

AN EARLY KUEHNEOSAURID REPTILE FROM THE EARLY TRIASSIC OF POLAND

SUSAN E. EVANS

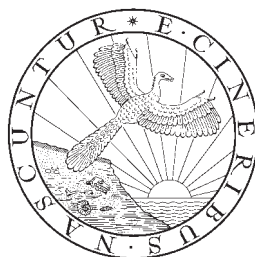
Evans, S.E. 2009. An early kuehneosaurid reptile (Reptilia: Diapsida) from the Early Triassic of Poland. *Palaeontologia Polonica* **65**, 145–178.

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

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

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Received 1 May 2006, accepted 15 August 2007



INTRODUCTION

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

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

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

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

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

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

GEOLOGICAL SETTING

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

MATERIAL AND METHODS

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

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

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

SYSTEMATIC PALEONTOLOGY

Clade Neodiapsida Benton, 1985

Clade Lepidosauromorpha Gauthier, 1984

Clade Lepidosauriformes Gauthier, Estes, *et* De Queiroz, 1988

Family **Kuehneosauridae** Robinson, 1962

Genus *Pamelina* gen. n.

Type species: *Pamelina polonica* sp. n.

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

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

Pamelina polonica sp. n.

Derivation of name: From Poland.

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

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

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

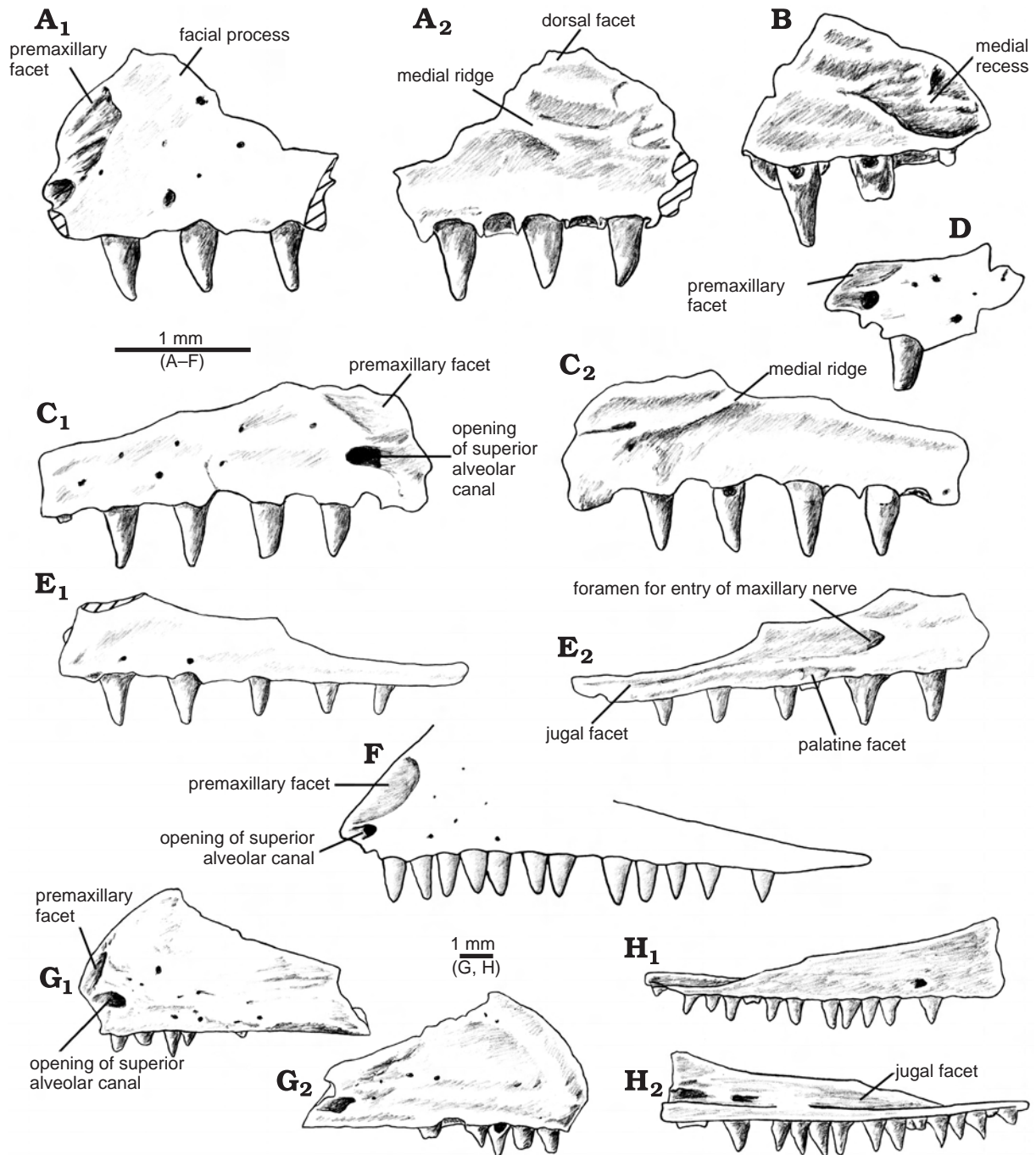


Fig. 1. **A–F.** *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A.** Holotype left maxilla ZPAL RV/1036, in lateral (**A₁**) and medial (**A₂**) views. **B.** Anterior tip of a left maxilla ZPAL RV/1039, in medial view. **C.** Right maxilla ZPAL RV/1034, in lateral (**C₁**) and medial (**C₂**) views. **D.** Anterior tip of a left maxilla ZPAL RV/1042, in lateral view. **E.** Orbital process of a left maxilla ZPAL RV/1035, in lateral (**E₁**) and medial (**E₂**) views. **F.** Partial reconstruction of *Pamelina* maxilla, in lateral view. **G, H.** *Kuehneosaurus*, Late Triassic, Emborough Quarry, England. **G.** Left anterior maxilla BMNH R.12900, in lateral (**G₁**) and medial (**G₂**) views. **H.** Orbital process of a right maxilla MBNH R.12903, in lateral (**H₁**) and medial (**H₂**) views.

