

A LONG-NECKED ARCHOSAUMORPH FROM THE EARLY TRIASSIC OF POLAND

MAGDALENA BORSUK-BIAŁYNICKA and SUSAN E. EVANS

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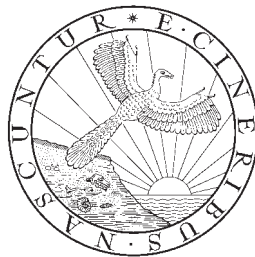
Czatkowiella harae gen. et sp. n. from the Early Triassic (earliest Late Olenekian) locality of Czatkowice 1, near Kraków, Poland, is characterised by a long slender neck, three headed ribs on some anterior dorsal vertebrae, and short broad neural spine tips in the dorsal vertebral series. Cladistic analysis suggests a relationship between *Czatkowiella* and the Late Permian long-necked reptile *Protorosaurus*, but fails to support a monophyletic Prolacertiformes. *Czatkowiella* and *Protorosaurus* do not group with either *Prolacerta* or the *Tanytropheus/Macrocnemus* clade of other workers, and fall at the very base of Archosauromorpha. Thus the long-necked morphology of many archosauromorph taxa should be regarded as a primitive state within this group, reversed in some daughter lineages such as rhynchosaurs and trilophosaurs.

Key words: Archosauromorpha, Reptile, *Protorosaurus*, Early Triassic, Poland, micro-vertebrates.

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INTRODUCTION

A small diapsid reptile *Czatkowiella harae* gen. et sp. n. is here described from the Early Triassic fissure deposits of southern Poland (Czatkowice 1 near Kraków; Paszkowski and Wieczorek 1982). It is a basal archosauromorph with a general similarity to a group of taxa once referred to as prolacertiforms. When the Early Triassic diapsid *Prolacerta* was first reported from South Africa (Parrington 1935), it was classified as a “thecodont”. Despite this, it was heralded as a lizard ancestor because of ventrally open lower temporal fenestra, although the long neck was unusual (Camp 1945). Its position remained controversial until Gow (1975) gave the first account of the postcranial skeleton. This information made it clear that *Prolacerta* was closer to archosaurs than to lizards. In his review, Gow linked *Prolacerta* to other genera, most notably the European Mid Triassic *Tanystropheus* and *Macrocnemus*. Over the next decades a broad series of other “prolacertiform” taxa were added: the Late Permian *Protorosaurus* (Britain and Germany; Seeley 1888) and *Eorasaurus* (Russia; Sennikov 1997); the Early Triassic *Boreoprincea* and *Microcnemus* (Russia; Tatarinov 1978; Benton and Allen 1997; Huene 1940), *Prolacertoides* (China; Yang 1973) and *Vritramimosaurus* (Russia; Sennikov 2005); the Early to Mid Triassic *Jesairosaurus* (Morocco; Jalil 1997); the Mid Triassic *Rhombopholis* (Britain; Benton and Walker 1997), *Malutinisuchus* (Russia; Otschev 1986), *Pamelaria* (India; Sen 2003), and *Cosesaurus* (Spain; Sanz and Lopez-Martinez 1984); the Mid–Late Triassic *Malerisaurus* (India and North America; Chatterjee 1980, 1986); the Late Triassic *Langobardisaurus* (Italy; Renesto 1994); and the Early Jurassic *Tanytrachelos* (North America; Olson 1979). The Early Triassic *Kadimarkara* (Australia, Bartholomai 1979) is actually a misinterpreted, and poorly preserved, specimen of *Prolacerta*, extending the pan-Gondwanan range of this genus from South Africa (Gow 1975) and Antarctica (Colbert 1987) to Australia.

As traditionally diagnosed, “prolacertiforms” form a large, impressive pan-Pangaeian assemblage, combining archosauromorph features (subthecodont teeth, presence of a posterolateral premaxillary process excluding or nearly excluding the maxilla from the narial margin, well developed transverse processes on dorsal vertebrae) with a characteristically long neck (elongation of individual vertebrae), dichoccephalous cervical vertebrae in which the rib heads are small and lie close together on the anterior margin of the centrum, and a ventrally open lower temporal fenestra (e.g., Benton 1985; Gauthier 1984; Evans 1987, 1988). However, there are problems. Many of the above named taxa (with the exception of *Macrocnemus*, *Tanystropheus*, *Prolacerta*, and *Protorosaurus*) are fragmentary and poorly known. In addition, recent cladistic analyses (e.g., Dilkes 1998; Müller 2004) have rejected the monophyly of Prolacertiformes (see also Discussion). Although some subsets of taxa may be related to one another (e.g., *Langobardisaurus*, *Macrocnemus*, *Tanystropheus*, *Tanytrachelos*), “prolacertiform” is essentially a gradal concept, with some taxa (notably *Prolacerta*) being closer to Archosauriformes than others (e.g., tanystropheids) (e.g., Dilkes 1998). Dilkes (1998) places the aberrant arboreal *Drepanosaurus* and *Megalancosaurus*, from the Late Triassic of Italy, in a clade with the main “prolacertiform” taxa (*Tanystropheus*, *Tanytrachelos*, *Macrocnemus*), but excludes *Prolacerta* itself.

Apart from *Czatkowiella*, the Czatkowice 1 assemblage includes a basal archosauriform *Osmolskina czatkowicensis* (Borsuk-Białynicka and Evans 2003, 2009) of *Euparkeria* size, procolophons (Borsuk-Białynicka and Lubka 2009), a kuehneosaurid (Evans 2009), a small lepidosauromorph reptile (Evans and Borsuk-Białynicka 2009b), a prefrog *Czatkobatrachus polonicus* of *Triadobatrachus* grade (Evans and Borsuk-Białynicka 1998, 2009a; Borsuk-Białynicka and Evans 2002), and some small temnospondyls (Szyszkin and Sulej 2009), and fish (Borsuk-Białynicka *et al.* 2003).

The objective of the present paper is to give an account of the morphology of those bones that may be confidently referred to *Czatkowiella harae*. The chemical preparation of the Czatkowice 1 breccia is finished. The material is housed in the Institute of Paleobiology, Polish Academy of Sciences.

Institutional abbreviations. — BPI, Bernard Price Institute for Palaeontological Research, University of Witwatersrand, Johannesburg, South Africa; PIN Institute of Paleontology, Russian Academy of Sciences, Moscow, Russia; ZPAL Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Acknowledgements. — We are indebted to Mariusz Paszkowski and Józef Wieczorek (Jagiellonian University, Kraków), who discovered the Czatkowice 1 breccia and offered it for study, and to the late Halszka Osmólska and Teresa Maryńska (Polish Academy of Sciences, Warsaw) who kindly transmitted the material to us. Thanks are also due to the referees for their helpful criticism, and particularly, to David Dilkes (Univer-

sity of Wisconsin) who did a major editorial work upon our manuscript. The following staff members of the Institute of Paleobiology, Polish Academy of Sciences in Warsaw helped us during our studies: Ewa Hara prepared the material, Cyprian Kulicki took SEM microphotographs, Marian Dziewiński photographs, Aleksandra Hołda-Michalska prepared most of the computer illustrations. We are grateful to colleagues from the Institute for their help in solving computer editorial problems, as well as Jane Pendjiky (UCL) for preparing computer Figs 14 and 15. We also thank Annalise Gottmann (Bonn) for advance information on *Protorosaurus*.

GEOLOGICAL SETTING

Discovered in 1978, the bone breccia of Czatkowice 1 was briefly studied by a team from the Institute of Geology of the Jagiellonian University in Kraków (Poland), and the geological setting was described (Paszowski and Wieczorek 1982). More exact data concerning the geology is included in this volume (Paszowski 2009). The material from the fissure exposure Czatkowice 1, described herein, has been dated as most probably Early Olenekian (Borsuk-Białynicka *et al.* 2003) in age, but has turned to come most probably from the earliest Late Olenekian (Shishkin and Sulej 2009). The deposition of the material of Czatkowice 1 probably occurred in a freshwater oasis within the arid circumequatorial belt of Northern Pangea.

MATERIAL AND METHODS

The description that follows is based on isolated and fragmentary bones extracted from a microvertebrate-bearing deposit containing the remains of at least four other small reptiles. Of these, *Czatkowiella* is overlapped by the archosauriform *Osmolskina* (Borsuk-Białynicka and Evans 2003) in the upper end of its size range, by *Pamelina* (Evans 2009) in the middle part of its range, and by *Sophineta* (Evans and Borsuk-Białynicka 2009b) at the extreme lower end. This presents something of a challenge in terms of attributing elements, particularly with *Osmolskina* which is the more closely related taxon. For the smaller diapsids, we have used a combination of fit for individual elements and the general rule that if a bone of the same morphology occurs through a wide size range it is more likely to be *Czatkowiella*, since there is little variation in jaw size for the two small lepidosauromorphs. The structure of the dentition (using scanning electron microscopy) permits association of tooth-bearing elements, the maxilla then forming a template around which to fit other skull bones.

SYSTEMATIC PALEONTOLOGY

Subclass **Diapsida** Osborn, 1903

Clade Archosauromorpha Huene, 1946

Family uncertain

Genus *Czatkowiella* gen. n.

Type and only species: *Czatkowiella harae*.

Derivation of name: From the name of the type locality, Czatkowice 1 in southern Poland.

Diagnosis. — As for type and only species.

Czatkowiella harae sp. n.

Derivation of name: The species name reflects our gratitude to Ewa Hara, Institute of Palaeontology, Warsaw, who has been responsible for most of the preparation of Czatkowice 1 remains.

Type specimen: ZPAL R.V/100, a right maxilla with almost complete tooth row.

Type locality and horizon: Czatkowice quarry, Kraków, Poland. Fissure/cave infill dated as earliest Late Olenekian (Shishkin and Sulej 2009).

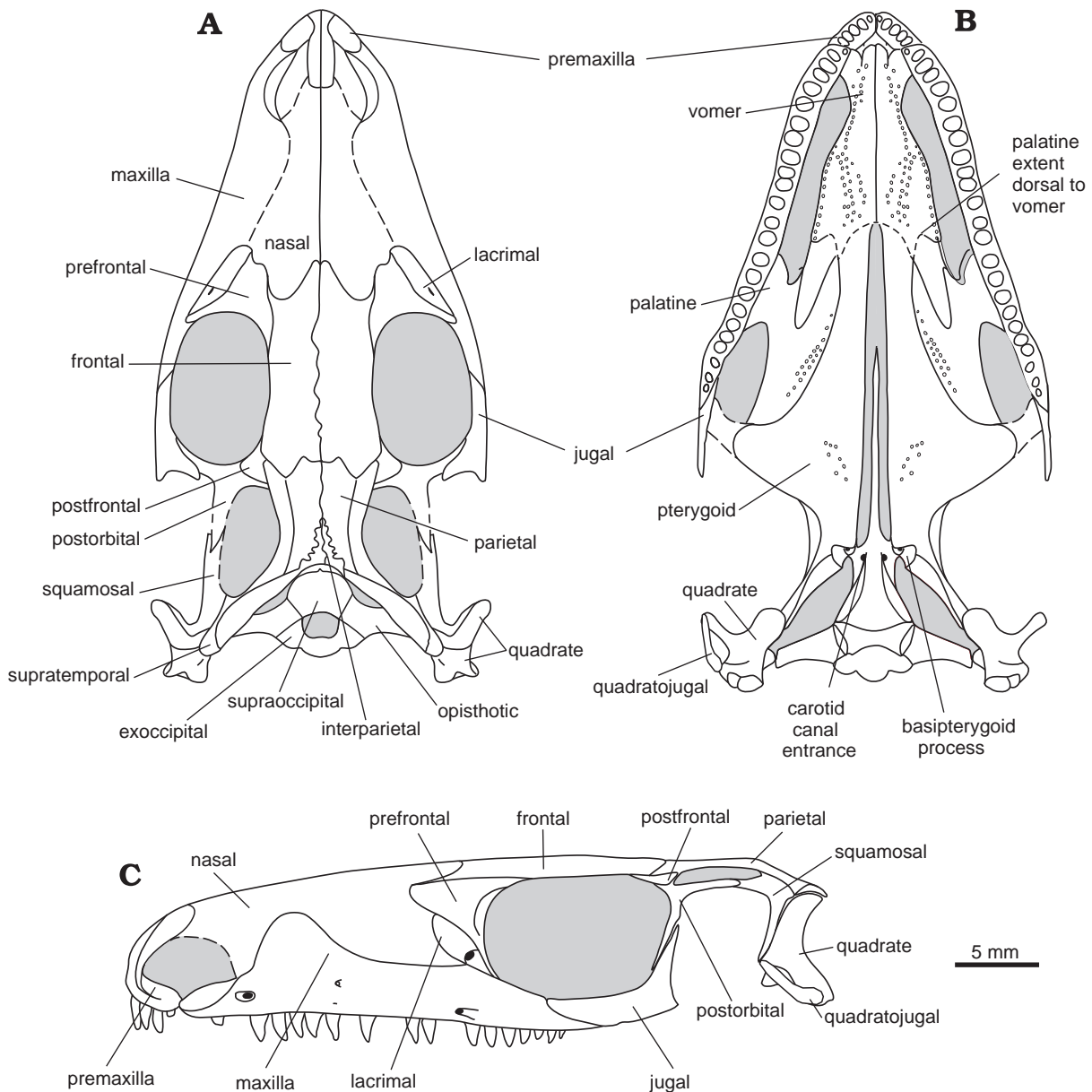


Fig. 1. *Czatковиella harae* gen. et sp. n., Early Triassic of Czatковице 1, Poland. Reconstruction of the skull, in dorsal (A), ventral (B), and lateral (C) views.

Diagnosis. — *Czatковиella* resembles early archosauromorphs (notably those traditionally grouped as “prolacertiforms”), and differs from lepidosauromorphs in having strongly elongated cervical vertebrae with long low neural spines and slender horizontally placed cervical ribs with an anterior process; it resembles the Late Triassic gliding kuehneosaurs and some archosauriforms, and differs from all described “prolacertiforms”, in having three-headed ribs on some anterior trunk vertebrae, but differs from kuehneosaurs in that these ribs do not attach to the ends of elongated transverse processes; resembles *Rhombopholis* (Benton and Walker 1997) in having expanded spines on the dorsal vertebrae, but differs in the other vertebral characters noted above; resembles the Late Permian *Protorosaurus* in combining long cervical vertebrae and slender horizontal cervical ribs with a primitive premaxilla lacking a posterolateral process, but differs in having a biradiate postorbital bone, paired parietals without a median crest, and cervical vertebrae that are proportionally longer in relation to their height, in the possession of some three-headed ribs, in having short dorsal vertebrae with a greater development of a spine table, and in lacking the bifid caudal neural spines that characterise all specimens of the Late Permian genus (SEE personal observation). In its combination of characters, *Czatковиella* is unique and justifies distinct generic status.

Dimensions. — As reconstructed in Fig. 1 on the basis of most frequent bones, the skull of *Czatkowiella harae* was about 40 mm in length (on average), and is thus much shorter than that of *Prolacerta broomi* B.P.I. 2675 (about 70 mm) as illustrated by Gow (1975, fig.12). However, the presence of very small (Fig. 3F) and very large (Figs 3E, 4F) maxillae demonstrates a range of variability that we consider to be intraspecific.

DERMAL SKULL ROOF BONES

Premaxilla. — There are many specimens of this bone, the best being ZPAL R/5 and 111 (Figs 2A, C, 4C, E), which are complete except for the end of the nasal process. The premaxilla has a dorsally convex oval body, bearing 3–5 tooth positions. The posterior margin of the premaxillary body is rounded, and the lateral surface bears no trace of a maxillary overlap facet. The connection between the premaxilla and maxilla was apparently weak and perhaps ligamentous (see below, maxilla). Thus almost the only bony attachment of the premaxilla to the skull is the weak joint with the nasal. The nasal process is a long, slim arcuate band of bone that rises first vertically and then runs back horizontally. This horizontal portion bears a slender ventral facet for the nasal. The nasal process is anteroposteriorly flattened with only a narrow medial edge for articulation with the contralateral bone (Figs 2A₂, C, 4E). The alveolar portion of the bone lacks any development of a palatal process. Assuming the two nasal processes lie side by side anteriorly, the bodies of the two premaxillae must have lain at an angle to one another (Fig. 2C), leaving a triangular posterior space to receive the vomers. The dorsal surface of the premaxillary body contributed to the floor of the external nares.

Maxilla. — This is represented by numerous fragments of differing individual size and age. The best preserved specimen, ZPAL R.V/100 (Figs 2A, 3C₂, C₃, 4A₁), has an almost complete alveolar margin, including the anterior tip, but lacks the dorsal facial process. The posterior end is also missing but this may be reconstructed from a juvenile specimen (ZPAL R.V/471; Fig. 3F) that is complete posteriorly. This bone has 13 tooth positions posterior to the palatine foramen, instead of the seven present in the holotype. On this basis, the total tooth count is about 26–28. The teeth are weakly pleurodont (under the definition that the labial wall is higher than the lingual wall as seen in lingual aspect) and show a simple alternating pattern of tooth replacement, the replacement teeth eroding the base of the existing tooth from the medial side. The replacement slowed down or ceased in old individuals (Figs 3E, 4F).

