophoninae gen. indet. I ZPAL RV /989. Lingual (**A**<sub>1</sub>, **A**<sub>3</sub>, **C**<sub>1</sub>, **D**<sub>1</sub>), labial (**B**, **E**<sub>2</sub>), and occlusal (**A**<sub>2</sub>, **C**<sub>3</sub>, **D**<sub>2</sub>, **E**) views. **A**<sub>2</sub>, **A**<sub>3</sub>, **C**<sub>3</sub>, **D**<sub>1</sub>, **D**<sub>2</sub>, **E**<sub>1</sub>, **E**<sub>2</sub>, SEM micrographs; all but **A**<sub>3</sub>, **E**<sub>2</sub> stereo-pairs.

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

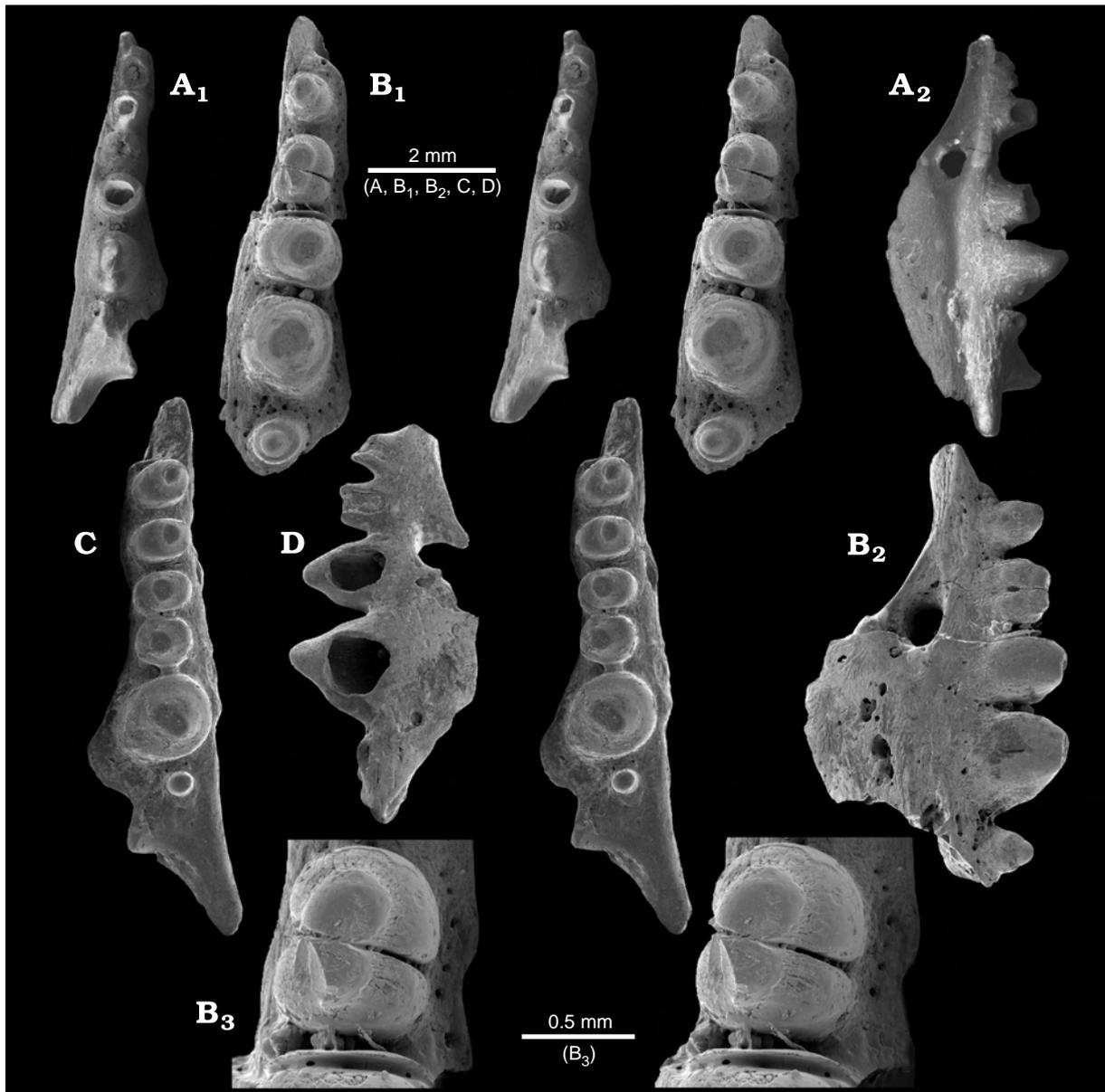


Fig. 12. *Procolina teresae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A, B**. Right maxillae: ZPAL RV/735 (**A**) and ZPAL RV/721 (**B**). **C, D**. Left maxillae: ZPAL RV/711 (**C**) and ZPAL RV/738 (**D**). Occlusal (**A**<sub>1</sub>, **B**<sub>1</sub>, **B**<sub>3</sub>, **C**) and lateral (**A**<sub>2</sub>, **B**<sub>2</sub>, **D**) views, fused premolariforms II and III (**B**<sub>3</sub>). SEM micrographs; all but **A**<sub>2</sub>, **B**<sub>2</sub>, **D** stereo-pairs.