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

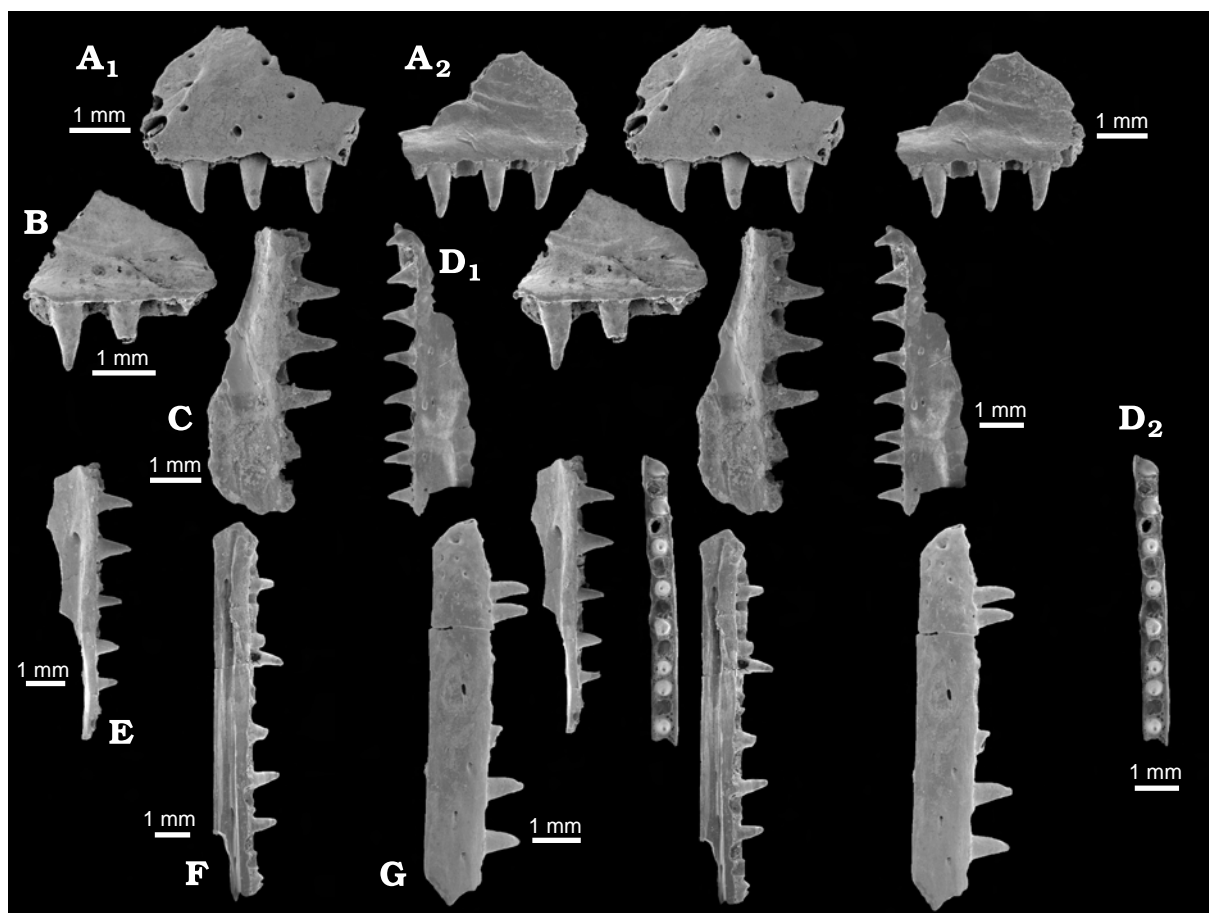


Fig. 2. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Maxilla and dentary. A. Holotype left maxilla ZPAL RV/1036, in lateral (A₁) and medial (A₂) views. B. Anterior tip of a left maxilla ZPAL RV/ 1039, in medial view. C. Mid-section of a right maxilla ZPAL RV/1034, in medial view. D. Midsection of a left maxilla ZPAL RV/1081, in lateral (D₁) and occlusal (D₂) views. E. Orbital process of a left maxilla ZPAL RV/1035, in medial view. F. Partial left dentary ZPAL RV/143, in lateral view. G. Right partial dentary ZPAL RV/144, in medial view. SEM stereo-pairs.

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

DESCRIPTION

SKULL

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

The skull reconstructions in Fig. 3 are based on isolated and incomplete elements from more than one individual. Clearly this has its limitations and should be regarded as providing an estimated, rather than exact, representation of proportions. The key relationships are those between the parietal and squamosal (*e.g.*, ZPAL RV/975 and 147); the frontal, parietal and postfrontal (*e.g.*, ZPAL RV/378, 157 and 978); the frontal and prefrontal (ZPAL RV/381 and 979); the premaxilla and maxilla (ZPAL RV/1044 and 1034); the squamosal and the quadrate (ZPAL RV/147, 1011, 1029); and the length of the maxilla (ZPAL RV/1034,

1035, 1036, and 1038). The ventral edge of the prefrontal lines up roughly with the anterior part of the palatine facet on the maxilla (because it met the anterior edge of the palatine in life) and the ventral condyle of the quadrate gives the outer limit of the lower jaw which, in itself, must run anteriorly on the same line as the maxilla. Without the nasals, the width and length of the skull would ideally be confirmed by palatal elements but this region is poorly known in *Pamelina*. The reconstructions in Fig. 3 were made without reference to *Kuehneosaurus* but, despite differing proportions, the result shows striking similarities, including the very small relative size and posterior position of the squamosal.

Premaxilla. — The premaxilla of *Pamelina* is a distinctive element represented by several good specimens (*e.g.*, ZPAL RV/146, 451, 1043, 1044, 1045, and 1082), and many more fragmentary ones. It is composed of three parts: a shallow, slightly curved alveolar ramus; a posterolateral maxillary process; and an elongate palatal flange (Figs 4A₁, 5). The narrow alveolar margin bears four or five strong, slightly recurved, teeth set in shallow circular pits (Figs 4A₃, 5A, C). Starting from a point roughly half way along its lateral edge, the alveolar margin is extended obliquely upwards and backwards (at roughly 45° to the horizontal) by a long laterally compressed blade of bone that fitted against a matching facet on the anterolateral margin of the maxilla and almost excluded it from the border of the external nares (Fig. 4A₂). In Fig. 3B, the ventral margins of premaxilla and maxilla are shown in alignment, but it is possible that there was a slight anteroventral angulation of the premaxilla in life. Ventromedially, the premaxillae met along a strong anteromedial symphyseal surface, but the only remnant of the dorsal nasal process is a slight medial elevation (Figs 4A₄, 5A₂, B₂); the nares were thus confluent. Posteromedially, each premaxilla is drawn into a horizontal palatal flange that floored the confluent nares and is separated from the alveolar margin by a narrow choanal embayment (Fig. 4A₃).