The facial process may be partly reconstructed on the basis of specimen ZPAL V/101 (Fig. 3B), but its posterior border is damaged. The specimen shows the lateral surface to be convex, and the medial one correspondingly concave in section. A flat dorsomedial concavity on the facial process probably received the nasal (Figs 2A₂, 3C₃). The outline and extent of this facet are unclear. The maxilla contributed to at least the posteroventral margin of the large external naris with a long narrow premaxillary process. This process is in-turned medially, and triangular in transverse section. Its end probably abutted the premaxilla in a joint that was held by ligaments. The dorsolateral surface of the premaxillary process bears an oval, ridged area separated from the medial surface by a distinct crest. This ridged area may have served as an attachment point for ligaments holding the bones together. The medial surface of the premaxillary process bears a horizontal, longitudinal furrow (Fig. 2A₂) that probably accommodated the vomer.

Along the anterior two-thirds of the bone, the alveolar margin is medially swollen to make the dental furrow deeply concave (Fig. 3C₃). In the posterior one third, the margin becomes dorso-ventrally flattened into a supra-alveolar shelf that bears facets and neurovascular furrows and foramina. The largest of these foramina is the palatine foramen, situated on the dorsomedial surface of the maxilla roughly one third of the distance from the posterior tip of the specimen ZPAL RV/100. In modern lizards and *Sphenodon*, this foramen opens into the superior alveolar canal and gives passage to the maxillary artery and vein, and the maxillary branch of the trigeminal nerve (CV5ii). These structures presumably ran forward in a conspicuous furrow that extends along the posteromedial part of the supra-alveolar shelf, in the angle between it and the facial process. From there, they would have passed *via* the infraorbital foramen (palatine and maxilla combined, see below) to enter the palatine foramen and the superior alveolar canal. Small neurovascular branches then passed to the teeth, to the soft tissues of the mouth (perhaps *via* a small oblique groove running anteroventrad from the palatine foramen), and to the external surface of the upper jaw (*via* the small lateral maxillary foramina). The superior alveolar canal exits *via* a slightly larger foramen (Fig. 2A₁) on the lateral side of the premaxillary process.

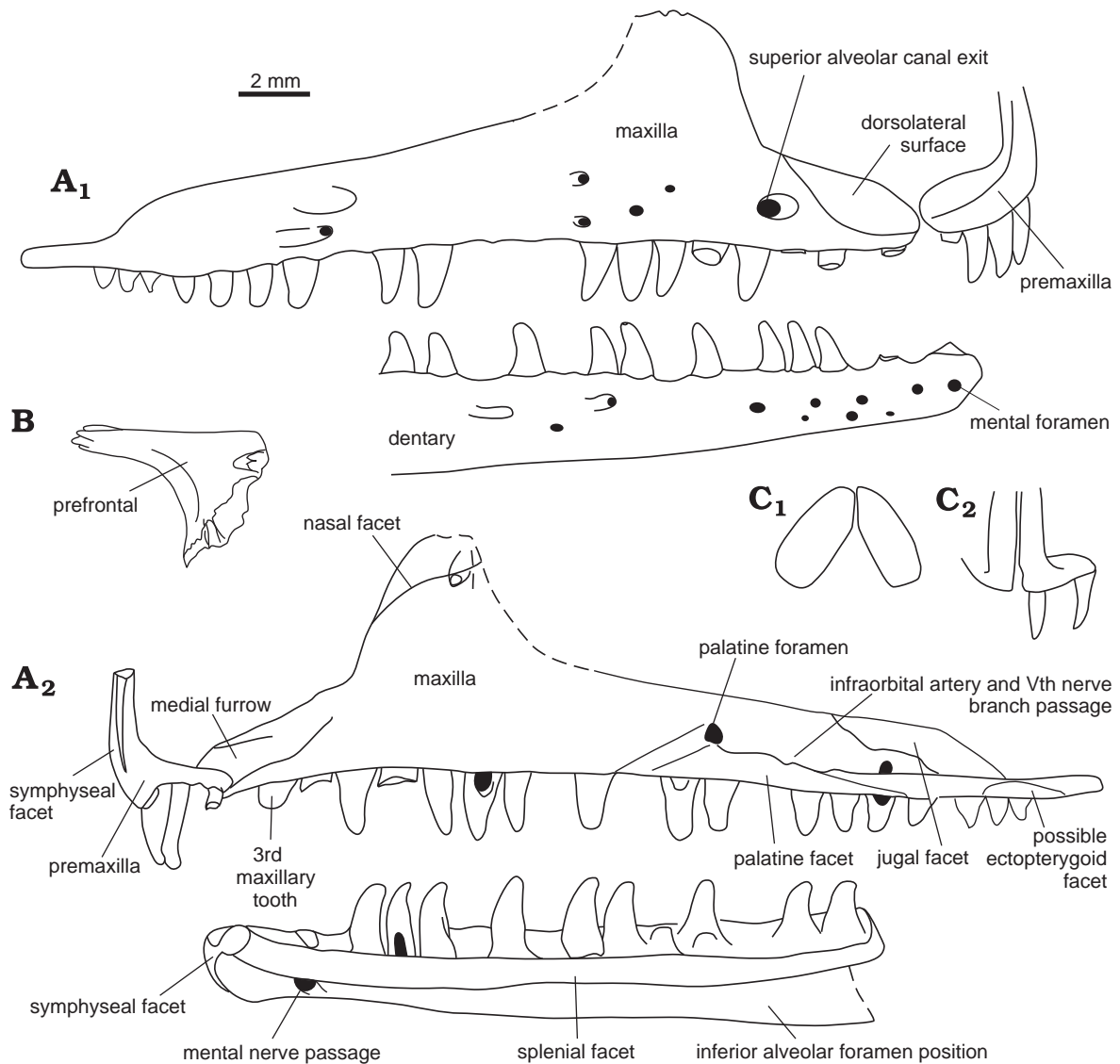


Fig. 2. *Czatkowiella harae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A.** Reconstruction of the jaws based on ZPAL RV/5, 100, 101, 102, 471, in labial (**A₁**) and lingual (**A₂**) views. **B.** Left prefrontal, ZPAL RV/466 reversed, in lateral view. **C.** Praemaxillae, the outline of articulated bones, in ventral view (**C₁**) and anterior view of the articulated bones (**C₂**).

Below the palatine foramen, the medial border of the supra-alveolar shelf bears a shallow triangular palatine facet (Figs 2A₂, 3C₃). This extends between the 13th and 18th tooth position and tapers posteriad. The ectopterygoid position may not be determined from the posteromedial border of the juvenile specimen ZPAL RV/471, and is conjectural (Figs 1B, 2A₂). The posterior process of the maxilla is low and of relatively constant height, but narrows abruptly in the posterior one sixth of its length. In this region, the medial surface of the lateral blade of the maxilla bears a furrow-like facet for the jugal (Fig. 2A₂). This facet is rather short which suggests a significant contribution of the maxilla to the orbital border.

Frontal. — Several frontal types have been recognised amongst the Czatkowice 1 bones. They are all relatively similar, in being paired with only light sculpture, and differ mainly in the shape and size of the various facets for adjacent bones. Only one type, however, shows a range of sizes (*e.g.*, ZPAL RV/340–344, 480) within the single morphology and these elements are tentatively referred to *Czatkowiella*.

Each frontal (Fig. 5D, E, I) is relatively robust with the dorsal surface perforated by numerous vascular foramina. A sinuous midline suture, in which the contralateral frontals alternate in overlapping and underlapping one another (Fig. 5I₂), with strong facets, demonstrates that the joint was strong. The prefrontal and postfrontal facets are separated by deep vascular foramina (Fig. 5A₂). In dorsal view, the prefrontal facet is

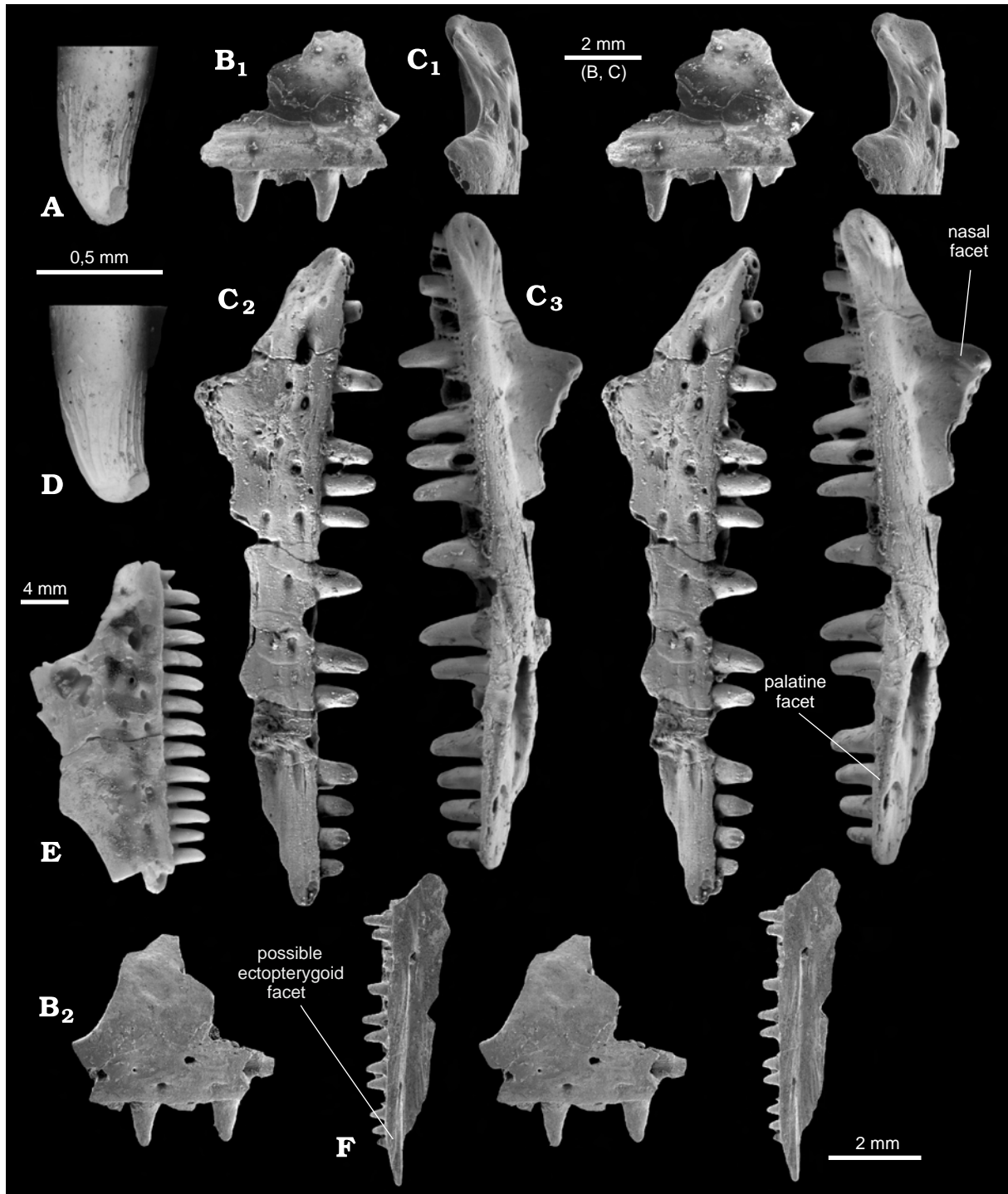


Fig. 3. *Czatkowiella harae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A, D.** Two premaxillary teeth ZPAL RV/5, in lingual view. **B.** A fragment of left maxilla ZPAL RV/101, in lingual (**B₁**) and labial (**B₂**) views. **C.** Anterior part of right maxilla ZPAL RV/100, in dorsal (**C₁**, anterior fragment), labial (**C₂**), and lingual (**C₃**) views. **E.** A fragment of an old adult specimen of maxilla ZPAL RV/1126, in labial view. **F.** Posteriormost part of right maxilla of small individual ZPAL RV/471, in lingual view. SEM micrographs; all but A, D, E stereo-pairs.

visible only as a narrow slot facet winding around the anterolateral margin of the bone although it comes onto the dorsal surface anteriorly where it grades into the nasal facet (Fig. 5D, E₂).

In ventral view, a relatively wide central part of the bone is divided into a deeper anterior concavity for the olfactory bulbs and a shallower, longer posterior surface which roofs the olfactory tracts as they pass forward to the nose. The central concavities are bordered by low sharp subolfactory crests (*cristae cranii*). About the

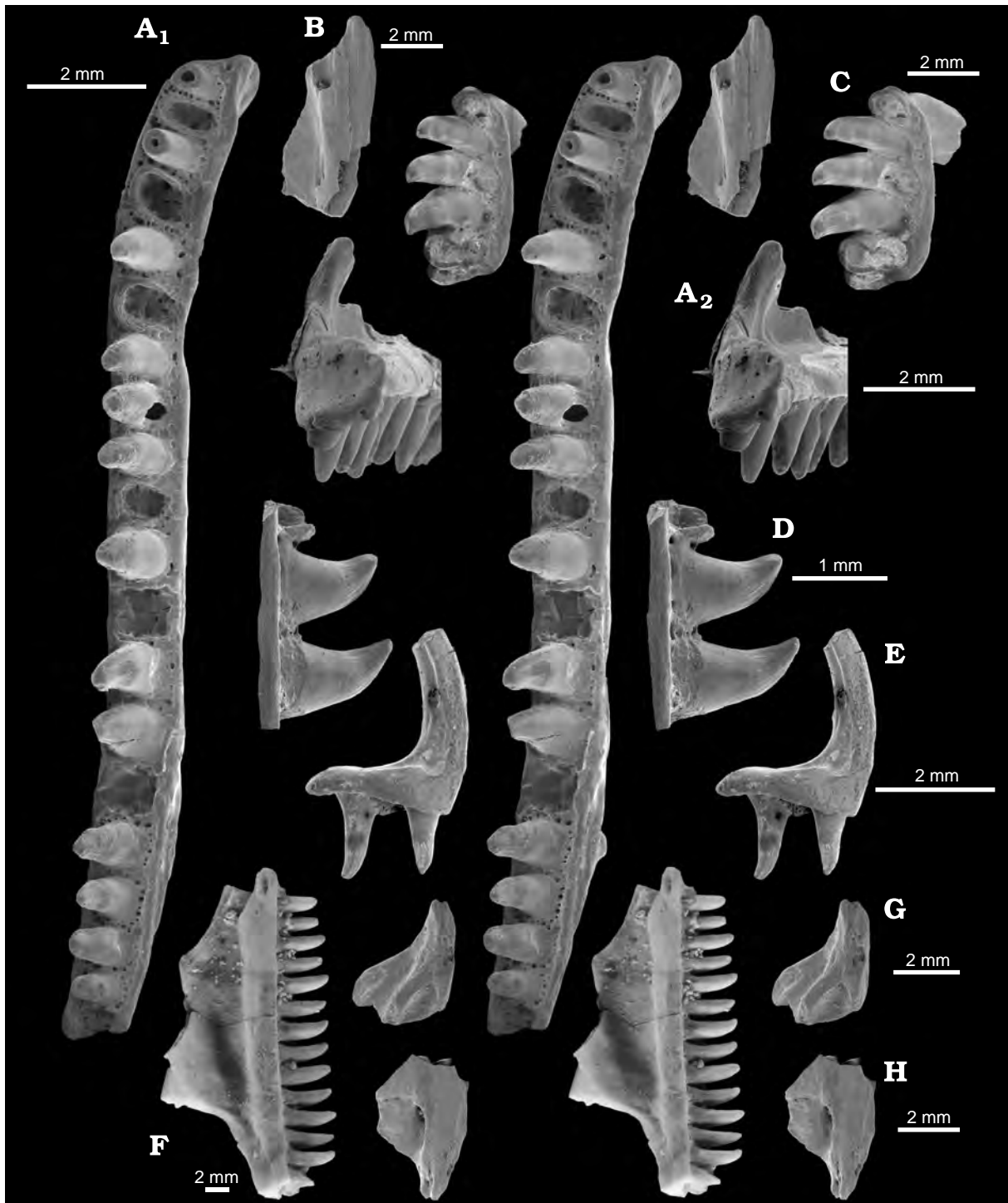
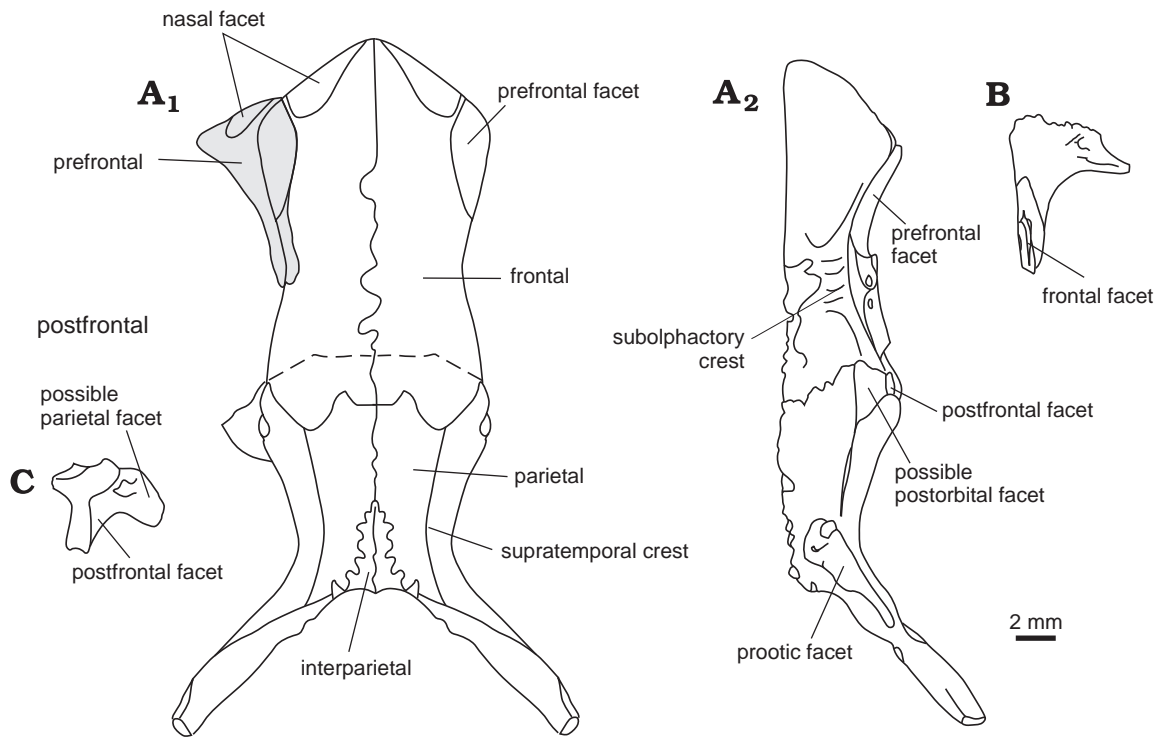