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

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

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

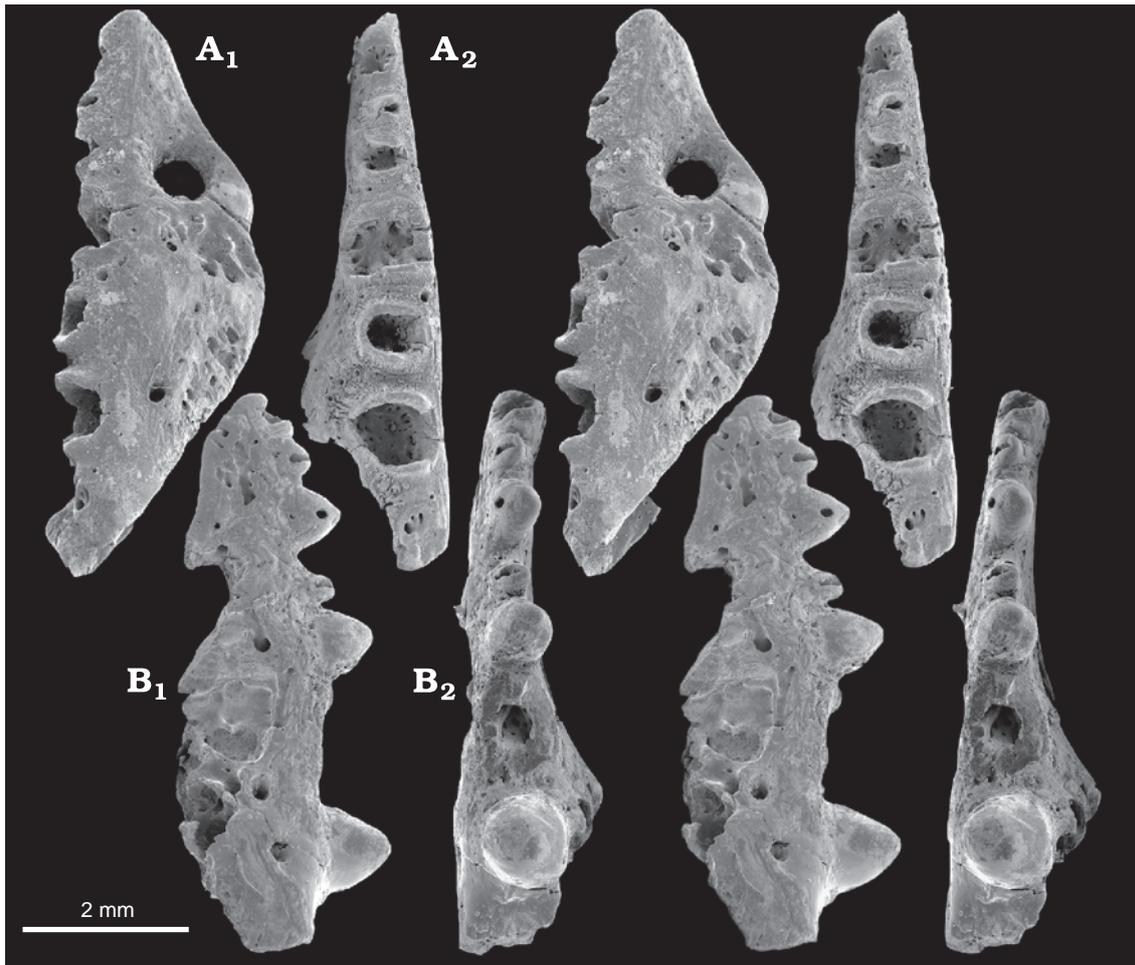


Fig. 13. Procolophonids from the Early Triassic of Czatkowice 1, Poland. Procolophonidae gen. indet. I. **A.** Left maxilla ZPAL RV/739. **B.** Right maxilla ZPAL RV/734. Lateral (A<sub>1</sub>, B<sub>1</sub>) and occlusal (A<sub>2</sub>, B<sub>2</sub>) views. SEM stereo-pairs.

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

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

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

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

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

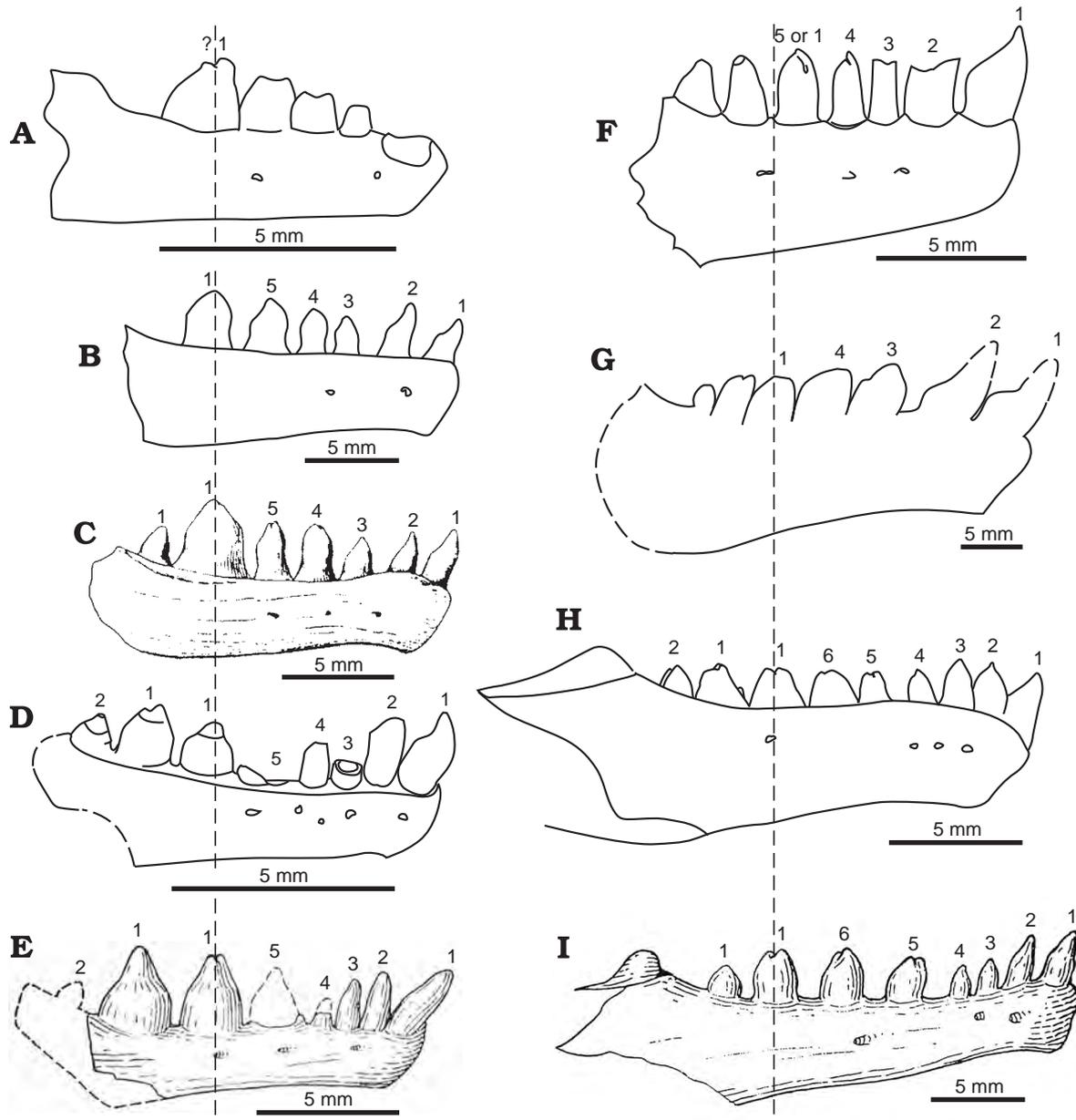


Fig. 14. Procolophonid dentaries in lateral view. **A.** *Kapes bentoni* Spencer *et* Storrs, 2002. **B.** *Kapes majmesculae* (Otschev, 1968). **C.** *Kapes amaenus* Ivakhnenko, 1975. **D.** *Procolina teresae* gen. et sp. n. **E.** *Burtensia burtensis* (Otschev, 1958). **F.** *Lestanshoria massiva*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

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

The third (first postaxial) vertebra has proportionally the longest centrum (Figs 16A, 17C<sub>1</sub>) comparable to the axial one, and centrum length decreases posteriorly to the seventh vertebra (Fig. 16C, first from the left), which has the proportions of a typical dorsal. All dorsals (Fig. 16C three vertebrae on the right) share the same centrum length, which is also retained in the anterior caudals, but sacrals are somewhat shorter.