Comparison with Late Triassic kuehneosaurs: The premaxilla of *Pamelina* resembles that of *Kuehneosaurus* (*e.g.*, BMNH R12879, 12880, Fig. 4B) in general shape (confluent nares, posterolateral maxillary process, median flange, five tooth positions), but differs in having a more conspicuous posterior palatine flange (small stub in *Kuehneosaurus*) and a posterolateral process that originates further back, so that the narial opening is wider and more U-shaped (compare Fig. 4A₂ and B₁). The precise shape of the premaxilla of *Icarosaurus* is uncertain as the bone is overlain by other elements (Colbert 1966, 1970; personal observations).

Maxilla. — No complete maxilla exists for *Pamelina* but it is represented by many anterior and posterior fragments (*e.g.*, ZPAL RV/1034–1042, Figs 1A–F, 2A–D). There were at least 20 tooth positions. The facial process is relatively deep (more than twice the height of the longest tooth) with an almost straight narial margin (*e.g.*, ZPAL RV/1034, 1036) that bears a long narrow premaxillary facet (most sharply defined in large specimens, *e.g.*, ZPAL RV/1036, Figs 1A₁, 2A₁). As the facet does not reach the top of the bone, the maxilla clearly entered the narial margin for a short distance dorsally. A large ventrolateral exit foramen for the superior alveolar canal opens into the lower edge of the premaxillary facet and below this, the anterior margin of the maxilla is notched (Fig. 1D). The maxillary teeth, like those of the premaxilla, are attached to the margins of shallow rounded pits and were replaced from the lingual side.

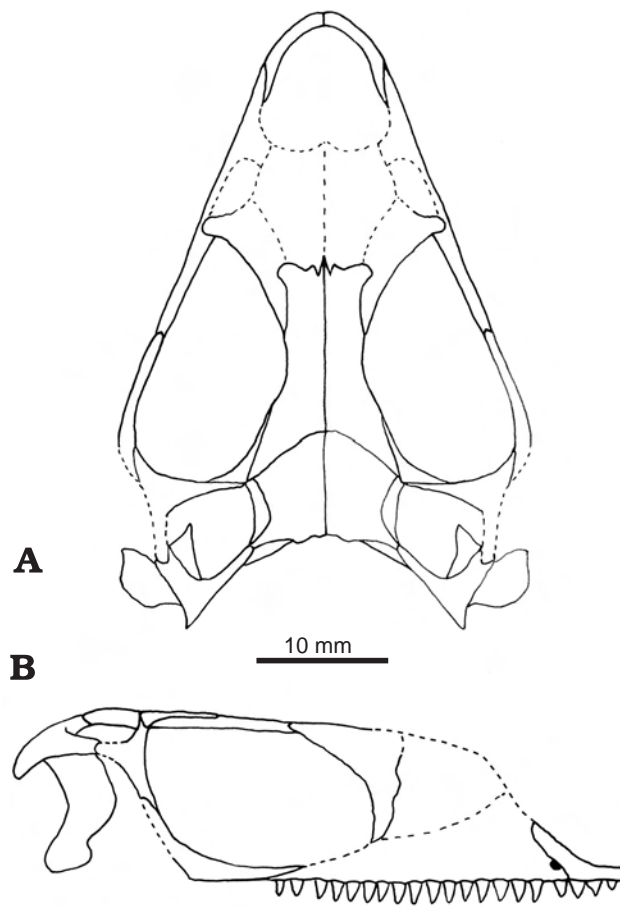


Fig. 3. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Reconstruction of the skull, in dorsal (A) and lateral (B) views.