Fig. 4. *Czatkowiella harae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A.** Maxilla ZPAL RV/100, in occlusal (A_1) and anterior (A_2) views. **B.** Anterior part of right lacrymal ZPAL RV/224, in medial view. **C.** Premaxilla ZPAL RV/5, in ventral view. **D.** Posterior maxillary teeth ZPAL RV/1119, in lingual view. **E.** Premaxilla ZPAL RV/111, in medial view. **F.** Maxilla fragment of old adult specimen ZPAL RV/1126, in lingual view. **G.** Supratemporal ZPAL R.V/1076. **H.** Posterior part of the right lacrymal ZPAL RV/225, in lateral view. SEM stereo-pairs.

Fig. 5. *Czatkowiella harae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A.** Reconstruction of a partial skull roof, in dorsal view (A_1) and ventral view of the left part of the same (A_2). **B.** Left prefrontal in medioventral view with the anterior part damaged. **C.** Postorbital, in direct dorsal view. **D.** Central part of the left frontal ZPAL RV/994, in ventral view. **E.** Anterior part of the left frontal ZPAL RV/995, in ventral (E_1) and dorsal (E_2) views. **F.** Right postfrontal ZPAL RV/1075, in ventral (F_1) and dorsal (F_2) views. **G.** Posterior part of the left parietal ZPAL RV/820, in dorsal (G_1) and ventral (G_2) views. **H.** Left parietal ZPAL →



RV/724, in dorsal (H₁) and ventral (H₂) views. I. Central part of the right frontal ZPAL RV/342, in dorsal (I₁) and ventral (I₂) views. J. Left postorbital ZPAL RV/1072, in medial view. K. Left interparietal ZPAL RV/1065, in ventral view. All but A–C SEM micrographs; all but E₂, F₂, J, K stereo-pairs.

mid-length of the bone the crests lie at roughly one quarter of the frontal width from the orbital margin, and slope very steeply toward the orbit (Fig. 5D, I₂). There is variation in this feature, as shown by specimens ZPAL RV/994 and 995, and the frontal table may have extended further over the orbit with age as the olfactory crests became thicker (Fig. 5D, E₁, I₂). The crests diverge anteriorly and posteriorly. Anteriorly, they bear complex prefrontal facets. Posteriorly, each postfrontal facet is subdivided into two concavities, the anterior one almost touching the prefrontal facet. Medial to the rear of the subolfactory crest is a parietal facet. It extends across towards the midline and shows that the frontoparietal overlap was extensive.

Parietal. — As with the frontal, there are several diapsid parietal types at Czatkowice 1. Of these, only one type fits the morphology of the designated frontal, reaches a corresponding adult size to other bones attributed to this taxon, and comes in a range of sizes. It is represented by specimens ZPAL RV/373, 367, 444, 724, and 820, the most complete of these being the latter two (Fig. 5G, H). ZPAL RV/724 is a nearly complete left bone missing only the distal end of the postparietal process; ZPAL RV/820 is another left bone preserving the rear end of the skull table and an almost complete postparietal process. The description that follows is based on these two specimens.

The parietals are paired. Each bone is elongate, with a long skull table and a long posterolaterally directed postparietal process. The anterior margin bears a rugose dorsal facet for the frontal (the total suture being W-shaped) and a smaller lateral slot facet for the postfrontal (Fig. 5H). On the ventral surface, there is another frontal facet (suggesting the two bones slotted firmly into one another) and a shallower facet, possibly for the postorbital. The anterior margin of the parietal is wider than the rest of the bone but there is no marked anterolateral parietal wing. The parietal plate is rather flattened, with the lateral adductor shelf lying at only a shallow angle to the dorsal surface. The concave lateral edge formed the margin of the upper temporal fenestra, with the greatest embayment towards the rear end of the bone — just anterior to the origin of the postparietal process. Medially, the interparietal suture is slightly sinuous anteriorly and then becomes more interdigitated posteriorly (Fig. 5G, H). There is no parietal foramen. In ZPAL RV/724, the medial border is straight from front to back, but in smaller specimens, including ZPAL RV/444 and 820, the borders diverge leaving a triangular gap in the back of the bone (Fig. 5A₁). This is particularly striking in ZPAL RV/820, where edge is strongly interdigitated both medially and then for a short distance posteriorly. This gap accommodates a pair of postparietal/interparietal elements (see below), but in more mature specimens (*e.g.*, ZPAL RV/724), the postparietal has become fully incorporated into the body of the bone. The postparietal process is long, running out almost horizontally from the parietal plate but at an angle of about 45°. From proximal to distal, the orientation of the process changes from horizontal to vertical, with the dorsal plate tapering sharply and the development of a ventrolateral flange. At the tip of this is a vertical slot facet for the supratemporal.

Postparietal/interparietal. — ZPAL RV/1065 (Fig. 5K) is a right postparietal bone that fitted into the triangular cleft described above in the back of the parietal plate. The bone has a rough ventral surface and a smoother dorsal surface. The posterior edge is sharp and curved, the medial margin bears an extension of the interparietal suture, and the lateral edge bears deep digitations matching those of the parietal.

Prefrontal. — Several types of small prefrontal have been recovered, differing in the length and robusticity of the orbital process and the size and position of facets for surrounding bones. The commonest and morphologically most consistent type of prefrontal, exemplified by specimens ZPAL RV/410 and 466 (Figs 5A₁, 6B, F), is found in a range of sizes. It has a frontal process and frontal facet that most closely fits the frontal type referred to *Czatkowiella*.

The bone is strongly curved with a long, relatively slender orbital (frontal) process and a broad, medially concave body that contributes to the lateral wall of the nasal chamber. The frontal process tapers posteriorly. On its medial surface (Fig. 6F) it bears a complex interlocking facet that wrapped around the anterolateral margin of the frontal. Anteromedially, this process expands horizontally into a faceted flange that could have supported the posterolateral part of the nasal. Whether the prefrontal met the maxilla anterodorsally is not known as this very thin region of the bone is generally broken. The remainder of the bone then curves anteroventrally to form the anterior margin of the orbit. The orbital flange is narrow and tapers at its tip into a relatively narrow curved process that met the palatine, but probably was not strongly sutured to it (if at all). The flange supports a broad facial region with a large anterolateral facet that is in two parts with a slight step between them. This large double facet is for the lacrimal (Fig. 6B₁).

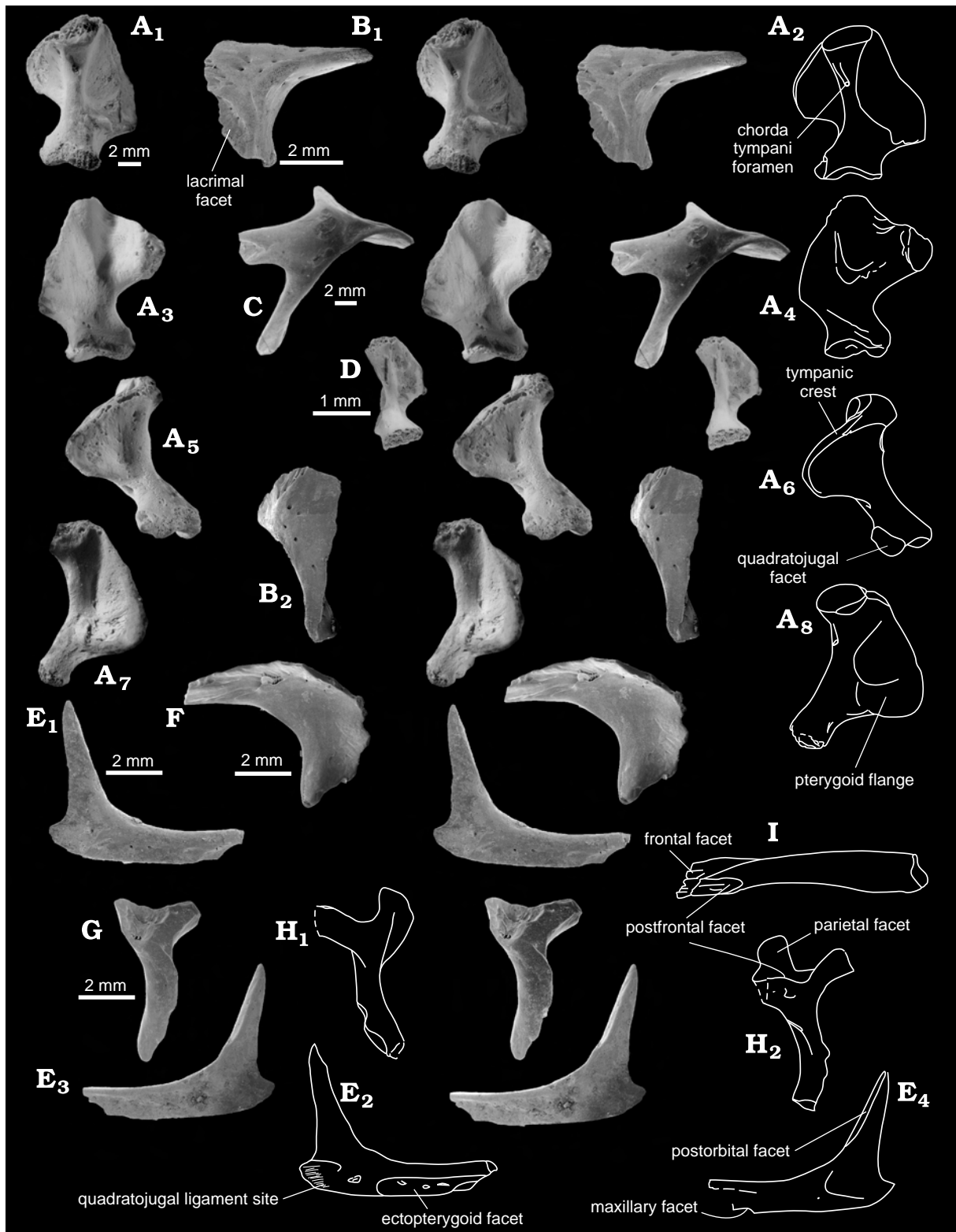


Fig. 6. *Czatkwiewella harae* gen. et sp. n., Early Triassic of Czatkwiewice 1, Poland. **A.** Left quadrate ZPAL RV/375, in posterior (A_1 , A_2) anterior (A_3 , A_4), lateral (A_5 , A_6), and medial (A_7 , A_8) views. **B.** Left prefrontal ZPAL RV/466, in lateral (B_1) and dorsal (B_2) views. **C.** Left squamosal ZPAL RV/27 possibly belonging to *Czatkwiewella harae*, in lateral view. **D.** Small left quadrate ZPAL RV/192, in posterior view. **E.** Left jugal ZPAL RV/113, in medial (E_1 , E_2) and lateral (E_3 , E_4) views. **F.** Left prefrontal ZPAL RV/410, in medial view. **G.** Left postorbital ZPAL RV/284, in lateral view. **H.** Left postorbital ZPAL RV/355, in medial (H_1) and lateral (H_2) views. **I.** Parietal ZPAL RV/724, in left side view. All but A_2 , A_4 , A_6 , A_8 , E_2 , E_4 , H_1 , H_2 , **I** SEM stereo-pairs.

Lacrimal. — The lacrimal of *Czatkowiella* is represented by several specimens (*e.g.*, ZPAL RV/1051, 1052; Fig. 4B, H respectively) attributed on the basis of size (too large to belong to the smaller diapsids) and fit. The lacrimal has a double facet on its medial surface that closely fits the facet morphology on attributed prefrontals in size and orientation. The lacrimal is an elongate and roughly triangular bone with a straight ventral maxillary edge, a curved posterior margin that was excluded from the orbit by the prefrontal, and a bilobed dorsal edge that curved downward and forward to meet first the prefrontal and then the maxilla. The opening of the lacrimal canal is set well forward on the face (Fig. 4H), requiring the presence of a deep groove to carry the duct from the orbital margin to the foramen. From here, the duct canalises the bone and presumably opened from the apex to cross the inner surface of the maxilla, but this region is not preserved in any specimen.

Postfrontal and postorbital. — The postorbital specimens ZPAL RV/284, 355, 377, 508, 1071–1074, 1084 are attributed to *Czatkowiella* on the basis that they are, on average, smaller than those of *Osmolskina* (Borsuk-Białynicka and Evans 2009), and display a range of sizes. The bone is a distinctive element that is bi- rather than triradiate (Fig. 6G, H), with a long, curved jugal process and a long straight squamosal process. The postorbital completed almost the entire posterior orbital margin *via* the elongated jugal process. The squamosal process is long and slender, and has a faceted posterior tip that slotted into a facet on the lateral surface of the squamosal. The dorsomedial process of the postorbital is very short and inclined medially. It bears a deep concavity that accommodated a small postfrontal. The concavity is extended by a median tongue-shaped process that turns posteromedially, possibly to contact the parietal (Fig. 5A₂, C).

Only one incomplete postfrontal bone (ZPAL RV/1075,) has been identified. It must have straddled the frontoparietal suture. Its slender anteromedial end is mediodorsally and laterodorsally faceted (Fig. 5F₁) and was thus overlapped by the frontal. Only posteriorly, does the postfrontal bear a postorbital facet (Fig. 5F).

Jugal. — Jugals are usually rather common and easily recognised elements in microvertebrate deposits of this type, but relatively few non-archosaurian jugals have been recovered. Of these, most are very small and belong either to the small lepidosauromorph or to juveniles of other taxa. However, one subset is larger and flatter, with weak ectopterygoid facets (*e.g.*, ZPAL R V/113; Fig. 6E₂). These bones have a strap like ventral component and a dorsal process rising subvertically at only a slight angle to the main axis of the bone. This dorsal process bears a strip facet along its anterior margin for the postorbital. The main body extends posteriorly into a short, rounded posterior process, and anteriorly into longer anterior maxillary process that fitted into a groove on the dorsomedial surface of the maxilla. The posterior process bears no articular facet for the quadratojugal. Instead, it is roughened for the attachment of a quadratojugal ligament that was the only structure closing the lower temporal fenestra ventrally.