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

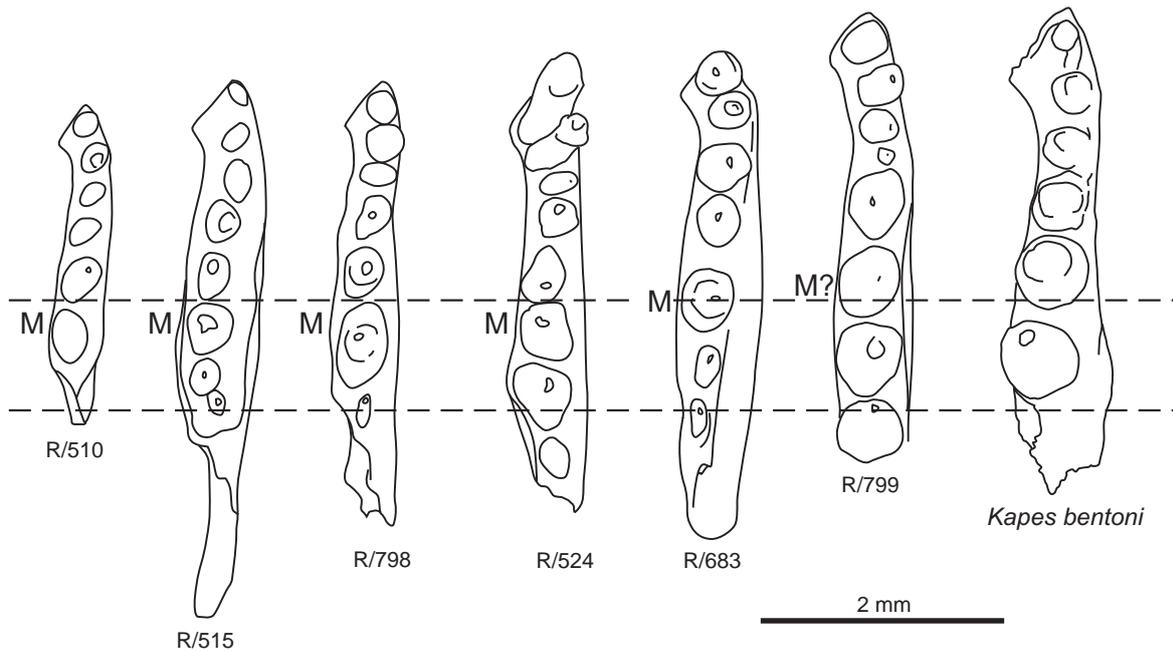


Fig. 15. *Procolina teresae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland, compared to *Kapes bentoni* Spencer *et* Storrs, 2002. Dentaries in occlusal view. The upper dashed-line denotes the level of the posterior alveolar foramen, the lower dashed-line denotes the level of the posterior limit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

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

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

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

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

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

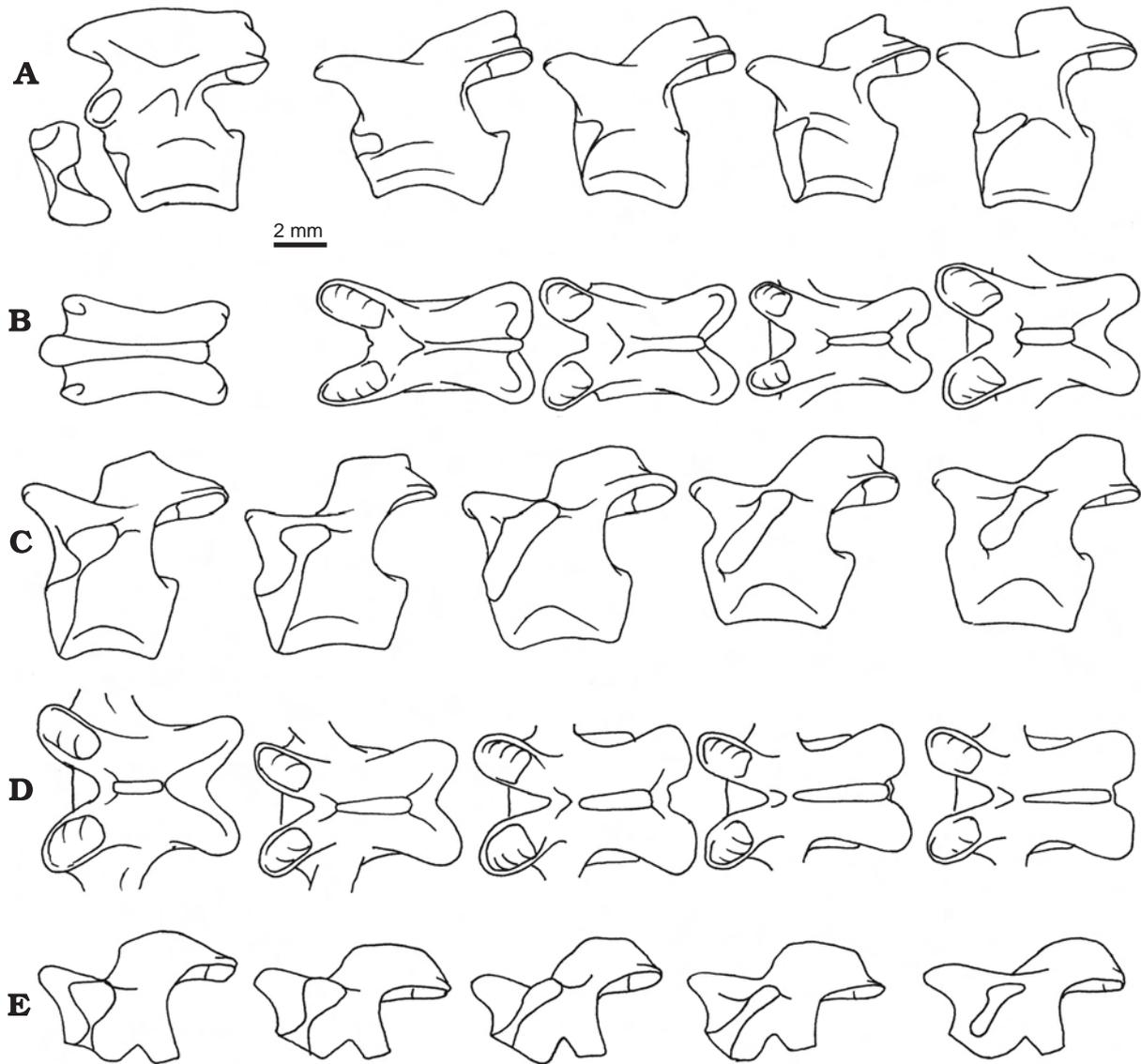


Fig. 16. **A–D.** *Procolina teresae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Vertebrae. From left to right: **A.** Atlas centrum + axis intercentrum ZPAL RV/825, and cervicals II–VI ZPAL RV/825–830 respectively, in left lateral view. **B.** Cervicals II–VI, in dorsal view. **C.** Possible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