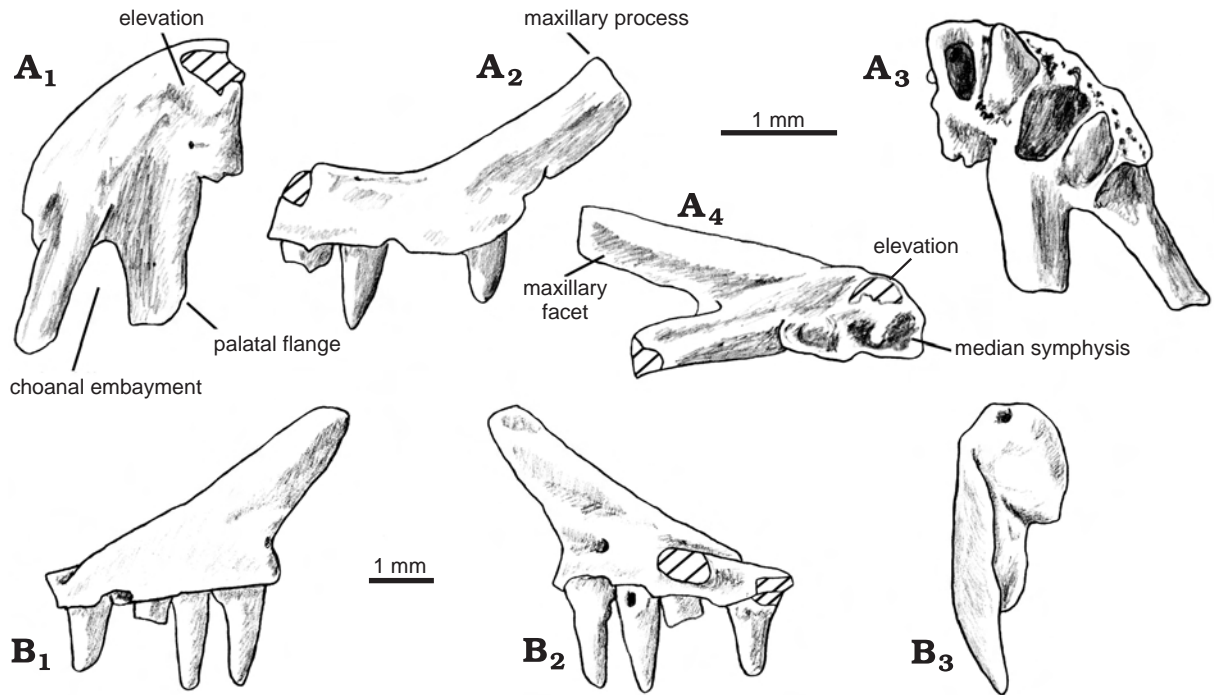


Fig. 4. **A.** *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Left premaxilla ZPAL RV1082, in dorsal (A₁), lateral (A₂), ventral (A₃), and medial (A₄) views. **B.** *Kuehneosaurus*, Late Triassic, Emborough Quarry, England. Left premaxilla BMNH R.12880, in lateral (B₁), medial (B₂) and dorsal (B₃) views.