Squamosal. — The squamosal is another problematic bone. While archosaurian squamosals are abundant, very few small reptile squamosals have been identified. None of these has a size range that matches other elements of *Czatkowiella*. However, two morphs exist for the squamosal of *Osmolskina* (Borsuk-Białynicka and Evans 2009) one with a narrow body and long anteroventral ramus, and one with a thicker (dorsoventrally) body and a shorter more ventrally directed ramus. Both display the same quadriradiate type with a lozenge-shaped body, anteriorly faceted postorbital process, and a bifid parietal process with its posterior part (*i.e.*, posteromedial process of the squamosal) overhanging the quadrate head. It seems likely that one or other of these squamosal types pertains to *Czatkowiella*. The finer outline and more open angle between the posterior and ventral processes of the longer type match the anterodorsal border of the *Czatkowiella* quadrate better than that of *Osmolskina* which is anteriorly less extensive and is directed more vertically (Borsuk-Białynicka and Evans 2009). The longer squamosal type (Fig. 6C) is therefore provisionally attributed to *Czatkowiella*.

Supratemporal. — Whichever squamosal morphology is referred to *Czatkowiella*, the angle and shape of the posteromedial process is such that it would not have fitted into the slot at the tip of the postparietal process. This suggests the presence of an intervening supratemporal bone. ZPAL RV/1076 (Fig. 4G) is a partial supratemporal tentatively attributed to *Czatkowiella*. It comprises a small curved body bearing a concavity that accommodated the medial tip of the squamosal and a posterodorsal sheet of bone that maintained the posterior edge of the upper temporal fenestra. The medial facet for the parietal is not preserved.

Quadrate and quadratojugal. — The quadrate is strongly arched (Fig. 6A₅–A₈) Its contact with the squamosal is fairly long. The cephalic condyle and the mandibular condyle are connected by a strong posterior pillar. A small foramen for the chorda tympani perforates the posterior face of this pillar at about one third of the

distance from the cephalic condyle (Fig. 6A₁, A₂). Both the pterygoid flange and tympanic crest diverge anteriorly from the pillar, so that the proximal half of the bone is very large and its anterior face is concave. The medial surface of the pterygoid flange bears a clear pterygoid facet (Fig. 6A₇, A₈). The ventral extremity of the quadrate projects laterally to contact the quadratojugal. Between it and the tympanic crest, the margin is deeply incised by a quadratojugal foramen. This was framed laterally by a reduced quadratojugal. A small oval quadratojugal facet lies on the ventrolateral margin of the quadrate (Fig. 6A₅, A₆), but the quadratojugal itself has not been recognized itself. Medial to this, the mandibular condyle bears an articular facet for the lower jaw. This articular facet extends onto the anterior surface of the bone. If this joint surface was horizontal in life, then the ventral half of the quadrate sloped posteriorly at an angle of about 45° (Fig. 1C). The lower margin of the pterygoid flange would then have extended subhorizontally (Fig. 6A₇, A₈) to contact the quadrate ramus of the pterygoid.

PALATAL COMPLEX

Vomer. — The vomer of *Czatkowiella* is attributed on the basis of size and fit between the anterior end and the maxilla. The anterior and middle parts of the bone are well represented (*e.g.*, ZPAL RV/159, 485, 518, 519, 753) but the posterior region is thin and tends to fragment. The anterior tip of the bone is bifid (Fig. 7F, L), the anterolateral lobe fitting into the posterior part of the medial furrow on the maxillary tip (Fig. 2A₂), and the anteromedial lobe directed forward, perhaps with a ligamentous attachment to the premaxilla. The medial edge of the bone is straight and bears a rugose sutural surface for the contralateral vomer (Fig. 7I₁), deep in the anterior quarter, very deep and forming a raised dorsal ridge in the second quarter, and shallower and grooved further posteriorly. The lateral edge is concave anteriorly (forming the narrowest part of the bone) and convex posteriorly as the bone widens out. The dorsal surface of the bone is guttered anteriorly between the raised medial and lateral edges, and then expands into a wider shallower concavity posteriorly (Fig. 7F, J). A small foramen consistently perforates the anterolateral edge in the second quarter of the bone (Fig. 7E, F), but it does not go through onto the palatal surface of the bone. It was probably for an emissary vein. In *Sphenodon* (O'Donoghue 1921), a large venous sinus occupies the dorsal concavity on the vomer and it is likely the same was true of *Czatkowiella*. The palatal surface of the vomer has a covering of small rounded denticles. A double row begins on the anteromedial edge (Fig. 7I₂, L), crossing the bone to the anterolateral edge and then running along this margin until the bone expands in its posterior half. At this point the rows divide, a single row continuing along the lateral margin with a double row extending into the central area. This double row continues backward and medially to the edge of the bone. In ZPAL RV/753, the dorsal surface bears facets for the palatine and pterygoid, although this thin region is not complete. The anterolateral tip of the palatine fitted into a slot facet on the dorsolateral edge of the vomer (Fig. 7F, J). Medially, at about the same level, the intervomerine suture thins abruptly creating a grooved shelf that accommodated the anterior tip of the pterygoid (Fig. 7F, J).

Palatine. — The palatine of *Czatkowiella* is represented by numerous bones in a range of sizes. It is a large elongated sheet of bone bearing a strong lateral maxillary process. The maxillary process is separated from the main body of the bone by two U-shaped incisions, the anterior one corresponding to the choana, the posterior one to the suborbital fenestra. The process is perforated centrally by an infraorbital foramen that lay adjacent to the palatine foramen of the maxilla (see above). The dorsal surface (Fig. 7A₂, C) of the bone is subdivided into two parts separated from each other by a transverse step. The anterior part is relatively flat, while the posterior one is concave. The anterior part has a low surface that may have had a ligamentous connection to the orbital process of the prefrontal but there is no prefrontal boss. A groove crosses the bone from medial to lateral. It carried branches of the palatine nerve towards the infraorbital foramen (joining the maxillary nerve). Lateral to the maxillary process, the ventral surface (Fig. 7A₁, D, G) is also divided into two, but medially and laterally. The lateral surface runs along the margin of the bone and carries a tooth row posteriorly but none anteriorly. The medial edge is covered by a large facet for the pterygoid, grading anteriorly into a shorter facet for the vomer. It is clear from the facet pattern that the pterygoid met the vomer anteriorly, separating the palatines for their complete length and excluding them from the interpterygoid vacuity.

Pterygoid. — Pterygoids are common in the material (*e.g.*, ZPAL RV/70, 71, 75, 76), but none is complete. Judging by eye, the variability range of the pterygoids attributed to *Czatkowiella* is larger than that of *Osmolskina* (Borsuk-Białynicka and Evans 2009). In this respect the *Czatkowiella* pterygoids correspond to the *Czatkowiella* braincase material (see p. 205).

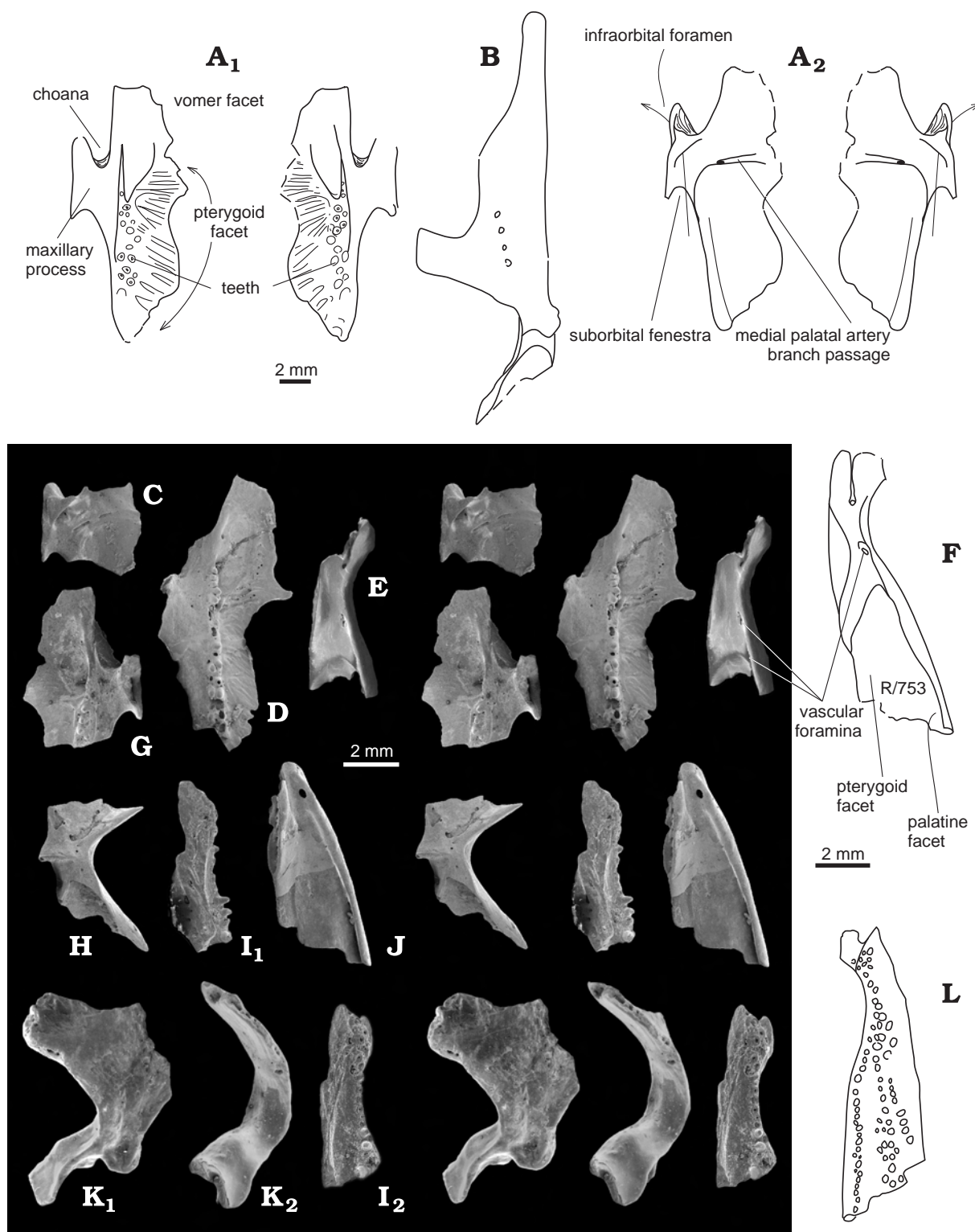


Fig. 7. *Czatkowiella harae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Reconstruction of palatines of both sides, in ventral (A_1) and dorsal (A_2) views. **B**. Reconstruction of the right pterygoid, in ventral view. **C**. Central part of the left palatine ZPAL RV/202, in dorsal view. **D**. Right palatine ZPAL RV/997 without maxillary process, in ventral view. **E**. Anterior part of the right vomer ZPAL RV/518, in dorsal view. **F**. Reconstruction of the right vomer, in dorsal view. **G**. Central part of the left palatine ZPAL RV/203, in ventral view. **H**. Central part of the left pterygoid ZPAL RV/334, in ventral view. **I**. Anterior part of the left vomer ZPAL RV/519, in medial (I_1) and ventral (I_2) views. **J**. Posterior part of the right vomer ZPAL RV/753, in dorsal view. **K**. Right pterygoid ZPAL RV/76, in ventral (K_1) and lateral (K_2) views. **L**. Reconstruction of the right vomer, in ventral view. All but A, B, F, L SEM stereo-pairs.

The palatal flange may be confidently reconstructed as a rather narrow triangle, its medial and lateral borders enclosing an angle of no more than 60° (Fig. 7H, K). The palatal surface of the wing bears a longitudinal concavity that turns gradually into a dentigerous field extending along the medial border (Fig. 7H, K₁). The dorsal surface of the wing is folded transversely, the main fold extending as a longitudinal convexity bordered medially and laterally by concavities. The anterior extent of the bone is reconstructed (Fig. 7B) on the basis of the rest of the ventral aspect of the skull but it is clear from the facets on the vomer that the pterygoids met in the anterior midline (Fig. 1B). Posteriorly, the ventral surface of the bone passes gently into the quadrate ramus without the bordering crest that occurs on the archosauriform pterygoids (Borsuk-Białynicka and Evans 2009). There is also no ligament tuberosity in this region. In these two respects, the pterygoids are similar to those of *Prolacerta broomi* (Gow 1975, fig. 11). At the junction between the palatal plate and the quadrate ramus is the medial basiptyergoid fossa. As a whole the pterygoid is dorsally concave (Fig. 7K₂). The quadrate ramus is angled laterally at roughly 90° to the lateral border of the palatal wing. At the base, the quadrate ramus is hemi-cylindrical in cross-section, and dorsally convex. It expands posteriorly into a bony blade, with thickened dorsal and ventral margins, although this region is usually broken.

BRAINCASE

The braincase bones are mostly disarticulated. In the Czatkowice 1 assemblage *Czatkowiella* is the second largest reptile after the archosauriform *Osmolskina*. Among the basioccipitals, the specimens more delicately built are always fused with the exoccipitals, and never with the opisthotic. The opisthotics with no conjoined exoccipital clearly belong with them. In *Osmolskina* the reverse is true: the exoccipital is always completely integrated with the opisthotic, and these bones are thus readily discriminated from those of *Czatkowiella*. The assignment of other braincase bones is mainly based on a size criterion. The braincase base of *Czatkowiella* is basically horizontally aligned, the parasphenoid rostrum extending in the same plane as parasphenoid ventrolateral crests. The angle between the basisphenoid and the basioccipital is more or less open depending on the amount of cartilage in the basisphenoid-basioccipital contact, which is unknown. All specimens display a well-ossified neurocranial surface.

Basioccipital and exoccipital. — The exoccipitals are tightly fused with the basioccipital (Fig. 8A, D), except in juveniles. The tripartite structure of the occipital condyle is evident only in eroded specimens. The exoccipital shafts first diverge dorsally, then they converge, but do not meet, above the large circular foramen magnum (Figs 8A₁, 9A). The exoccipitals are subtriangular in transverse section, with the surfaces facing medially, posterolaterally and anterolaterally. Their upper ends are only rarely preserved. Roughly level with the dorsal margin of the condyle, the exoccipital is perforated by the main hypoglossal nerve foramen, with one or two much smaller accessory foramina below it (Figs 8A₁, 9A). Ventrally, the exoccipitals are separated in the midline by a narrow strip of basioccipital (Figs 8D, 9D). This zone expands a little towards the occipital condyle and much more so anteriorly where the basioccipital becomes the only element of the braincase floor. It bears a sagittal crest that protrudes anteriorly. On either side of the protruding part, inclined slightly laterally, the anterior margins of the basioccipital fit the posterior surfaces of the basisphenoid, although the bones may have been separated by cartilage in life. Ventrally, the gap was bridged by the posterior lamina of the parasphenoid (Figs 8H, 9G). This overlapped the basioccipital and left a parabolic trace on its ventral surface. Anterior to the base of each exoccipital, and below its suture with the basioccipital (ZPAL R.V/423), there is a transverse furrow corresponding to the floor of the metotic fissure (cranial nerves IX and X). The braincase floor is covered by finished bone which evidently appeared early in ontogeny. Together, the basioccipital and exoccipitals form a sub-quadrangular occiput (Fig. 8A) the ventral corners of which bear strong basal tubera for the attachment of hypaxial muscles, most notably *m. longus colli ventralis*. These tubera are laterally flattened and are united ventrally by a concave crest. The crest separates the neck of the occipital condyle from the anteroventral concavity that continues onto the parabasisphenoid.