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

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

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

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

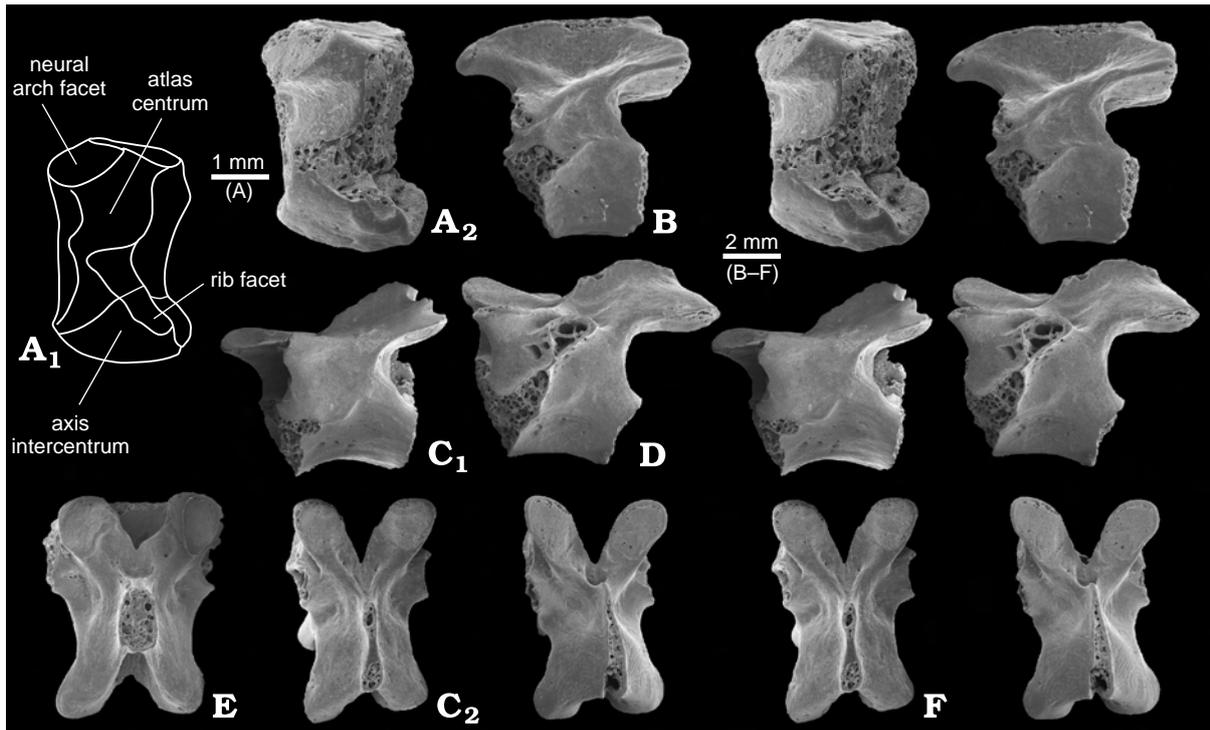


Fig. 17. **A–D.** *Procolina teresae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A.** Atlas centrum + axis intercentrum ZPAL RV/825. **B.** Axis ZPAL RV/826. **C.** Cervical vertebra III ZPAL RV/827. **D.** Dorsal vertebra ZPAL RV/833. **E.** Anterior dorsal vertebra ZPAL RV/845. **F.**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

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

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

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

Three sacral vertebrae (Fig. 18) were present in *Procolina teresae*. In all sacrals, the ribs are firmly connected to the transverse processes, and the line between them is indicated by a roughened raised surface. Un-

fortunately, none of the sacral vertebrae in the collection has the distal part of the sacral rib preserved. The first sacral rib is the stoutest. Its massive base is oval in cross-section and its end is greatly expanded craniocaudally and somewhat dorsoventrally (Fig. 18A<sub>1</sub>, D). The base of the second sacral rib is stout (Fig. 18B<sub>1</sub>, E). As preserved, it does not show much expansion of its end. The massive base of the third sacral rib projects laterally. Its distal part is the slimmest and is curved cranially (Fig. 18C, F).

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

#### Genus indet. I

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

**Jaws.** — ZPAL RV/734 (Figs 3D, 13B) is a right maxilla about the size of adult specimens of *Procolina teresae* (6 mm in tooth row length). The tooth formula is 6.1.0. Instead of four premolariforms, which is considered the maximum adult count in *P. teresae*, the maxilla ZPAL RV/734 bears six premolariforms, that alternate in size as do the hatchling teeth in *Sphenodon* (Robinson 1976). The dominant tooth, the VIIth, is implanted posterior to the largest portion of the maxilla, slightly posterior to the usual position. The labial surface and the whole dorsal portion is strongly damaged by the resorption process (Fig. 13B<sub>1</sub>).

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

ZPAL RV/989 (Figs 9F, 11E) is a very small left dentary (5.3 mm in dtl) displaying juvenile features. Its assignment is problematic. The tooth count is 7, the dominant tooth being situated at the VIIth tooth position posterior to the posterior alveolar canal (Fig. 9, arrow). The teeth are small and widely spaced. Between them, at three intermediate tooth positions, there are scars invaded by bony tissue (Figs 9F, 11E). The scars show that the tooth count was higher at still earlier stages of ontogeny. The fifth tooth position bears scars that probably mark the lingual course of a replacement tooth (Fig. 9F). The inferior alveolar canal is open laterally (Fig. 11E<sub>2</sub>), which indicates the poor ossification of the element.

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

**Vertebrae type B2.** — The Czatkowice 1 material includes many specimens closely similar to *Procolina teresae*, but in which neurocentral suture is open and neural arch and centrum are separated from each other (Figs 16E, 19G). Neural arches are more inflated at the spine base than in *Procolina*. Dorsal centra are half-cylindrical with only slight lateral concavities and without a ventral medial ridge (Fig. 19B<sub>4</sub>). Possible cervical centra are not oblique and are somewhat dorsoventrally flattened. On the other hand those specimens share some similarities with *Procolina*, such as the shallow hourglass-shaped concavity on the dorsal side (Fig. 19I), scars on the anterior and posterior faces, the shape of neurocentral suture, and amphicoely.