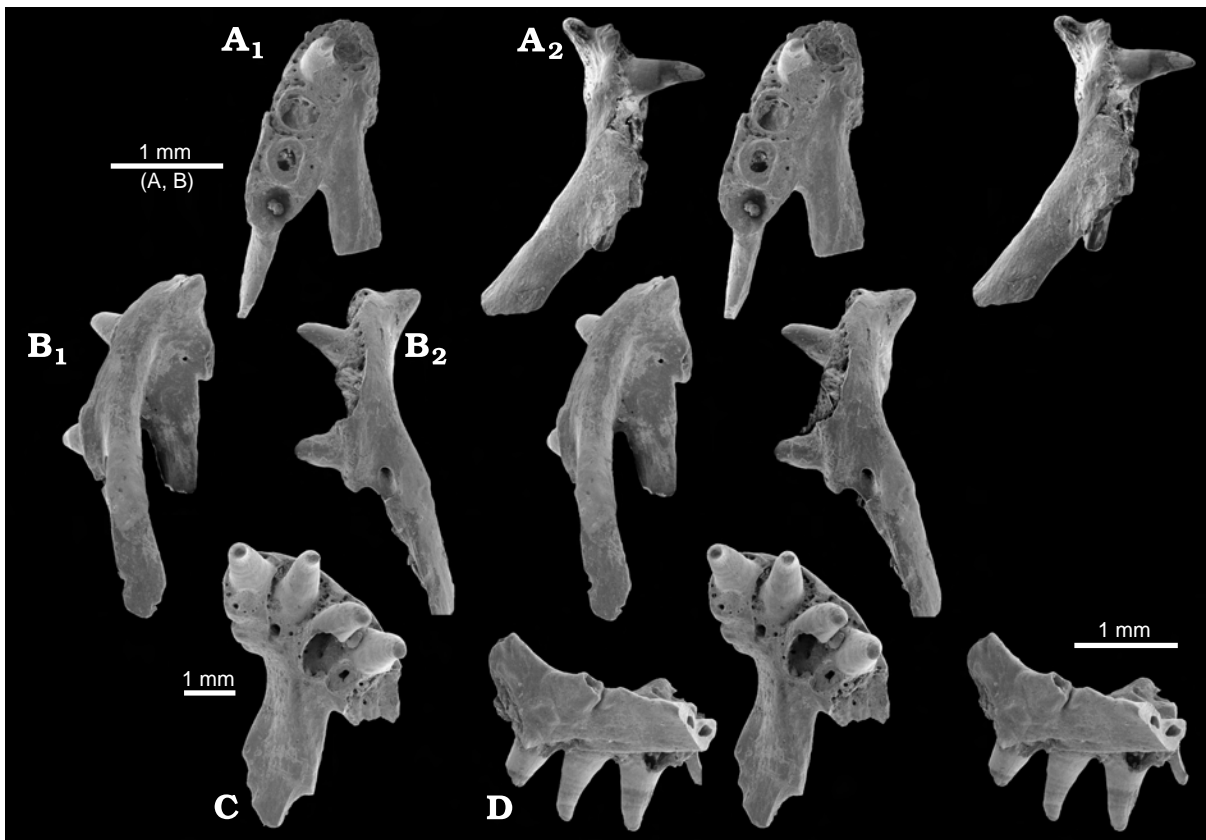


Fig. 5. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Premaxilla. **A.** Right bone ZPAL RV/146, in ventral (A₁) and lateral (A₂) views. **B.** Left bone ZPAL RV/1039, in dorsolateral (B₁) and lateral (B₂) views. **C.** Left bone ZPAL RV/451, in ventral view. **D.** Partial right bone ZPAL RV/1043, in lateral view. SEM stereo-pairs.