Supraoccipital. — The supraoccipital attributed to *Czatkowiella* is a subhexagonal blade of bone, wider than long, with the opisthotic and prootic borders enclosing an angle of approximately 90° , and separated from each other by a small incision (*e.g.*, Fig. 8B₁). The concave posterior border of the supraoccipital is laterally incised by small exoccipital facets that do not meet each other. Between them, is the fairly long supraoccipital border of the foramen magnum. The anterior border is sinuous (Fig. 8B₂), with bilateral con-

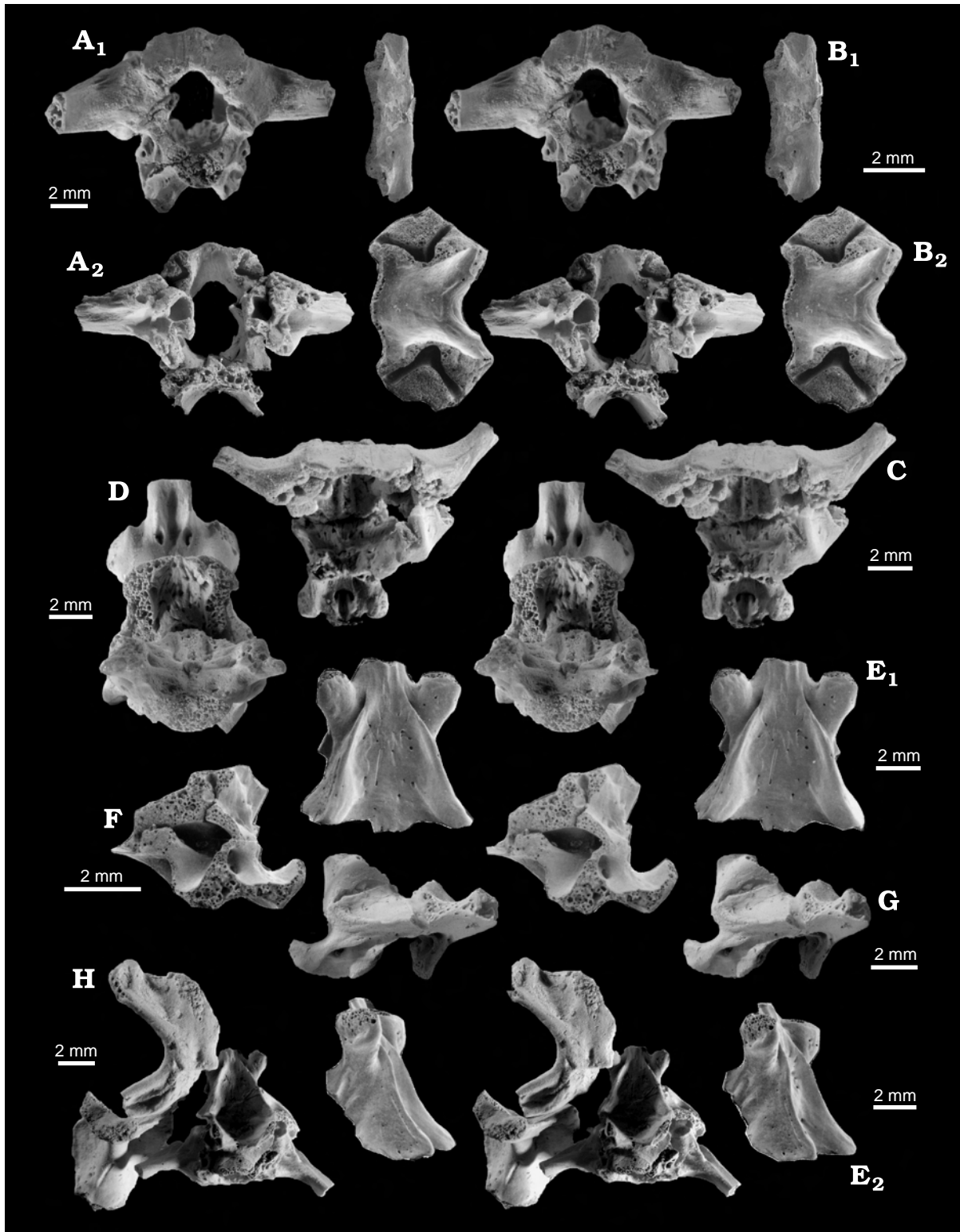


Fig. 8. *Czatkowiella harae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A.** Braincase ZPAL RV/433 combined from different individuals, in posterior view (A_1), the same in anterior view with the parabasisphenoid and prootics omitted (A_2). **B.** Supraoccipital ZPAL RV/126, in anterior (B_1) and ventral (B_2) views. **C.** Braincase ZPAL RV/433 combined from different individuals with the parabasisphenoid and the left prootic included, in anterior view. **D.** An incomplete braincase ZPAL RV/430 in dorsal view combined from different individuals, with the supraoccipital and prootics omitted. **E.** Parabasisphenoid ZPAL RV/433, in ventral (E_1) and lateral (E_2) views. **F.** Left prootic ZPAL RV/119, in medial view. **G.** Left prootic combined with opisthotic ZPAL RV/432, in lateral view. **H.** A braincase ZPAL RV/999 combined from different individuals with a quadrate and a pterygoid ZPAL RV/76 added, in ventral view. All stereo-pairs; B, E, F, G SEM micrographs.

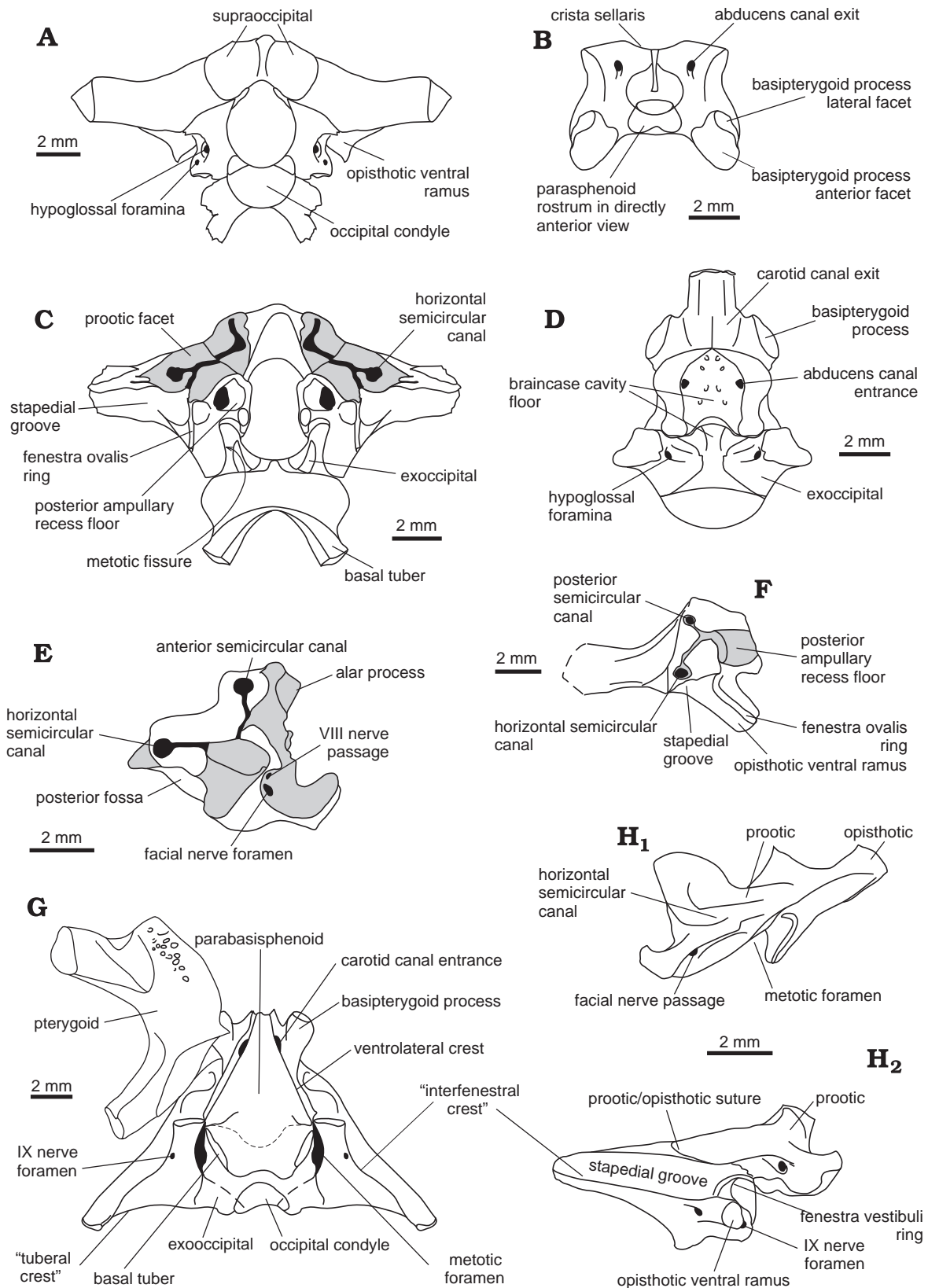


Fig. 9. *Czatkowiella harae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Explanatory schemes to Fig. 8. **A.** Braincase, in posterior view. **B.** Parabasisphenoid, in anterior view. **C.** Posterior part of the braincase, in anterior view with parabasisphenoid and prootics omitted. **D.** Partial braincase, in dorsal view with supraoccipital and prootics omitted. **E.** Left prootic, in medial view. **F.** Left opisthotic, in anteromedial view. **G.** Braincase with pterygoid articulated, in ventral view. **H.** Left prootic and opisthotic articulated, in lateral (H_1) and ventral (H_2) views.

cavities separating the anteriorly protruding central part from the prootic facets. The thin anterior surface of the bone was probably continued forward in cartilage and bears no special cavities for venous sinuses. Instead, the dorsal surface of the bone is grooved by two concavities extending posteriad from the anterior border, and two extending laterad towards the notch between the prootic and opisthotic facets. Further furrows, perhaps associated with veins, run on the ventral surface of the bone (Fig. 8B₂), parallel to the posterior border. The whole plate is well ossified even at a small size, matching the condition of other parts of the cranium attributed to *Czatkowiella*. The facets for neighbouring bones and for the internal labyrinthine walls are very distinct. Bilaterally, the supraoccipital provides the dorsal components of the otic capsules. The prootic and opisthotic margins are perforated by entrance foramina of the anterior and posterior semicircular canals respectively. On each side of the bone, the internal surface of the capsule is grooved by the semicircular canals.

Parabasisphenoid. — In ventral view, the parabasisphenoid forms a long triangle of bone (Figs 8E, 9G). Two straight blunt ventrolateral crests converge anteriorly from the posterolateral parasphenoid wings towards the bases of the basiptyergoid processes, and then run in parallel along the ventral surface of the parasphenoid rostrum (cultriform process). Between the crests, the ventral surface is concave, deep posteriorly but becoming shallower towards the rostrum. The surface then becomes convex rostrally. A possible parasphenoid component is long, its posteromedial part overlapping the ventral surface of the basioccipital almost to the level of the basal tubera.

The basiptyergoid processes are short, broad and somewhat dorsoventrally flattened. They are widely separated from each other by the base of the parasphenoid rostrum. Seen in anterior view, they are also ventrally deflected with the articular surfaces for the pterygoids on the anteroventral and ventrolateral surfaces. In anterior view, the rostrum seems tripartite — the dermal parasphenoid ossification (or ossifications) underlying the paired trabeculae cranii, represented by their ossified ovoid bases. Between the basiptyergoid processes and the ventrolateral crests, there are distinct furrows that transmitted the internal carotid arteries and the palatine branches of the facial nerve (VII). At the base of the parasphenoid rostrum and lateral to the ventrolateral crests are paired carotid foramina (Figs 8E, 9G). At the level of these foramina, each artery must have divided. A palatine branch accompanied the nerve forward along the ventrolateral edge of the rostrum, while the cerebral branch entered the carotid foramen and ran through a short vertical canal to reach the dorsal side of the cultriform process just anterior to the hypophysial fossa (Figs 8C, 9B). The fossa which is an excavation of the anterior wall of the basisphenoid is divided by a, vertical, sagittal crest into two concavities, which give the surfaces of origin for retractor muscles of the eye. Each surface is perforated by a short canal for the abducens nerve (Figs 8C, 9B). The intracranial surface of the basisphenoid is subrectangular in outline, concave, and covered by finished bone. The lateral walls of the parabasisphenoid (Fig. 8E₂) are fairly deep but horizontally aligned. They bear elongated facets for the prootic. These extend towards the midline along the crest of the dorsum sellae but it is not clear whether or not they met.

Posteriorly, the basisphenoid bears oblique, more or less finished, posterior surfaces for the basioccipital, whereas a ventral sheet of finished bone, roughly corresponding to parasphenoid, extends onto its ventral surface. When articulated, the parabasisphenoid and basioccipital together form a longitudinally concave neurocranial cavity floor. The ventral ramus of the opisthotic probably entered the space left between the basioccipital and parabasisphenoid on each side.

Opisthotic. — The opisthotic attributed to *Czatkowiella* is represented by a number of specimens (*e.g.*, ZPAL RV/179–182, 432, 449) permitting an accurate reconstruction. The main body of the opisthotic extends into a slightly bilaterally flattened paroccipital process. In life, the contralateral processes extended directly laterad, while changing posterolaterally in the distal parts only. The exoccipital facet faces ventromedially, and the supraoccipital facet dorsomedially. The supraoccipital facet bears the circular opening of the posterior semicircular canal. The prootic facet cuts obliquely through the anterolateral edge of the bone (Figs 8A₂, 9C). It contains the opening for the horizontal semicircular canal, and below it lies the wide entrance of the vestibular cavity containing the posterior ampullary recess. Posteroventral to the prootic facet, the surface of the paroccipital process is flattened and sculptured by heavy longitudinal crests. A still more ventral wall of the opisthotic bears a longitudinal stapedial groove directed towards the fenestra vestibuli. The groove is bordered anterolaterally by a distinct crest extending in line with the prootic crest, posteriorly by another crest, (roughly corresponding to the intertuberal crest, Oelrich 1956), that continues proximally onto the ventral ramus of the opisthotic (Figs 8A₂, 9F, H₂), and still more medially by a crest analogous to the crista tuberalis of lizards.

A circular convexity or ring (Figs 8A₂, 9C, F, H), that cuts transversely through the stapedial groove, demarcates the attachment area of the membrane covering the fenestra vestibuli. The ring continues onto the anterior surface of the ventral ramus of the opisthotic.

The ventral ramus of the opisthotic is a fairly long, subvertically oriented, blade (Figs 8G, 9F, H). It extends into a large anteromedially directed flange (denoted as the posterior ampullary recess floor in Fig. 9C, F), that protrudes from the ventral corner of the posterior ampullary recess. The ventral ramus also forms the anterolateral border of the metotic foramen, with the exoccipital providing its posteromedial wall. Close to its base, the ventral ramus is perforated by a short, superficially placed, lateral canal (Fig. 9G). This may have carried the glossopharyngeal nerve (IX), or one of its branches, while the vagus (X) passed through the main part of the foramen. This is not, however, homologous to the condition in lizards where a separate ventral channel is created for the glossopharyngeal nerve and perilymphatic duct by the apposition of the opisthotic (posterior ampullary prominence) and exoccipital below the vagus foramen. A similar small canal can be found on the opisthotic of the basal rhynchocephalian, *Gephyrosaurus* (SEE unpublished data).

Prootic. — The prootic is exemplified by specimens ZPAL RV/119–121, 461, 462. These are attributed mainly on the basis of their subhorizontal alignment, as determined by the course of the horizontal canal (Fig. 8F). This matches the basically horizontal alignment of the braincase floor in *Czatkowiella*. The lateral surface of the main body has distinct elongated convexities covering the anterior and horizontal semicircular canals. Above the anterior canal, there is a small but distinct triangular alar process. A well-developed anterior inferior process extends anteriorly, separated from the main part of the bone by the wide incisura prootica marking the position of the trigeminal nerve ganglion (V). This contains a small, subtriangular supra-trigeminal process. In its upper part, a small notch marks the exit of the *vena cerebialis media* from the interior of the brain case. The lateral face of the prootic (Figs 8G, 9H₁) is partially divided by a weak *crista prootica* that extends posterodorsally from the lower margin of the anterior inferior process. It converges posteriorly with the ventral margin of the bone as it passes into the lateralmost crest of the opisthotic, but gradually fades out. The *crista prootica* overhangs the small facial foramen and the grooves into which the anterior (palatine) and posterior (hyomandibular) branches of the nerve pass.

In medial aspect, the prootic (Figs 8F, 9E) is excavated for the inner ear structures. The main cavity, the *cavum vestibulae*, receives the anterior semicircular canal dorsally, horizontal semicircular canal posteriorly where it contacts the opisthotic, and is open posteroventrally. Anterodorsal to the anterior semicircular canal is a funnel-shaped excavation, the subarcuate fossa, for the cerebellar flocculus and part of the dural venous sinus system. Anteroventral to the fossa, and posterior to the incisura, a third excavation housed the ganglia of the facial and vestibulocochlear nerves. The excavations are separated from one another by flat surfaces of unfinished bone representing internal sutures or divisions continued in cartilage. The openings of the anterior and horizontal semicircular canals are located within the supraoccipital and opisthotic surfaces respectively. Ventral to the base of the posterior process, and posterior to vestibular cavity, is a triangular shelf labelled as posterior fossa in Fig. 9E, that provides the anterolateral wall of the stapedial fossa.

MANDIBLE

The lower jaw of *Czatkowiella* is known from the dentary, surangular, and less certainly, parts of the angular and perhaps splenial.