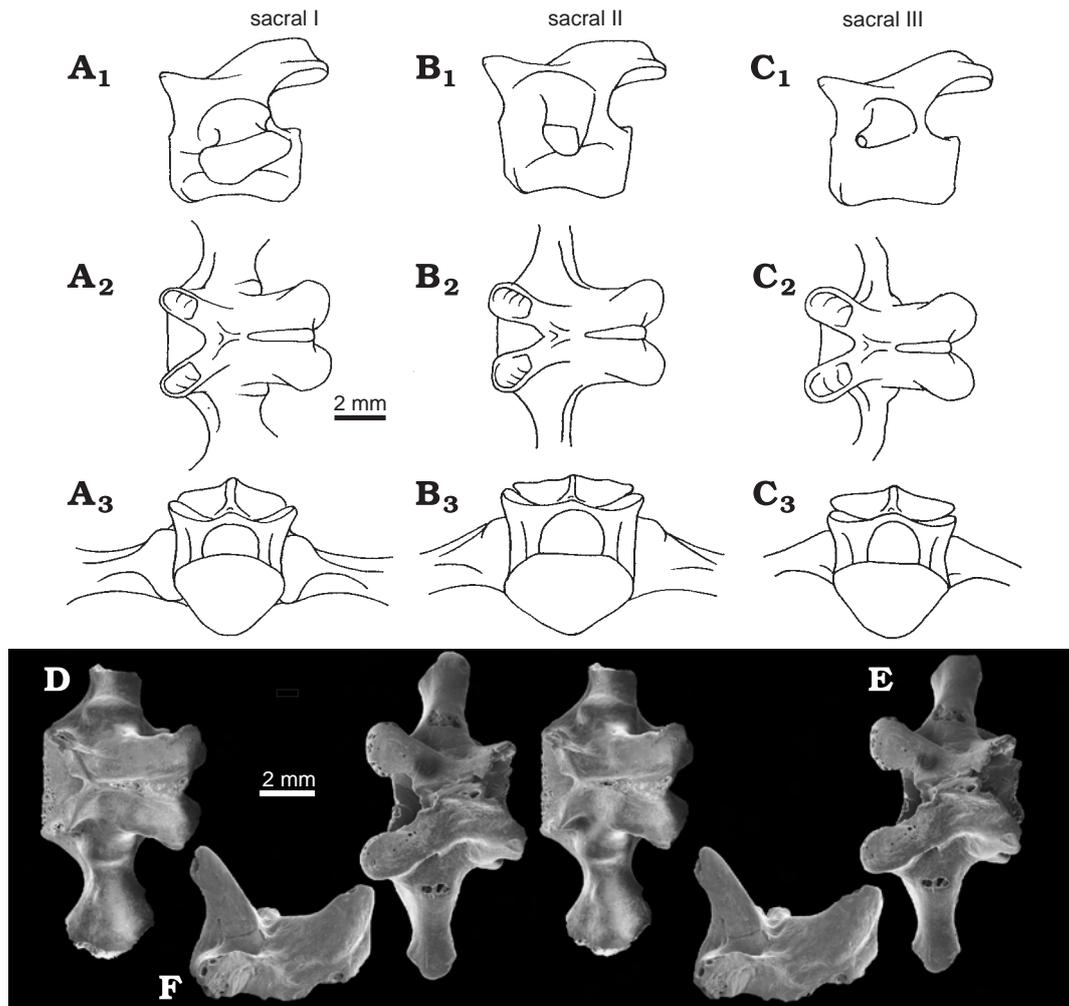


Fig. 18. *Procolina teresae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland, sacral vertebrae. A. Sacral I. B. Sacral II. C. Sacral I–III. D. Sacral I ZPAL RV/836. E. Sacral II ZPAL RV/835. F. Sacral III ZPAL RV/837. Left lateral (A<sub>1</sub>, B<sub>1</sub>, C<sub>1</sub>), dorsal (A<sub>2</sub>, B<sub>2</sub>, C<sub>2</sub>, D–F), and cranial (A<sub>3</sub>, B<sub>3</sub>, C<sub>3</sub>) views. D–F, SEM stereo-pairs.

The isolated neural arches from Czatkowice 1 material excluded from *Procolina teresae* on the basis of relatively late fusion with the centra are similar to those of *Procolina* in shape, except that they are more swollen above the postzygapophyses, more rectangular in dorsal view (Fig. 19B<sub>2</sub>) and bear relatively more posteriorly located spines (Fig. 16E). However, these differences are distinct only on the anteriormost dorsals. The distal ends of the neural spines are poorly ossified.

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

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

No mandible can be associated with confidence with ZPAL RV/734, but ZPAL RV/733 (Fig. 9A), more slender than the average, and bearing smaller and more numerous teeth is perhaps a match. Notewor-

thy is the tooth formula of this specimen, which is either 6.1.4. or 7.1. 3. Except for the formula, this specimen has a much less ascending postmolariform tooth row than *Procolina*, and bears three accessory teeth ready to erupt. How this profile might have changed in ontogeny is obscure, because this region is often damaged.

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

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

#### Genus indet. II

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

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

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

The centra are amphicoelous and, in contrast to adult *Procolina*, notochordal. They are disproportionately small compared to the neural arch. As in *Procolina*, the anterior and posterior articular facets are not well ossified, and the centra as preserved are trapezoidal in lateral view, with their ventral length smaller than the dorsal one. The prominent excavations on the ventrolateral sides of the centrum, separated by the blunt ventral ridge make it nearly triangular in transverse section (Fig. 19C<sub>3</sub>, E). The ridge is similarly developed in all vertebral regions and the small notochordal canal runs through the base of the ridge, which distinguishes these centra from those of *Procolina*. On the dorsal surface of the centrum there is a deep conical excavation, while in *Procolina* this concavity is shallow and hourglass-shaped. In the smallest specimens the arch may be separated from its centrum.

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

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

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

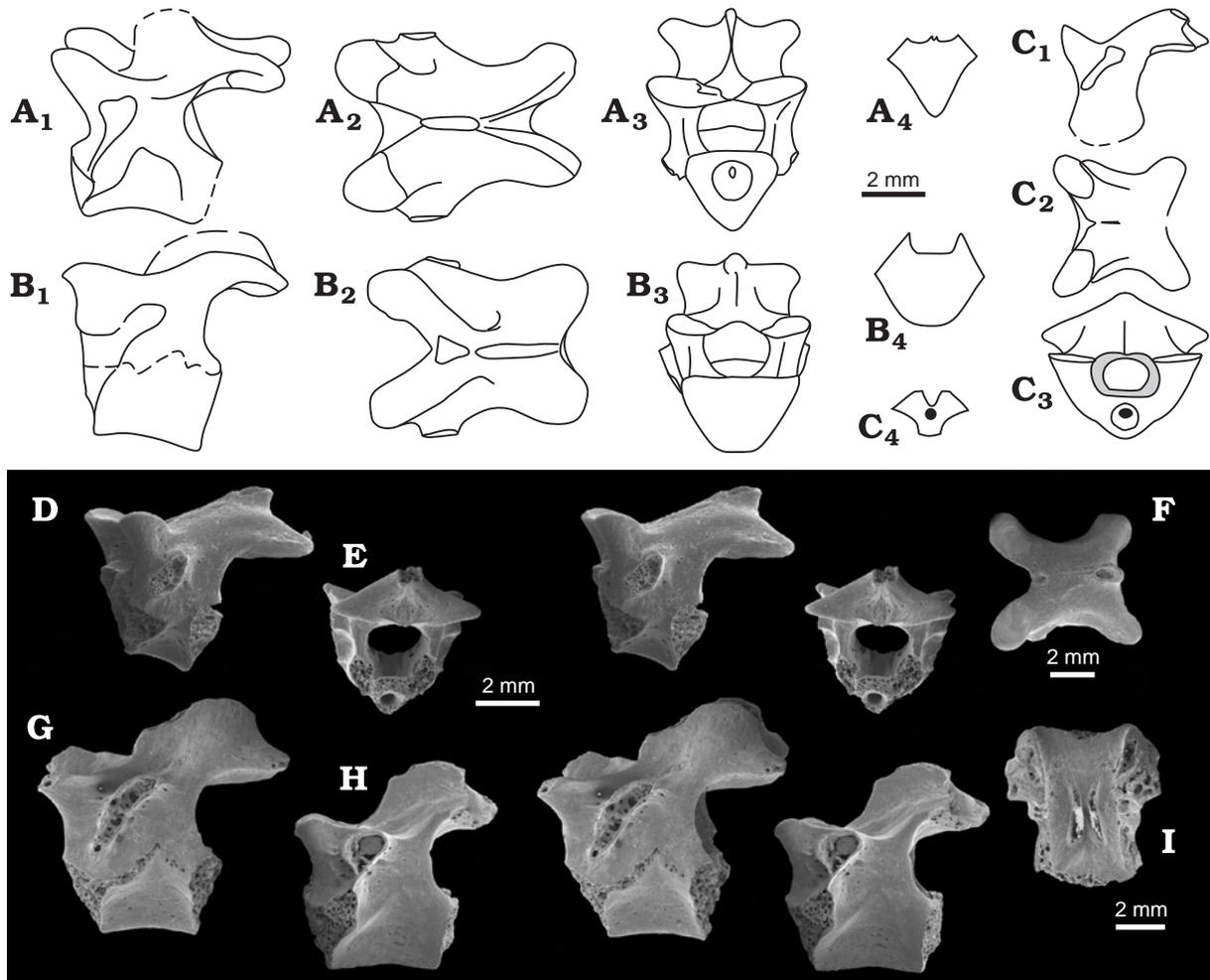


Fig. 19. Procolophonids from the Early Triassic of Czatkowice 1, Poland. Comparison of *Procolina teresae* gen. et sp. n., anterior dorsal type vertebrae (A, H, I) with those of Procolophonidae gen. indet. I (B, G) and gen. indet. II (C–F). Left lateral (A<sub>1</sub>, B<sub>1</sub>, C<sub>1</sub>, D, G, H), dorsal (A<sub>2</sub>, B<sub>2</sub>, C<sub>2</sub>, F), anterior (A<sub>3</sub>, B<sub>3</sub>, C<sub>3</sub>), and posterior (E) views. Transversal section of centrum about the mid-length (A<sub>4</sub>, B<sub>4</sub>, C<sub>4</sub>), dorsal view of the centrum without neural arches (I). D–I, SEM micrographs; all but F, I stereo-pairs.