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

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

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

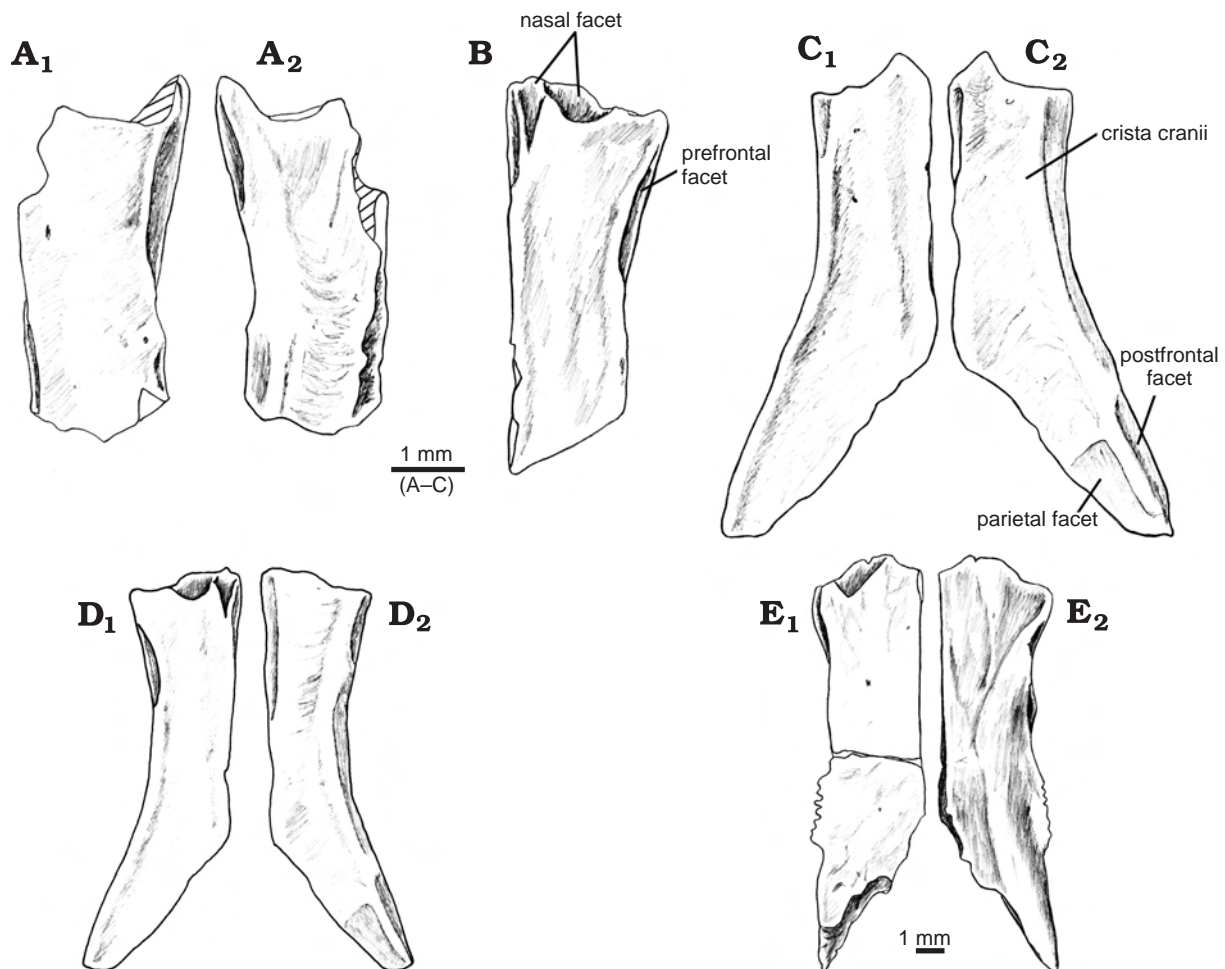


Fig. 6. **A–D.** *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A.** Anterior part of right frontal ZPAL RV/387, in dorsal (A₁) and ventral (A₂) views. **B.** Anterior part of right frontal ZPAL RV/383, in dorsal view. **C.** Posterior region of a left frontal ZPAL RV/378, in dorsal (C₁) and ventral (C₂) views. **D.