Dentary. — The dentary of *Czatkowiella* is represented by a large number of specimens, including adult and juvenile examples (Fig. 10). None is complete and we can therefore only estimate the tooth count but it was probably between 20 and 30 in adult animals. The anterior teeth are elongate cones with a slight curvature and apical striae, as in the upper teeth (Fig. 3A, D), but the teeth become more robust and more recurved (*e.g.*, Fig. 4D) towards the posterior end of the dentary, especially with age. The jaw ramus is shallow. In lateral view, the bone is lightly sculptured, at least in adults, and bears a series of neurovascular foramina, that are particularly numerous at the anterior end of the bone, below the first 6–8 tooth positions. This region of the bone is also somewhat unusual in that the dorsolateral and ventrolateral surfaces meet at an angle to form a slight crest. In medial view, the tooth row lies above a strong, slightly rounded subdental ridge that thickens anteriorly and contributes to a strong rugose symphyseal surface in adult animals. This surface is less rugose in immature specimens. Below tooth position 6–7 (depending on the age of the animal and the size of the

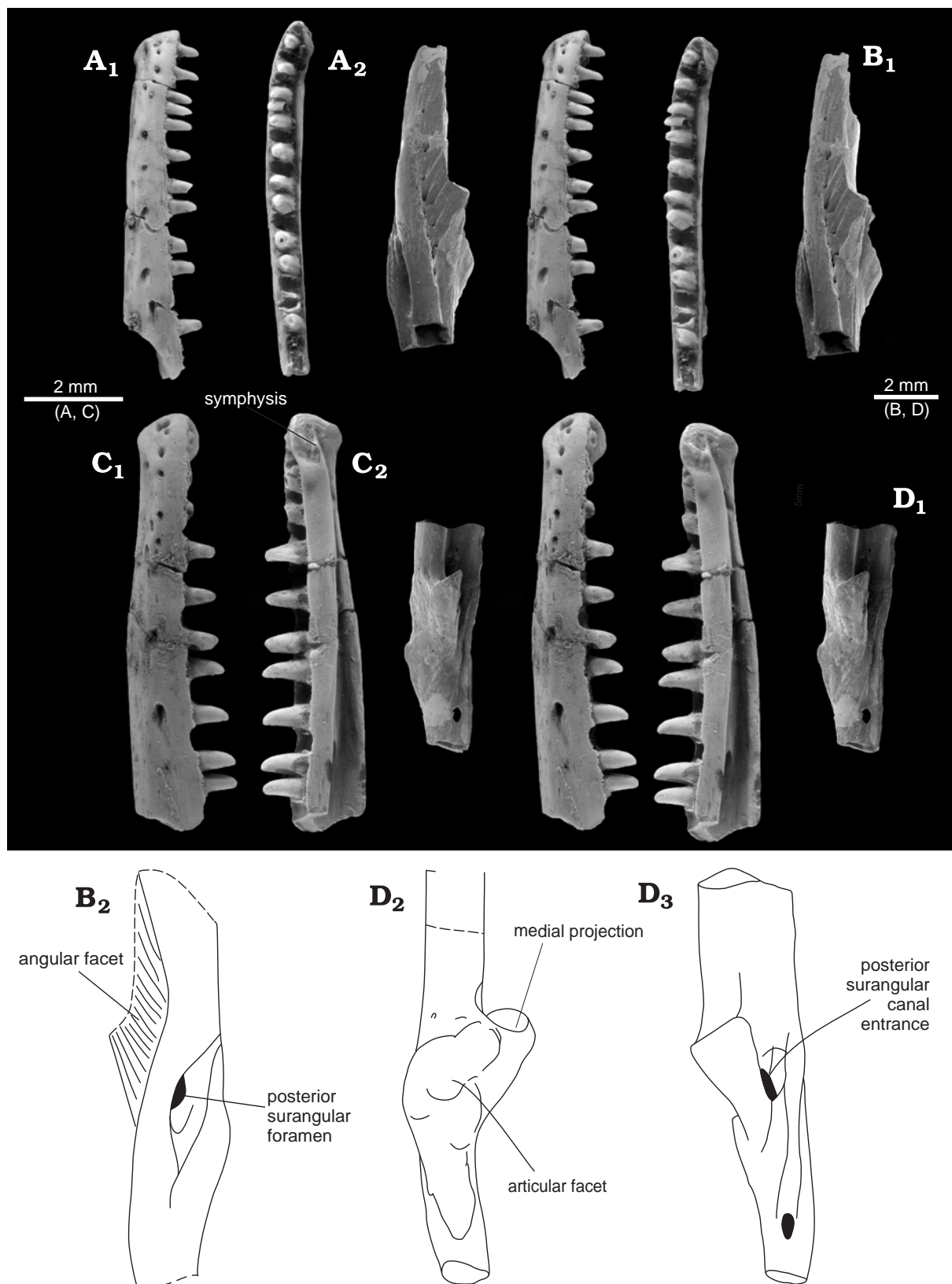


Fig. 10. *Czatkowiella harae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A.** Left dentary ZPAL RV/107, in labial (A₁) and occlusal (A₂) views. **B.** Posterior fragment of the right surangular ZPAL RV/486, in ventrolateral (B₁) view; morphological diagram of the same (B₂) reversed. **C.** Left dentary ZPAL RV/106, in lateral (C₁) and lingual (C₂) views. **D.** Posterior fragment of the left surangular ZPAL RV/166, in mediadorsal (D₁) view; morphological diagram of the same in dorsal (D₂) and medial (D₃) views. All but B₂, D₂, D₃ SEM stereo-pairs.

teeth), the subdental ridge develops a facet, more obvious in the juvenile than the adult, which clearly supported the splenial. This suggests that the splenial did not reach the symphysis, leaving the Meckelian fossa open for a short distance anteriorly. In this region, roughly at the level of the second or third tooth position, the medial wall of the fossa is perforated by a conspicuous nutrient foramen. The Meckelian fossa is generally deep but low. It is open ventrally in young animals although the ventral margin shows a slightly incurving in more mature individuals. Further posteriorly, at around the level of tooth position 15–16, the fossa is perforated by a small foramen representing the opening into the inferior alveolar canal, carrying branches of the mandibular division of the trigeminal nerve (Viii) and accompanying blood vessels. There were at least four tooth positions behind this point, but the posterior end of the bone is not preserved in any specimen.

Surangular. — The surangular is represented by several fragments (Fig. 10B₁, D₁) distinguished by their narrow proportions. They show a size range corresponding to those of other *Czatkowiella* bones. A thick dorsal ridge passes posteriorly into a hook-like medial projection. On its posterior surface, this projection bears a rather poorly determined dorsomedial facet for the articular. The large canal, for the mandibular division of the trigeminal nerve and associated blood vessels, enters at the base of the hook-like projection (posterior surangular canal entrance Fig. 10D₃), and exits by a large posterior surangular foramen situated further posteriorly within a furrow on the ventrolateral face of the posterior process (Fig. 10B₂). A smaller foramen, of unknown function, opens on the medial surface of the bone, still further posteriorly, at the end of a furrow that parallels the medioventral border of the facet for the articular bone.

Dentition. — The marginal teeth of the adult animal are large and recurved with a slight labiolingual compression. Under Scanning Electron Microscopy, the teeth (premaxilla, maxilla, dentary) are shown to have finely striated tips (Figs 3A, C₁, D, 4A, E), but the striation becomes less obvious with age (*e.g.*, Figs 3C₂, 4F). The labial margin of the jaw is higher than the lingual one giving a subpleurodont implantation in smaller individuals, but in larger individuals the teeth approach a subthecodont condition. Tooth replacement occurs from the lingual side of the tooth. It is active in small animals but may have slowed down in adults (*e.g.*, ZPAL RV/1126; Fig. 4F).

VERTEBRAE

The vertebrae of *Czatkowiella* range in size but are characterised by having very dense bone (much heavier and denser than that of either of the smaller diapsids), bicipital cervical ribs and three-headed ribs in the anterior part of the trunk. Further posteriorly, the two ventral rib facets consolidate into a single parapophysis that eventually merges with the diapophysis towards the end of the dorsal vertebral series. The cervical vertebrae attributed to *Czatkowiella* are much elongated whereas the dorsal vertebrae overlap to some degree in their proportions and centrum shape with those of the basal kuehneosaurid from the same material (Evans 2009, see also Fig. 16 herein), but they differ in having a shorter and wider neural arch, shorter wider spine (Fig. 11B), and more strongly divergent zygapophyses separated by a deep V-shaped triangular cleft posteriorly.

Axis. — There is a single common axis type (*e.g.*, ZPAL RV/615; Fig. 11E) and, logically, this should belong to *Czatkowiella*, given the robusticity of the bone and the shape and position of the anteriorly placed rib facets. The bone has a long neural spine with a horizontal dorsal margin that extends forward beyond the anterior tip of the centrum to form a distinct anterior spur. The lateral faces of the spur are planar but the median part becomes more rugose so that it seems to form the posterodorsal limit to a small anterolateral surface. Conceivably this marks the attachment of a proatlas, an element reportedly present in *Prolacerta* (Gow, 1975). The flanks of the neural arch splay out ventrally and bear surfaces for the atlas arches on their anterior shoulders (Fig 11E₁). Posteriorly, the zygapophyses are larger, longer, and divergent, with a ventrally shelved cavity between them. The axis centrum is much narrower than the arch with a strong midventral keel that renders the centrum triangular in cross-section (Fig. 11E₂). The centrum is weakly amphicoelous but not notochordal, and its anterior face forms a planar attachment surface for the odontoid. The lateral surface of the axis is marked by three weak anteroposterior crests, one at the inferior margin of the arch which probably corresponds to the zygapophysial crest in later vertebrae, one at the neurocentral boundary, and one marking the lower limit of the centrum proper, below which is the keel. The central ridge bears a tubercle where it meets the anterior edge of the centrum and this must correspond to one head of an atlantal rib. Below it the

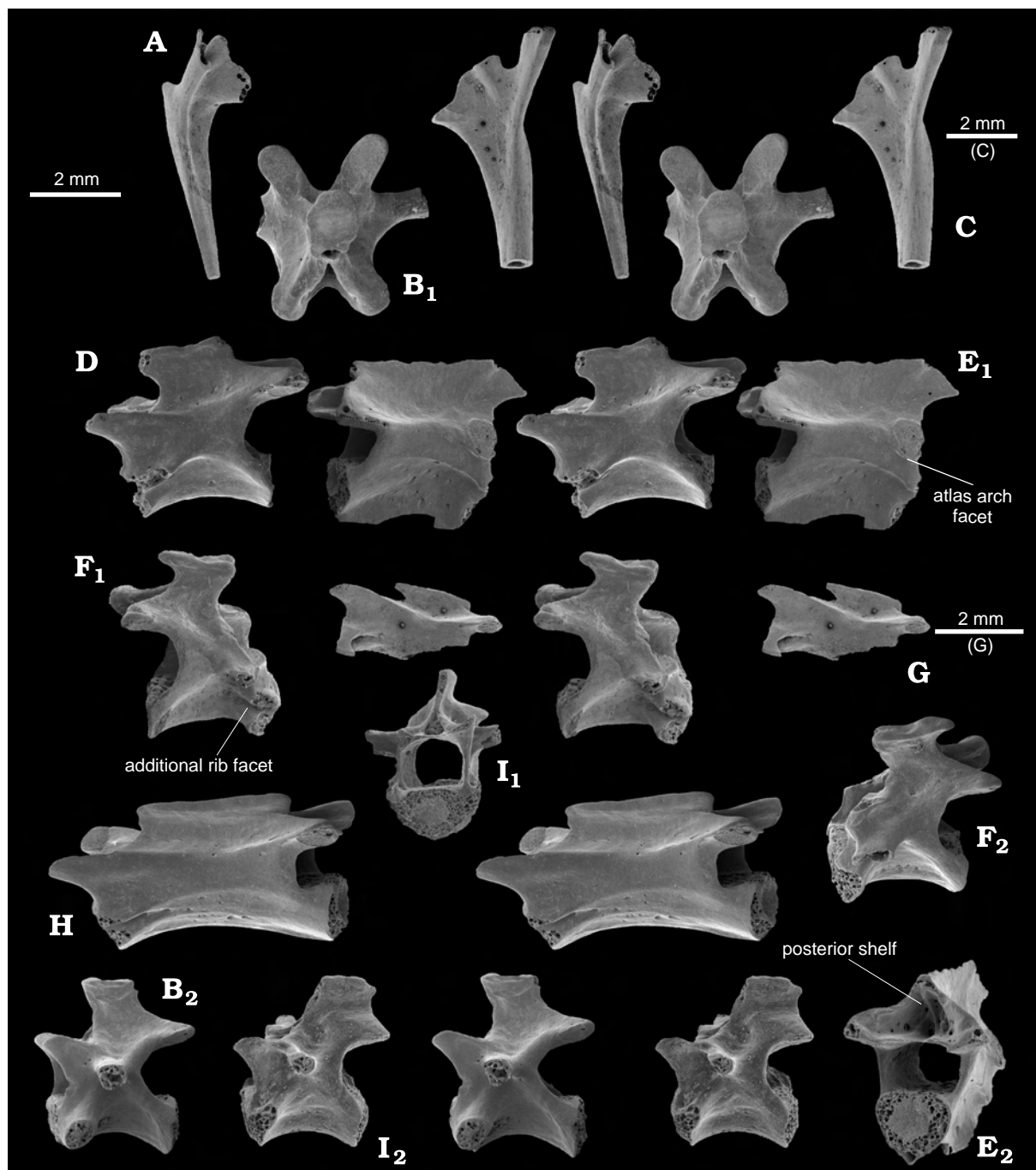


Fig. 11. *Czatkowiella harae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Right three-headed anterior dorsal rib ZPAL RV/934. **B**. Anterior dorsal vertebra ZPAL RV/618. **C**. Right three-headed dorsal rib ZPAL RV/1122. **D**. Anterior cervical vertebra ZPAL RV/613. **E**. Axis ZPAL RV/615. **F**. Dorsal vertebra ZPAL RV/619. **G**. Juvenile mid-cervical vertebra ZPAL RV/616 with proximal fragment of rib fused. **H**. ?Midcervical vertebra ZPAL RV/616. **I**. Posterior dorsal vertebra ZPAL RV/221. Right lateral view (**A**, **E**₁, **F**₁), left lateral view (**D**, **F**₂, **G**, **H**, **I**₂), dorsal view (**B**₁), posterior view (**E**₂), and anterior (**I**₁) views. SEM micrographs; all but **E**₂, **I**₁ stereo-pairs.

edge of the centrum is usually damaged, but there is a hint of a second, weaker tubercle, suggesting the axial rib was dichoccephalous with the two heads close together.

Atlas intercentrum. — This is a small compact, transversally enlarged, body that is trapezoid in outline (ZPAL RV/1100; Fig. 12C). The shorter side bears a concave articular surface that probably met the occipital condyle, and the anterolateral sides bear facets for the atlantal arches. The dorsal surface is convex and spongy and probably contacted the atlas centrum. The fully ossified ventral surface is sculptured and concave

in longitudinal section. The bone is smaller than the atlantal intercentra attributed to *Osmolskina* (Borsuk-Białynicka 2009) and displays a more elaborate morphology, but it is too large to belong to any of the smaller Czatkowice 1 taxa.

Postaxial cervical vertebrae. — The cervical vertebrae of *Czatkowiella* are well represented in the collection. There is a common morphology, with some differences in vertebral length in relation to height, centrum shape, and the shape of the neural spine. Vertebral number cannot be reconstructed, but there is a limited number of cervical morphotypes and it seems likely that the neck was fairly conservative (7–9 segments).

A typical cervical vertebra (*e.g.*, ZPAL RV/616; Fig. 11H) is roughly twice as long (anterior to posterior length of the centrum) as it is high (lower margin of centrum to tip of neural arch midvertebrally). The centrum is solid with weakly convex anterior and posterior surfaces (amphiplatyan). It is subcircular in transverse section with a small ventral angulation when the ventral crest exists, but this is usually absent or very weak. The ventral margin of the centrum slopes posteroventrally, so that the posterior articular surface is lower than the anterior one. The ventral surface is concave, a shape that is accentuated by the anteroventral protrusion of the facets for dichocapalous cervical ribs. These facets are situated bilaterally on the anteroventral borders of the centrum, and are joined to the posterior margin of the centrum by weak curved anteroposterior ridges (see *e.g.*, Fig. 11D, H). Neurocentral sutures are always fully closed. The arch is elongate with a low more or less horizontal spine that has a very long base extending over the whole length of the vertebra. The anteroposterior length of the spine is slightly greater at its apex than at its base, creating a slight overhang at each end (Fig. 11D, G), which is most evident in the anterior dorsals (Fig. 11F). Both zygapophyses extend slightly beyond the end of the centrum. Laterally, the zygapophyses are joined by an anteroposterior crest, although this may be disjunct in some of the longer elements. Seen in dorsal view, the median edge of the cervical neural spine is narrow but it becomes wider in dorsals, particularly so in the anterior part of the dorsal series (Fig. 11B). The triangular recesses between the zygapophyses are shelved with bone. Between the postzygapophyses the shelf extends well back, creating a deep posterior recess that extends below the spine and forms one of the most consistent features of *Czatkowiella* vertebrae (Fig. 11E₁). Between the prezygapophyses the corresponding shelf is very short and bears a slight longitudinal furrow, probably a trace of ligament. No accessory articulations (*e.g.*, like the zygosphene-zygantrum system of lepidosaurs) are developed between successive vertebrae.