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

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

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

#### Genus indet. III

ZPAL RV/716 is a posteriorly incomplete, fairly large and very thick dentary (Fig. 11C) with a dental formula hardly comparable with *Procolina*. It bears basal parts of three anterior teeth that sink deep into the

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

## DISCUSSION

### COMPOSITION OF THE PROCOLOPHONID CZATKOWICE 1 FAUNA

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

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

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

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

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

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

#### PROCOLOPHONID GENERIC LEVEL TAXONOMY

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

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

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

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

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

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

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

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

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

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

## CZATKOWICE 1 PROCOLOPHONID TOOTH REPLACEMENT

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

In the Czatkowice 1 procolophonid material, gaps that are more likely to be due to replacement than to post mortem loss do occur, but neither *Procolina* nor genus indet. material display resorption pits on the lingual side of the crown bases or tooth-bearing bones (*e.g.*, in some durophagous reptiles *Dracaena guianensis* or some dinosaurs; Edmund 1960, figs 18, 48). A regular replacement of functional teeth by the tooth buds developed on the lingual side of the jaws is typical of both synapsids and diapsids (Edmund 1960, 1969), but not of earlier representatives of Amniota (Captorhinidae; Bolt and DeMar 1975) which may have multiple rows of functional teeth. In the procolophonids, the multiple tooth rows are rare (*e.g.*, in *Thelegnathus contritus*, Gow 1977b), and not found in the Czatkowice 1 material. The lack of replacement perforations in

juveniles of *Procolina* and in genus indet. I suggests an instantaneous replacement. The buds must have matured within a thick lingual mucosa to be shifted to the final tooth position only after a total resorption of their predecessors as shown by ZPALRV/739 (Fig. 13A<sub>2</sub>). The hypothesis that the single replacement act was quick (Bolt and DeMar 1975; Li 1983, p. 580) is thus supported in this case.

In the Czatkowice 1 procolophonids, the teeth to be shed are perforated apically and/or labially (Figs 3C, D, F, 12B<sub>2</sub>, D, 13A). In the undetermined procolophonid material, and in tiny juveniles of *Procolina*, but less so in the adult *Procolina*, distinct traces of tooth resorption are associated with erosion of the tooth-bearing bones, and thus the whole organism could have been involved in resorption process. Interestingly, the process affected the labial side of jaws and teeth (Figs 12D, B<sub>2</sub>, 13).

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

We hypothesise that the temporary deterioration of tooth-bearing bones appeared as a solution to the difficulties with tooth replacement that resulted from the development of tooth permanency. Our material suggests that the expression of this process was subject to variability, possibly at a generic or specific level. If not a manifestation of pathology, a fusion of two or more smaller tooth buds to develop a single larger tooth, demonstrated by the maxilla ZPAL RV/721 (Fig. 12A), might be a process that made for a decrease in the premolariform tooth count. Posterior (Fig. 10C<sub>2</sub>), or posterolabial (Fig. 10A<sub>2</sub>) to the molariform tooth, the development of new accessory teeth, probably paralleled the posterior elongation of the dentary, as already suggested by Gow (1977a) in *Procolophon* and by Li (1983) in *Eumetabolodon*. Associated with the jaw elongation, and the eruption of new accessory teeth, was a certain amount of anterior shift of the molariform tooth, which is best illustrated by the *Procolina* mandibles (Fig. 15). A possible anterior shift of the molariform tooth is also suggested by the young specimens of the procolophonid genus indet. I that display an unusual posterior position of this tooth (Fig. 13). In the maxilla of *Procolina teresae* the number of accessory teeth, and the position of the molariform tooth, are noticeably stable.

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

#### BIOSTRATIGRAPHICAL COMMENTS

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

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

## CONCLUSIONS

### TAXONOMY

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

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

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

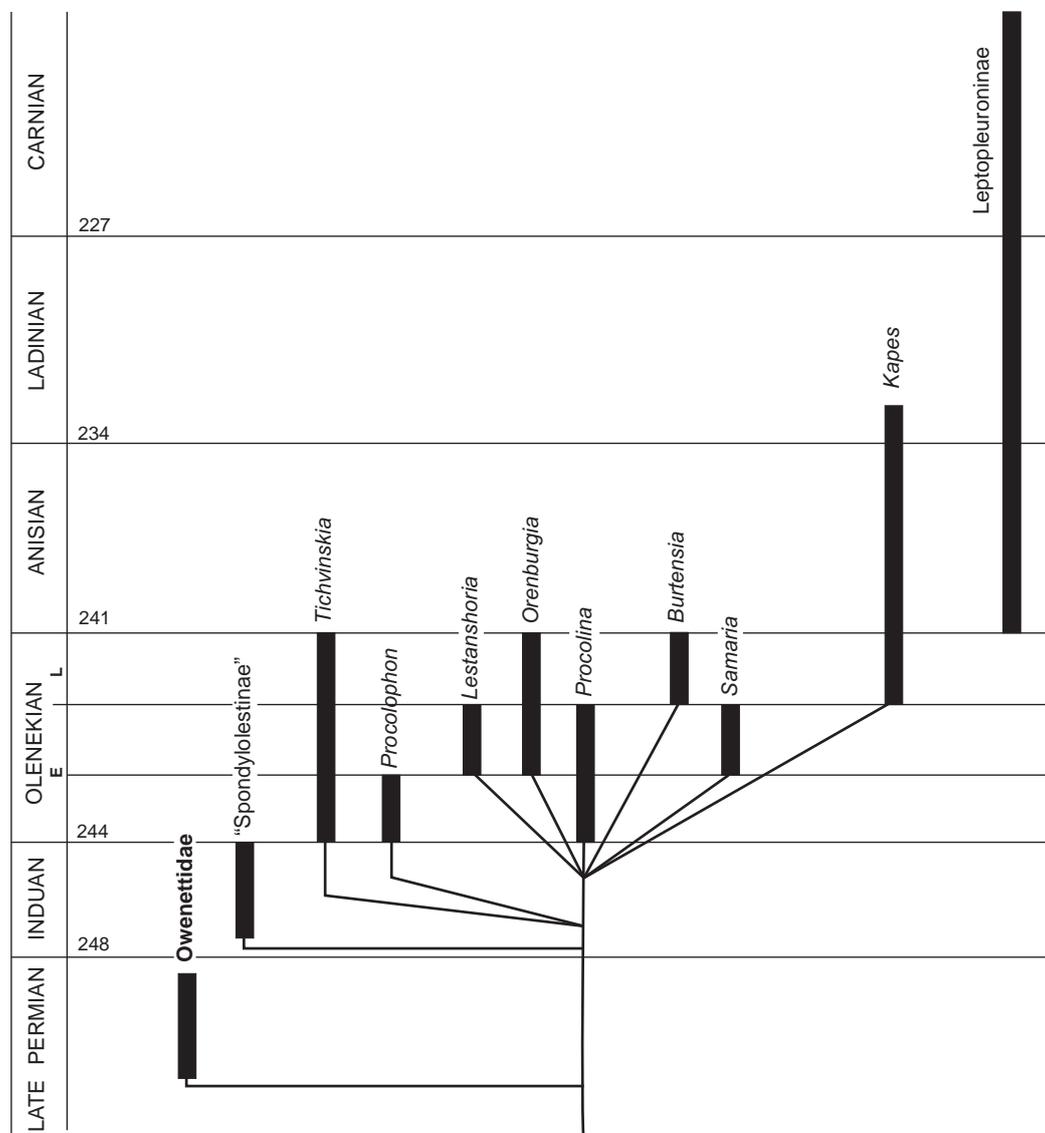


Fig. 20. Possible phylogenetic relationships within the Procolophonidae according to this study combined with a pattern of biochronology based mainly on Spencer and Benton (2000) and Shishkin *et al.* (2000) with *Procolina* included.