** Partial reconstruction of a left frontal, in dorsal (D₁) and ventral (D₂) views; out of scale. **E.** *Kuehneosaurus*, Late Triassic, Emborough Quarry, England. Left frontal BHNH R.12864, in dorsal (E₁) and ventral (E₂) views.

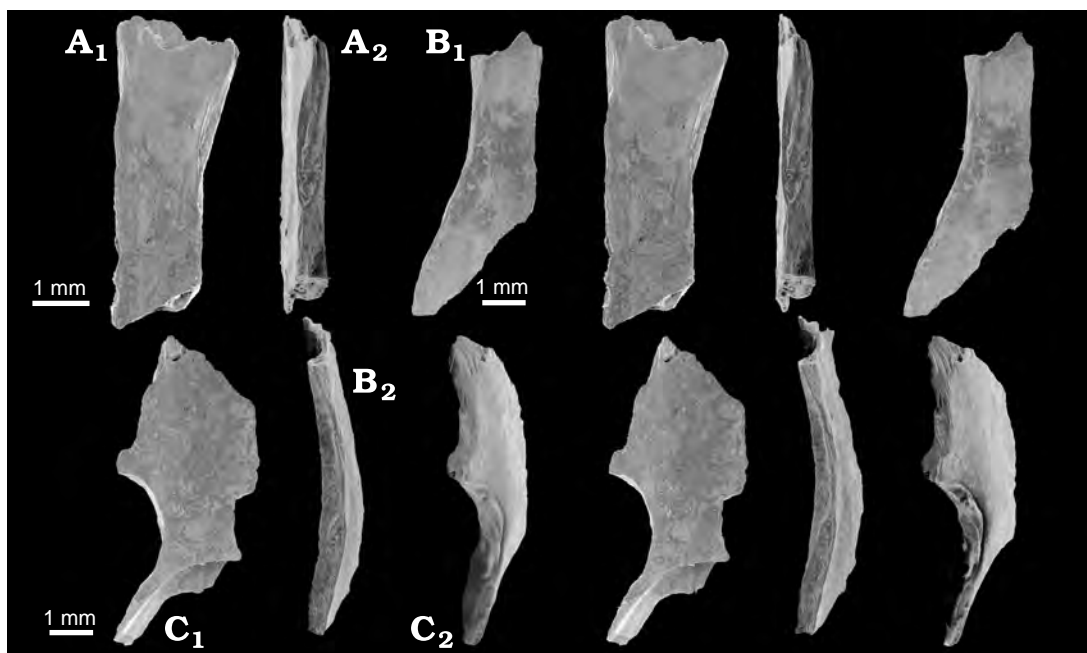


Fig. 7. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Frontal and parietal. A. Anterior end of a right frontal ZPAL RV/384, in dorsal (A₁) and lateral (A₂) views. B. Posterior region of a left frontal ZPAL RV/378, in dorsal (B₁) and lateral (B₂) views. C. Left parietal ZPAL RV/157, in dorsal (C₁) and dorsolateral (C₂) views. SEM stereo-pairs.