In other long necked taxa, and particularly in the articulated neck of *Malerisaurus langstoni* (Chatterjee 1986), the most anterior cervicals are shorter than those in the middle of the neck, with vertebral length increasing backwards, before shortening again towards the beginning of the trunk. This pattern is supported by *Amotosaurus rotfeldensis* (Fraser and Rieppel 2006) in which the first cervical is about half the length of the next one and the midcervicals are the longest. This might be the case in *Czatkowiella* as well. The typical elongated cervicals (ZPAL RV/1132, 1133; Fig. 12) are thus considered middle neck vertebrae. However, how much shorter the anterior cervicals were than the middle ones is obscure. In the Alla Cascina specimen of *Macrocnemus bassani*, the third vertebra is more than 30% longer than the axis, while being only 10% shorter than the next cervical (Peyer 1937, p. 90). This means that the typically elongated cervicals in *Czatkowiella* (*e.g.*, ZPAL RV/1132) might have followed the axis directly. Among other criteria of vertebral position, the development of the ventral keel (similar to the axis keel) is the least useful, because the keel is weak at best, and might be size dependent. The position of rib facets, and the width of the neural spine barely change along the cervical series, except at the posterior end. The gradient of the neural spine along the vertebral column is most helpful. The neural spine forms a long narrow crest in mid-cervicals, then becomes anteroposteriorly shortened with an anterior spur (Fig. 11D), and finally develops an anterodorsal inclination (Fig. 11B₂) to become subvertical in the anterior dorsals (Fig. 11F). At the end of the cervical series, the proportions of arch and centrum are more like those of the dorsal vertebrae, the centrum has become wider and somewhat dorsoventrally compressed, and the spine has a much shorter base but is taller. The diapophysis starts a posterior shift that becomes obvious only in dorsals. The parapophysis, that has the form of a thin crest in the anterior cervicals, becomes a conspicuous tuber on the anteroventral margin of the centrum (Figs 11, 12) at the transition to the dorsal series.

Dorsal vertebrae. — These can be divided roughly into anterior, middle, and posterior vertebrae, mainly on the basis of their rib facets and the robusticity of the centra. ZPAL RV/619 (Fig. 11F) probably represents a vertebra from the beginning of the dorsal series. This vertebra bears a third rib facet (Fig. 11F₂). between

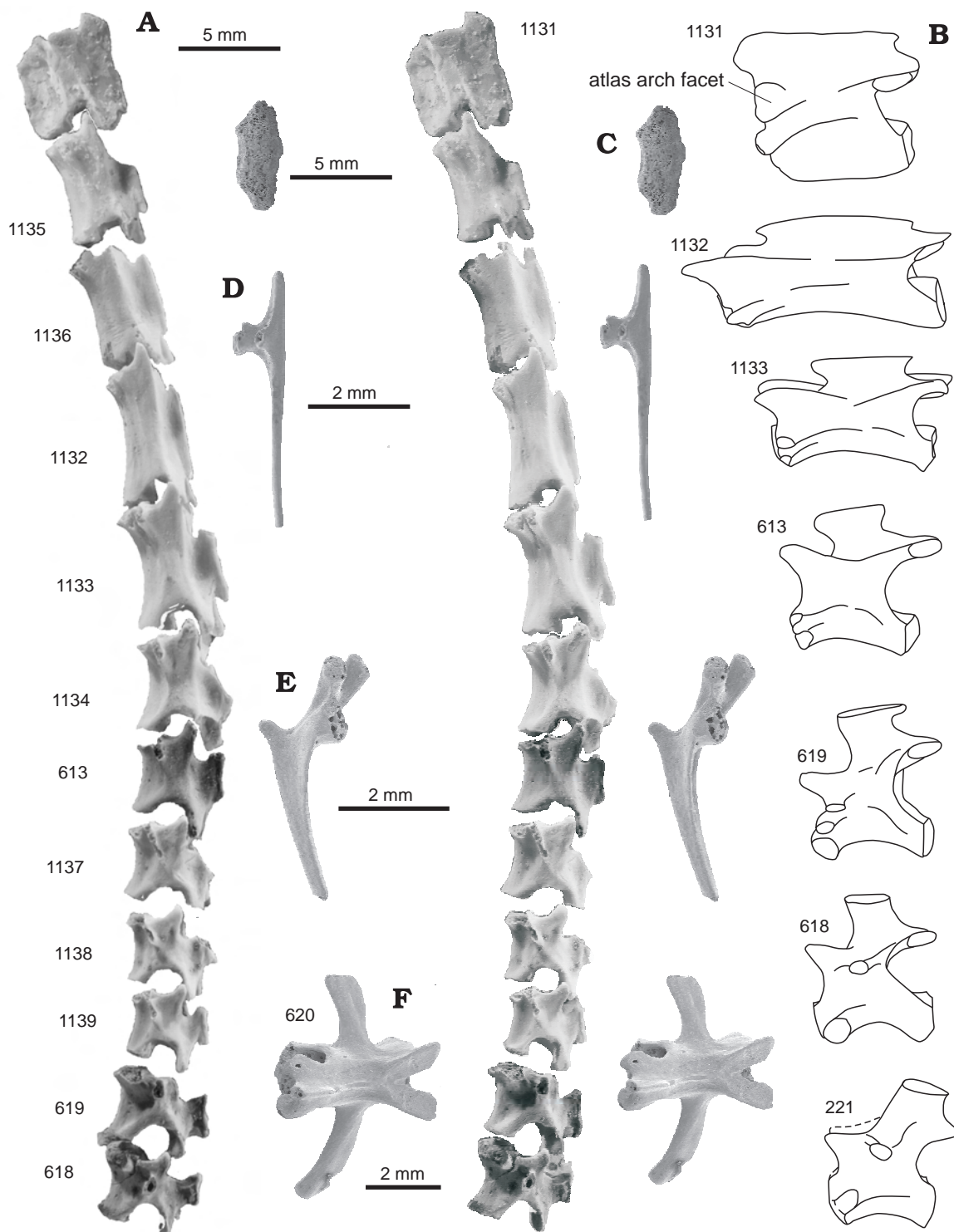


Fig. 12. *Czatkowiella harae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A.** Disarticulated cervical and anterior dorsal vertebrae arranged in a possible anatomical sequence. **B.** Morphological diagrams of cervical and dorsal vertebrae. **C.** Atlas intercentrum ZPAL RV/1100. **D.** Cervical rib ZPAL RV/937. **E.** Left anterior dorsal rib. **F.** Anterior caudal vertebra. Left lateral (A, B), dorsal (C, F), and ventromedial (E) views. All but B - stereo-pairs; C-F SEM micrographs. ZPAL RV/numbers alongside.

the main ones. The facet is preserved on the right side only, but the frequency of the three-headed ribs in the material suggests this was a normal feature of the *Czatkowiella* vertebral column. However, vertebrae with three rib heads are still rare and it seems likely that the three-headed ribs were limited to the transition between cervical and dorsal series in the living animal. The centrum is wider than in cervicals and somewhat

dorsoventrally compressed. The spine is anteroposteriorly short with transversally broadened tip. Two rib facets are still present at the anterior margin of the centrum but the diapophysis has started to move posterodorsally. ZPAL RV/618 (Fig. 11B₂) probably followed ZPAL RV/619 (Figs 11F₂, 12) as shown by the more posterior position of the diapophysis.

Caudal vertebrae. — Caudal vertebrae are similar to the dorsals in terms of central shape, but they are longer, with longer neural spines. Anterior caudals have broad based transverse processes (Fig. 12F) that represent fused caudal ribs. The processes are supported anteriorly and posteriorly by horizontal crests. In more posterior caudals, the transverse process decreases in length until it is no more than a raised area on the anteroposterior crest. Behind that point, only the lateral crest remains. The neural spine similarly decreases in height until it is little more than a median ridge. At no point is there any trace of an autotomy septum.

RIBS

The ribs of the neck and anterior dorsal region have a distinctive morphology. ZPAL RV/937 is the anterior part of a cervical rib. The two small heads lie together, between a short tapering anterior process and a long, very slender horizontal posterior shaft (Fig. 12D). These slender shafts are solid in cross-section and the many fragments present in the sample suggest that the neck of *Czatkowiella* was supported by a series of overlapping ribs, as in other long-necked genera such as *Protorosaurus*, *Prolacerta*, *Macrocnemus*, and *Tanystropheus*. Further posteriorly the rib heads enlarge and begin to separate, but a small subset of vertebrae and ribs (e.g., ZPAL RV/934 and 1122; Figs 11A, C, 12E respectively) show a three-headed morphology. In these ribs, the proximal head is divided into three parts — a large round upper facet, a second smaller facet, also rounded, and separated from the first by a shallow notch, and then a third smaller, offset facet, more sharply separated from the other two (Fig. 11C). A strong posteromedial crest runs from the smaller, lower, facet and curves back onto the shaft, which is much narrower. At the point of the angle there is a strong anterolaterally directed process. The angulation suggests this rib was directed as much backward as outward. Another subset of ribs shows a very similar morphology, but the two upper heads have coalesced. The three-headed ribs, and their vertebrae, are rare suggesting that there were only one or two such elements close to the neck-trunk boundary. Three-headed ribs also occur in this region in the Late Triassic kuehneosaurs and in a number of archosauriforms. Their distribution in the latter group is reviewed by Thulborn (1979) who suggests that these necessarily immobile ribs may have provided an important point of stability at the base of the neck.

LIMBS AND GIRDLES

There are a large number of limb and girdle elements in the Czatkowice 1 assemblage and these are more difficult to associate than skull remains. Work on this material is ongoing, but here we tentatively attribute a humerus and an ilium to *Czatkowiella*.

Humerus. — Among four humeral morphologies recognized to date from the Czatkowice 1 material, the type most safely attributable to *Czatkowiella* is a medium sized bone (e.g., ZPAL RV/1146; Fig. 13C) with a strongly enlarged, rather flat distal end perforated by a large entepicondylar foramen. The slender shaft is strongly twisted, so that estimated angle of the distal upon the proximal plane is almost 90°. Only a slight furrow for the radial nerve grooves the lateral border of the distal head, but there is no enclosed ectepicondylar foramen. The bone ranges in length from roughly 10–30 mm (7 specimens), which is smaller on average than the limb bones of *Osmolskina* (Borsuk-Białynicka and Sennikov 2009). On the basis of a skull length/humerus length ratio of 7:4 in *Prolacerta* (Gow 1975), this humerus might fit *Czatkowiella*, given our reconstructed skull length (Fig. 1) of 40 mm. Morphologically, it is quite similar to that of *Petrolacosaurus* (Reisz 1981), and more primitive than that of *Prolacerta*, which shares the loss of entepicondylar foramen with Archosauriformes.

Ilium. — Five iliac morphologies have been identified amongst the Czatkowice 1 reptile remains: that of the euparkeriid *Osmolskina* (clearly identified on the basis of size, number and morphology); those of procolophonoids (identified by their short, broad vertical blades); those of the smallest lepidosauromorph (identified by its size, frequency and morphology: slender angled blade and prepubic process); and two other types of rather similar morphology but differing size range. Both have subhorizontal iliac blades, a supra-acetabular buttress less developed than in *Osmolskina*, and first sacral rib facets positioned anterior and

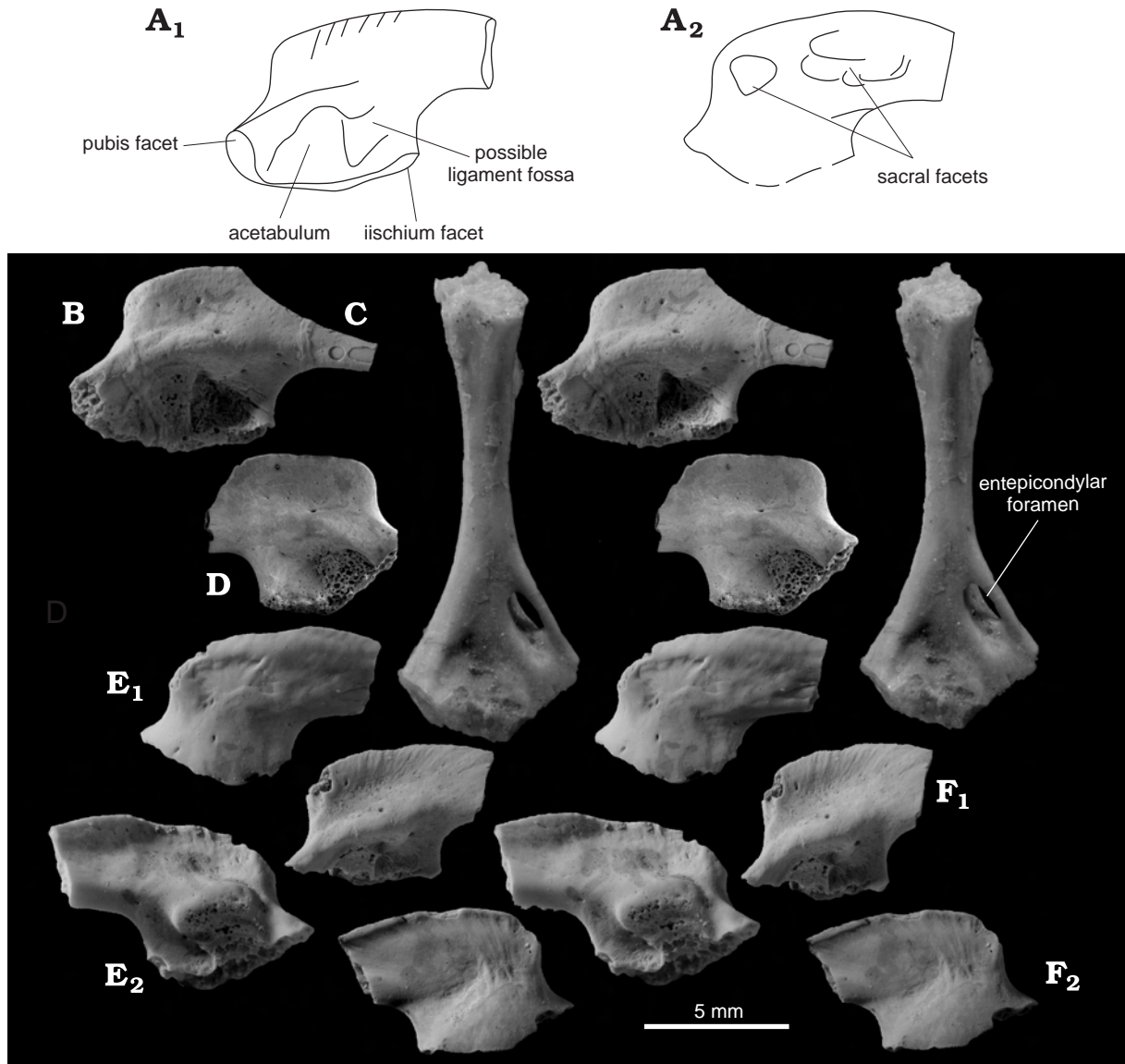


Fig. 13. *Czatkowiella harae* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A, B, D–F**. Ilium. **A**. Morphological diagrams. **B**. ZPAL RV/941. **D**. ZPAL RV/982. **E**. ZPAL RV/994. **F**. ZPAL RV/943. Left lateral (**A₁**, **B**, **F**), right lateral (**D**, **E₂**), right medial (**A₂**, **E₁**), and left medial (**F₂**) views. **C**. Left humerus ZPAL RV/1146, in dorsal distal view. All but **A₁** and **A₂** stereo-pairs.

just above the level of the acetabulum. However, although both types show a range of sizes, the largest examples of one type (Fig. 13), here referred to *Czatkowiella*, are much too large for the kuehneosaurid. The ilium referred to *Czatkowiella* is heavier than that referred to the kuehneosaurid, its acetabular part is relatively anteroposteriorly longer and less waisted, and its posterior process extends horizontally almost perpendicular to the posterior border of the acetabular part instead of ascending posterodorsally. Its anterodorsal part is obliquely cut off, the border descending anteroventrally with no anterior protrusion of any sort, in contrast to the smaller type that bears a conspicuous anterolateral tubercle in this region.

DISCUSSION

Czatkowiella shows a combination of features usually associated with basal archosauromorph reptiles — elongate neck vertebrae with closely associated dichoccephalous ribs, cervical ribs with an anterior process, and strong transverse processes on the dorsal vertebrae. The long low cervical vertebrae are of a type tradi-

tionally associated with those described as “prolacertiforms”, while differing from those of some long-necked archosauriforms in having more elongate and very low spines. The lack of a thecodont tooth implantation and the absence of an antorbital fenestra definitely preclude *Czatkowiella* from the latter group. In most recent phylogenies, “prolacertiforms” lie close to the base of Archosauriformes, whether as a monophyletic clade (e.g., Jalil 1997) or a series of successive outgroups to the crown (Dilkes 1998; Rieppel *et al.* 2003; Müller 2004).