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

#### TOOTH REPLACEMENT PHENOMENA

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

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

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

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

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

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

#### BIOSTRATIGRAPHIC IMPLICATIONS

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

### REFERENCES

- Bolt, J.R. and De Mar, R. 1975. An explanatory model of the evolution of multiple rows of teeth on *Captorhinus aguti*. *Journal of Paleontology* **49**, 814–832.
- Borsuk-Białynicka, M. and Evans S.E. 2003. A basal archosauriform from the Early Triassic of Poland. *Acta Palaeontologica Polonica* **48**, 649–652.
- Borsuk-Białynicka, M. and Evans, S.E. 2009a. Cranial and mandibular osteology of the Early Triassic archosauriform *Osmolskina czatkowicensis* from Poland. *Palaeontologia Polonica* **65**, 235–281.
- Borsuk-Białynicka, M. and Evans, S.E. 2009b. A long-necked archosauriform from the Early Triassic of Poland. *Palaeontologia Polonica* **65**, 203–234.
- Borsuk-Białynicka, M. and Sennikov, A.G. 2009. Archosauriform postcranial remains from the Early Triassic karst deposits of southern Poland. *Palaeontologia Polonica* **65**, 283–328.
- Borsuk-Białynicka, M., Cook, E., Evans, S.E., and Maryańska, T. 1999. A microvertebrate assemblage from the Early Triassic of Poland. *Acta Palaeontologica Polonica* **44**, 167–188.
- Borsuk-Białynicka, M., Maryańska, T., and Shishki, M.A. 2003. New data on the age of the bone breccia from the locality Czatkowice 1 (Cracow Upland, Poland). *Acta Palaeontologica Polonica* **48**, 153–155.
- Brochu, C.A. 1996. A closure of neurocentral suture during crocodylian ontogeny; implications for maturity assessment in fossil archosaurs. *Journal of Vertebrate Paleontology* **16**, 49–62.
- Broili, F. and Schröder J. 1936. Beobachtungen an Wirbeltieren der Karooformation. XXI. Über *Procolophon* Owen. *Sitzungsberichte der mathematisch-naturwissenschaftlichen Abteilung der Bayerischen Akademie der Wissenschaften zu München* **2**, 239–256.
- Carroll, R.L. and Lindsay, W. 1985. Cranial anatomy of the primitive reptile *Procolophon*. *Canadian Journal of Earth Sciences* **22**, 1571–1587.

- Chow, M. and Sun, A. 1960. A new procolophonid from north-western Shansi. *Vertebrata Palasiatica* **4**, 11–13.
- Colbert, E.H. and Kitching, J.W. 1975. The Triassic Reptile *Procolophon* in Antarctica. *American Museum Novitates* **2566**, 1–23.
- Cook, E. and Trueman, C. 2009. Taphonomy and geochemistry of a vertebrate microremains assemblage from the Early Triassic karst deposits at Czatkowice 1, southern Poland. *Palaeontologia Polonica* **65**, 17–30.
- DeBraga, M. and Rieppel, O. 1997. Reptile phylogeny and the interrelationships of turtles. *Zoological Journal of the Linnean Society* **120**, 281–354.
- Edmund, A.G. 1960. Tooth replacement phenomena in the lower vertebrates. *The Royal Ontario Museum, Life Science Division — Contribution* **52**, 1–190.
- Edmund, A.G. 1969. Dentition. In: C. Gans (ed.) *Biology of the Reptilia 1: Morphology*, 117–200. Academic Press, London.
- Evans, S.E. 2009. An early kuehneosaurid reptile (Reptilia: Diapsida) from the Early Triassic of Poland. *Palaeontologia Polonica* **65**, 145–178.
- Evans, S.E. and Borsuk-Białynicka, M. 1998. A stem-group frog from the Early Triassic of Poland. *Acta Palaeontologica Polonica* **43**, 573–580.
- Evans, S.E. and Borsuk-Białynicka, M. 2009a. A small lepidosauromorph reptile from the Early Triassic of Poland. *Palaeontologia Polonica* **65**, 179–202.
- Evans, S.E. and Borsuk-Białynicka, M. 2009b. The Early Triassic stem-frog *Czatkobatrachus* from Poland. *Palaeontologia Polonica* **65**, 79–105.
- Gauthier, J., Kluge, A.G., and Rowe, T. 1988. The early evolution of the Amniota. In: M.J. Benton (ed.) *The Phylogeny and Classification of the Tetrapods. Vol. 1*, 103–155. Clarendon Press, Oxford.
- Gow, C.E. 1977a. Tooth function and succession in the Triassic reptile *Procolophon trigoniceps*. *Palaeontology* **20** (3), 695–704.
- Gow, C.E. 1977b. New procolophonids from the Triassic Cynognathus Zone of South Africa. *Annals of the South African Museum* **72**, 109–124.
- Gow, C.E. 1978. The advent of herbivory in certain reptilian lineages during the Triassic. *Palaeontologia Africana* **21**, 133–141.
- Huene F. von 1911. Über die Procolophoniden, mit einer neuen Form aus dem Buntsandstein. *Zentralblatt für Mineralogie, Geologie und Paläontologie* **3**, 78–83.
- Huene F. von 1939. Ein neuer Procolophonide aus dem deutschen Buntsandstein. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilage-Band, Abt. B* **81**, 501–511.
- Ivakhnenko, M.F. [Ивахненко, М.Ф.] 1974. Новые данные по проколофонидам раннего триаса СССР [New data on the procolophonids from the Early Triassic of USSR]. *Палеонтологический журнал* **1974** (3), 68–74.
- Ivakhnenko, M.F. [Ивахненко, М.Ф.] 1975. О родовом составе проколофонид раннего триаса Приуралья [On the generic contents of the Procolophonidae from the Early Triassic of the Cis-Uralian region]. *Палеонтологический журнал* **1975** (1), 88–93.
- Ivakhnenko, M.F. [Ивахненко, М.Ф.] 1979. Пермские и триасовые проколофоны Русской платформы [Permian and Triassic procolophonoids of the Russian platform]. *Труды Палеонтологического Института АН СССР* **164**, 1–80.
- Ivakhnenko, M.F. [Ивахненко, М.Ф.] 1983a. Пермские парарептилии СССР [Permian parareptiles of USSR]. *Труды Палеонтологического Института АН СССР* **223**, 1–159.
- Ivakhnenko, M.F. [Ивахненко, М.Ф.] 1983b. Новые проколофоны Восточной Европы [New procolophonids of the Eastern Europe]. *Палеонтологический журнал* **1983** (2), 130–133.
- Laurin, M. and Reisz, R.R. 1995. A reevaluation of early amniote phylogeny. *Zoological Journal of the Linnean Society* **113**, 165–223.
- Lee, M.S.Y. 1995. Historical burden in systematics and the interrelationships of “parareptiles”. *Biological Reviews* **70**, 459–547.
- Li, J. 1983. Tooth replacement in a new genus of procolophonid from the Early Triassic of China. *Palaeontology* **26**, 567–583.
- Lubka, M. 1999. *Rozpoznanie taksonomiczne fauny kęgowców lądowych z dolnotriasowej brekcji kostnej z Czatkowic koło Krakowa na podstawie elementów kręgosłupa* [Taxonomic composition of terrestrial vertebrate fauna from the Lower Triassic bone breccia from Czatkowice near Cracow on the basis of backbone elements]. Unpublished Ms Dissertation. 100 pp. Institute of Paleobiology, Polish Academy of Sciences, Warsaw.
- Modesto, S.P., Damiani, R.J., and Sues H.-D. 2002. A reappraisal of *Coletta seca*, a basal procolophonid reptile from the Lower Triassic of South Africa. *Palaeontology* **45**, 883–895.
- Novikov, I.W. [Новиков, И.В.] 1991. Новые данные по проколофонидам СССР [New data on the procolophonids from USSR]. *Палеонтологический журнал* **1991** (2), 73–85.
- Novikov, I.W. [Новиков, И.В.] 1994. Биостратиграфия континентального триаса Восточной Европы на основании фауны тетрапод [Biostratigraphy of the continental Triassic of Eastern Europe on the basis of tetrapod fauna]. *Труды Палеонтологического Института АН СССР* **261**, 1–139.
- Novikov I.W. [Новиков, И.В.] 1995. Проколофониды [Procolophonids]. In: М.А. Шишкин, В.Г. Очев и В.П. Твердохлебов [M.A. Shishkin, V.G. Ochev and V.P. Tverдохлебов] (eds) *Биостратиграфия континентального триаса Южного Приуралья* [Biostratigraphy of the continental Triassic of the Southern Cis-Urals], 72–77. Наука, Москва.
- Novikov I.W. and Orlov, A.N. [Новиков, И.В. и Орлов, А.Н.] 1992. Новые данные по раннетриасовым позвоночным острова Колгуев [New data on Early Triassic vertebrates from Kolguyev Island]. *Палеонтологический журнал* **1992** (1), 133–136.