Dilkes (1998) included the five most completely known “prolacertiform” taxa in a phylogenetic analysis: *Prolacerta* (Early Triassic; South Africa, Antarctica, Australia), *Protorosaurus* (Late Permian; Europe), *Langobardisaurus*, *Macrocnemus* and *Tanystropheus* (Mid Triassic; Europe). Amongst these, he recognised a clade incorporating tanystropheids (*Tanystropheus*, *Langobardicus*) and *Macrocnemus*, to which the climbing non-“prolacertiform” *Megalancosaurus* and *Drepanosaurus* formed a sister clade. The Permian *Protorosaurus* formed the sister taxon to this heterogenous clade, while *Prolacerta* itself emerged as the sister taxon of Archosauriformes (Fig. 13). However, Dilkes’ analysis was completed prior to new work on the Late Permian genus *Protorosaurus* (Gottmann-Quesada and Sander 2009). The skull of this genus has remained very poorly known because the skull of the holotype is badly damaged. A second, more complete skull has existed in the collections of the Naturkundemuseum Kassel for more than thirty years (Haubold and Schaumberg 1985, p. 184) but has only recently been fully studied (Annalise Gottmann, Bonn).

Czatkowiella has been coded into Dilkes’ data matrix and the codings for *Protorosaurus* (Dilkes, 1998) have been updated, using information and photographs supplied by Annalise Gottmann (personal communication 2002, 2005). One of the most important changes is in Dilkes (1998) character 8. Like *Czatkowiella*, the new material shows that *Protorosaurus* lacks a posterolateral process on the premaxilla. We first ran a heuristic search using the full matrix (PAUP 3.1: random addition sequence, Tree-bisection-reconnection [TBR], multistate characters treated as polymorphism) and obtained four equally parsimonious trees (Length = 399, consistency index [CI] = 0.439, rescaled consistency index [RC] = 0.268). The strict consensus tree placed *Czatkowiella* as the sister group of *Protorosaurus*, with the two forming a small clade at the base of Archosauromorpha (Fig. 14A). The original matrix is too large for a more rigorous Branch-and-Bound search, so its size have been reduced by removing the archosauriform *Euparkeria*, the long-necked *Langobardisaurus* that always groups with *Macrocnemus* and *Tanystropheus*, and all of the rhynchosaur taxa (the main focus of Dilkes’ 1998 study) except the basal *Mesosuchus*. The analysis yielded two Maximum Parsimony Trees (MPT) (L = 289, CI = 0.554, RC = 0.288) that differed only in the placement of the archosauromorph *Trilophosaurus* (as a sister taxon to the *Macrocnemus/Tanystropheus/drepanosaurid* clade or as the sister taxon of all archosauromorphs crownward of *Protorosaurus*). The strict consensus of these trees is shown in Fig. 14B.

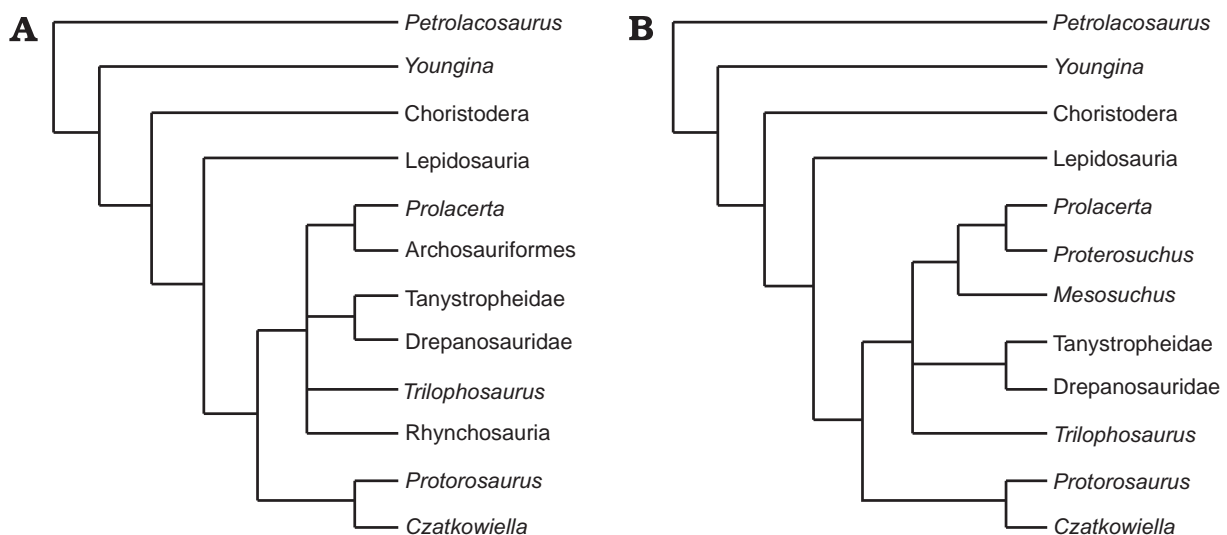


Fig. 14. Cladograms resulting from analyses using the matrix of Dilkes (1998) with data for *Protorosaurus* updated and with the inclusion of *Czatkowiella*. **A.** Strict consensus of four equally parsimonious trees resulting from a heuristic search using the full matrix (but with smaller clades grouped subsequently where appropriate to simplify the tree). **B.** Strict consensus of two maximum parsimony trees obtained from a branch-and-bound analysis using a reduced version of the Dilkes (1998) matrix (see text for details).

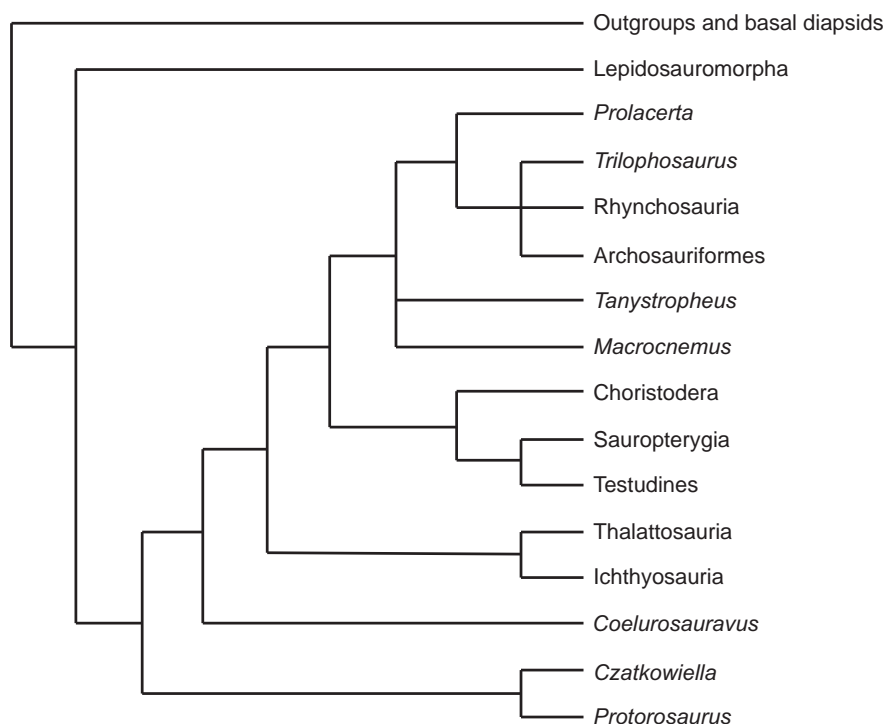


Fig. 15. Strict consensus of three equally parsimonious trees resulting from a heuristic search using the data matrix of Müller (2004), with *Czatkowiella* added and *Protorosaurus* updated.

A second, more general, diapsid analysis has recently been published by Müller (2004). Again, *Czatkowiella* has been coded into this data matrix, the codings for *Protorosaurus* updated, and an analysis run using the same format as the original analysis (heuristic search option, random addition sequence — 100 replicates, TBR branch swapping, trees rooted by outgroup [Synapsida, Seymouriidae], and with multistate characters interpreted as polymorphism). The analysis produced 3 equally parsimonious trees (TL = 1008; CI = 0.425; RC = 0.232), the strict consensus of which (Fig. 15) again places *Czatkowiella* and *Protorosaurus* as sister taxa, but at the base of a clade that incorporates Archosauromorpha, Sauropterygia, Testudines, ichthyosaurs, and the Permian glider *Coelurosauravus*, but not Lepidosauromorpha.

These two taxa (*Protorosaurus* and *Czatkowiella*) may thus represent a small clade of basal Permo-Triassic diapsids (*Protorosauria sensu stricto*) that are not closely linked to long-necked archosauromorphs like *Prolacerta*, *Tanystropheus* and *Macrocnemus*. Vertebral elongation would thus be a primitive rather than a derived trait within diapsids, reversed in several subsequent lineages (*e.g.*, rhynchosaur, trilophosaur). *Protorosaurus* and *Czatkowiella* share a similar skull morphology (long nasals, large lacrimal fully or partially excluded from the orbit by the prefrontal, maxillary tooth row not extending far beyond the anterior margin of the orbit, jugal with only a short posterior process, loss of the parietal foramen, reduction of the quadratojugal, slender dentary), but most of these features are not unique and occur in other diapsids of this grade (*i.e.*, around the base of Neodiapsida). Images of the Kassel skull (Annalise Gottmann, photograph) suggest that *Protorosaurus* may share the unusual premaxillary morphology of *Czatkowiella* in that in both the articular surface between the premaxillae appears weak. However, they differ in parietal morphology (fused with a sagittal crest in *Protorosaurus*, no evidence that the postparietals were incorporated). The teeth of both taxa have a similar shape and implantation. None of the teeth in the Kassel skull shows the mediolateral compression and grooving seen in mature teeth of *Czatkowiella*, but a partial dentition from a British *Protorosaurus* specimen (Evans and King 1993) has this morphology, and tooth shape may vary with age.

Postcranially, *Protorosaurus* and *Czatkowiella* share a long neck constructed of elongated cervicals with long, low spines, and slender, horizontally orientated cervical ribs. The cervical vertebrae of *Czatkowiella*, however, are more gracile and have much lower neural spines. In the trunk, the spines are also shorter while those of the caudal series lack the deeply bifid spines that characterise much of the tail in *Protorosaurus*. In its turn, *Protorosaurus* lacks the three-headed ribs found in the anterior trunk of *Czatkowiella* (Fig. 11A).

Thus *Czatkowiella* and *Protorosaurus* share few, if any, unique derived characters. They show similarities that may indicate relationship or may simply reflect a similar evolutionary grade. A more complete description of *Protorosaurus* (Gottmann-Quesada and Sander 2009) will help to resolve the issue.

CONCLUSIONS

Czatkowiella is relatively well known compared to other early diapsids but it has still proved difficult to classify. It shows skull and vertebral characters once thought diagnostic of the long-necked “prolacertiforms” (loss of the parietal foramen, distinct transverse processes on the dorsal vertebrae, double-headed ribs), but most recent cladistic analyses, including those presented here, have failed to support a monophyletic Prolacertiformes (Dilkes 1998; Rieppel 2002; Müller 2004). Our analysis using the matrices of Dilkes (1998) and Müller (2004) suggests a relationship between *Czatkowiella* and the Late Permian *Protorosaurus* at the base of Archosauromorpha. *Czatkowiella* is thus to be considered a survivor of the Permian stage of archosauromorph phylogeny (Fig. 16). However, this needs to be confirmed with a more detailed analysis at the new material of *Protorosaurus* (Gottmann-Quesada and Sander 2009). If this hypothesis of relationship is correct, then the similarities found between the cervical vertebrae and ribs of *Protorosaurus* (*sensu stricto*) and traditional “prolacertiforms” probably represent the retention of primitive character states, possibly synapomorphic for Archosauromorpha, or, given the cervical morphology of the basal diapsid *Petrolacosaurus* (Reisz 1981), for a more inclusive group. The challenge for the future will be to resolve the phylogenetic relationships of the other, more fragmentary, taxa previously classified as prolacertiform.

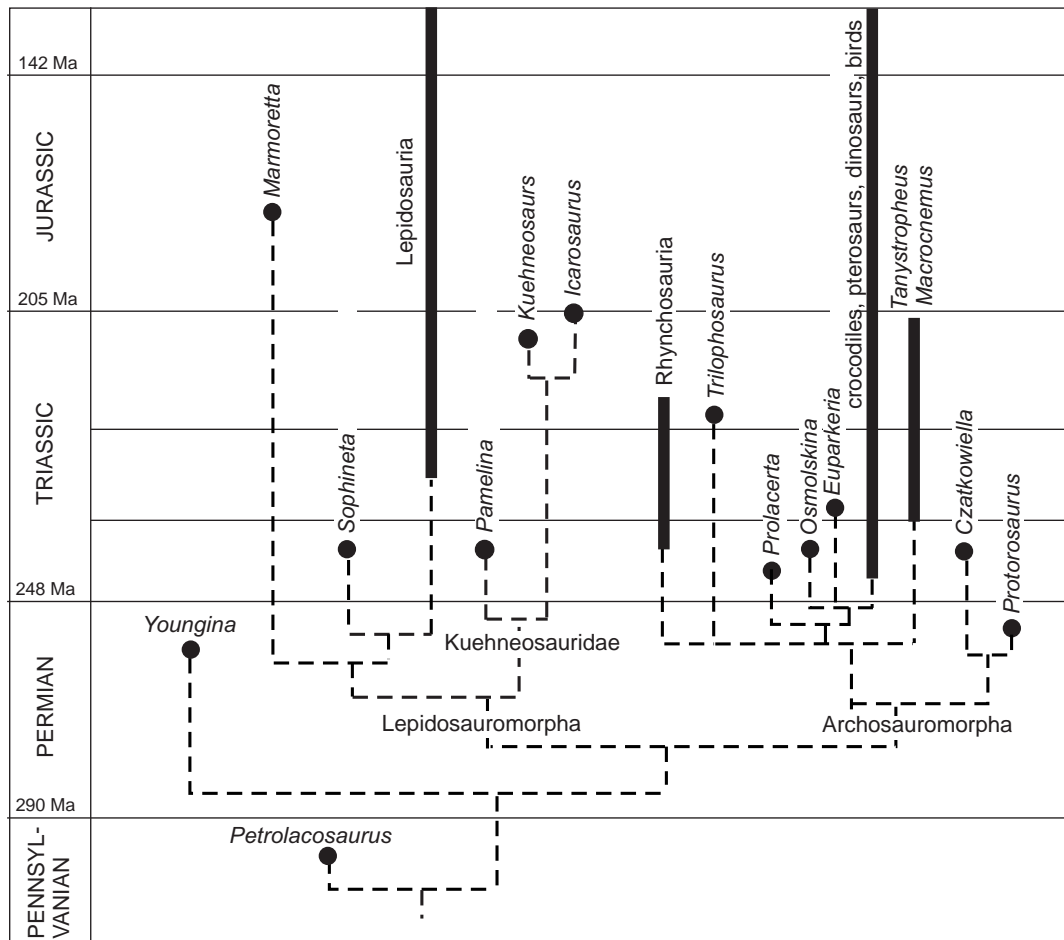


Fig. 16. Early diapsid phylogeny on a stratigraphic scale based on the current consensus, and present analysis of the Olenekian Czatkowice 1 taxa. Czatkowice stem kuehneosaur (Evans 2009); Czatkowice stem lepidosaur (Evans and Borsuk-Białynicka 2009).

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APPENDIX 1

Supplementary data matrix for *Czatkowiella* and *Protorosaurus*.

A. Codings for *Czatkowiella* and *Protorosaurus* in the data matrix of Dilkes (1998). Non standard entries: A = 1 or 2;

Czatkowiella 00010 00000 00??A 001?0 00??0 11011 010?1 1210? 0?011 01110 0??00 10100
00000 00?20 000?? 011?? 21101 0???1 ???? ???? ?1?? ???? ???? ????
????0 00000 0001? 0A?01 ??00

Protorosaurus 01010 00000 000?1 00100 00001 210?1 ?101? 11?? ???? ???? 00?00 10000
00000 ????0 00010 0111? 21??0 102?3 21?? ???? 1???0 110?1 00?00 00000
11000 ?000? 00?01 0?000 0?00

B. Codings for *Czatkowiella* and *Protorosaurus* in the data matrix of Müller (2004). Non standard entries: A = 1 or 2, B = 1 or 3.

Czatkowiella 00010 10110 02101 02001 0?100 11?1? 1010? ?1011 0??00 001?? ?1?? ????
???? ?0?? ???? ???? ?0000 0?0?? 210?? 01?00 ?110? ???? ?1?0 000??
00?00 10100 0???0 10?00 ???? ???? ?0001 11200 00200 0??? ???? ?0010
00?1

Protorosaurus 00010 10110 22B?1 020?1 ?0?00 01?? ????1 0?011 0100? 0?10? 11?00 0?00
??00? 200?0 ?0?00 01010 00000 0?010 1?? ???? 0100? 0?20? ?0?? 0000?
1100? 00?? ???? ???? ???? 11100 ?0001 ?100? ???? 00?? 0?12? ?0100
1011