- Oelrich, T.M. 1956. The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). *Miscellaneous Publications Museum of Zoology, University of Michigan* **94**, 9–122.
- Olson, E.C. 1947. The family Diadectidae and its bearing on the classification of Reptiles. *Fieldiana: Geology* **11**, 1–53.
- Ochev, V.G. [Очев, В.Г.] 1958. Новые данные по фауне триасовых позвоночных Оренбургского Приуралья [New data on the Triassic vertebrate fauna from the Orenburg of Cisuralien]. *Доклады Академии Наук СССР* **122**, 485–488.
- Paszkowski, M. 2009. The Early Triassic karst of Czatkowice 1, southern Poland. *Palaeontologia Polonica* **65**, 7–16.
- Paszkowski, M. and Wieczorek, J. 1982. Fossil karst with Mesozoic bone breccia in Czatkowice 1 (Cracow Upland, Poland). *Kras i Speleologia* **3**, 32–38.
- Pineiro, G., Rojas, A., and Ubilla, M. 2004. A new procolophonoid (Reptilia, Parareptilia) from the Upper Permian of Uruguay. *Journal of Vertebrate Paleontology* **24**, 814–821.
- Reisz, R.R. and Scott, D. 2002. *Owenetta kitchingorum* sp. n. a small parareptile (Procolophonia: Owenettidae) from the Lower Triassic of South Africa. *Journal of Vertebrate Paleontology* **22**, 244–256.
- Robinson, P.L. 1976. How *Sphenodon* and *Uromastyx* grow their teeth and use them. In: A. D'A. Bellairs and C.B. Cox (eds) *Morphology and Biology of Reptiles. Linnean Symposium Series* **3**, 43–64.
- Romer, A.S. 1956. *The Osteology of the Reptiles*. 772 pp. The University Chicago Press, Chicago.
- Shishkin, M.A. and Sulej, T. 2009. The Early Triassic temnospondyls of the Czatkowice 1 tetrapod assemblage. *Palaeontologia Polonica* **65**, 31–77.
- Shishkin, M.A., Ochev, V.G. Lozovskii, V.R., and Novikov, I.V. 2000. Tetrapod biostratigraphy of the Triassic of Eastern Europe. In: M.J. Benton, M.A. Shishkin, D. Unwin, and E.N. Kurochkin (eds) *The Age of Dinosaurs in Russia and Mongolia*, 120–139. Cambridge University Press, Cambridge.
- Spencer, P.S. and Benton, M.J. 2000. Procolophonoids from the Permo-Triassic of Russia In: M.J. Benton, M.A. Shishkin, D. Unwin, and E.N. Kurochkin (eds) *The Age of Dinosaurs in Russia and Mongolia*, 160–176. Cambridge University Press, Cambridge.
- Spencer, P.S. and Storrs, G.W. 2002. A re-evaluation of small tetrapods from the Middle Triassic Otter Sandstone Formation of Devon, England. *Palaeontology* **45**, 447–467.
- Sues, H.-D., Olsen, P.E., Scott, D.M., and Spencer, P.S. 2000. Cranial osteology of *Hypsognathus fenneri*, a latest Triassic procolophonid reptile from the Newark Supergroup of eastern North America. *Journal of Vertebrate Paleontology* **20**, 275–284.
- Waldman, M. and Evans, S.E. 1994. Lepidosauromorph reptiles from the Middle Jurassic of Skye. *Zoological Journal of the Linnean Society* **112**, 135–150.
- Young, Ch.-Ch. 1957. *Neoprocolophon asiaticus*, a new cotylosaurian reptile from China. *Vertebrata Palasiatica* **1**, 1–7.
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## APPENDIX 1

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

<i>Procolina teresae</i> dentaries ZPAL RV/	Tooth formula	Largest tooth position	Ontogenetic age	Posterior alveolar foramen position	Coronoid facet position behind	Dentary tooth row length (dtl)	Figs
510	5.1.0	VI	juvenile	VI	?	7.0	11A
511	5.1.2	VI	?adult	VI	VI	8.0	
513	6.1.2	VII	young adult	VI/VII	VII	7.4	11D
514	5.1.2	VI	young adult	V	VI	7.5	
515	5.1.2	VI	juvenile	VI	VI	7.5	9C, 10A
516	6.1.0?	VII	juvenile	VI/VII	VII	6.5	9B
517	6.1.1	VII	adult	?	VII	8.5	
524	5.1.2	VI, VII	adult	VI	VI	10.5	9D, 10C
683	4.1.2	V	adult	V	VI	9.5	9E
717	5.1.2	VI	adult	VI	VI	7.9	
740	6.1.2	VII	adult.	?	VI	8.0	
741	5.1.1	VI	adult	VI	VI	9.0	
762	5.1.2	VI	adult	?	VI	9.5	
763	5.1.1	VI	adult	VI	?	8.5	
764	5.1.?	VI	adult	VI	VI	est. 8.2	
791	6.1.1	VI	adult	VI/VII	VI	8.9	
792	5.1.1	VI	young adult	?	VI	7.0	
798	5.1.1	VI	adult	VI	VII	7.8	
799	5.1.2	V–VIII	adult	?	?	c. 10.0	
801	5.1.1		adult	VI	VII	8.1	
802	5.1.1	VI	adult	VI	VI	7	
Genus indet.							
989	6.1.0	VII	juvenile	VII	?	6.0	9F, 11E
716	4.1.?	IV, V	adult	IV/V	V	est. 9	11C
733	6.1.4	VII, VIII	juvenile	VII	VII	8.1	9A

## APPENDIX 2

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

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

## APPENDIX 3

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

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