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

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

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

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

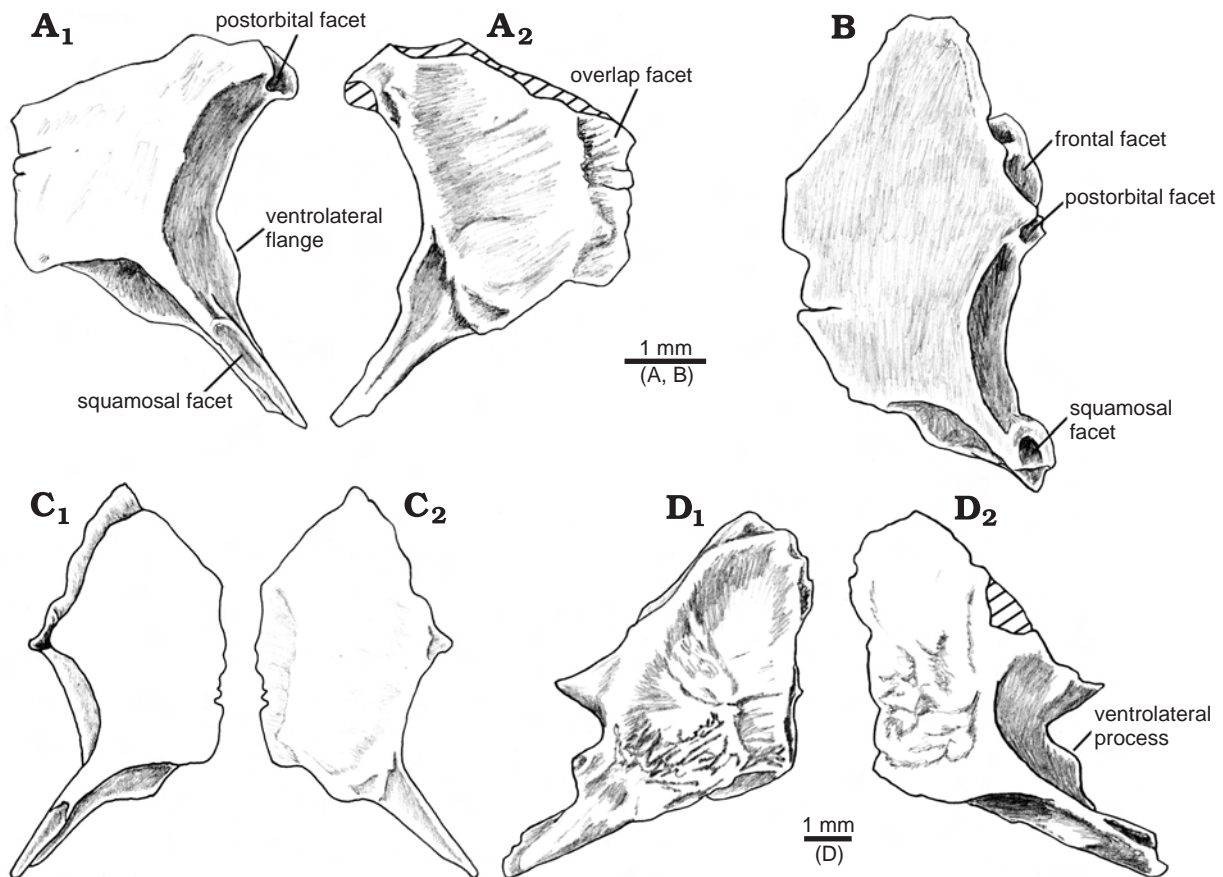


Fig. 8. A–C. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland, parietal. A. Right parietal ZPAL RV/975, in dorsal (A₁) and ventral (A₂) views. B. Right parietal ZPAL RV/1028, in dorsal view. C. Reconstruction of left parietal, in dorsal (C₁) and ventral (C₂) views, out of scale. D. *Kuehneosaurus*, Late Triassic, Emborough Quarry, England. Right parietal BMNH R.12861, in ventral (D₁) and dorsal (D₂) views.

unsculptured (Figs 7C₁, 8A–C); the ventral surface is concave and grooved by cranial blood vessels (Fig. 8A₂, C₂). Overall, the bone is relatively short and broad, with short tapering postparietal processes and smaller anterolateral wings separated by the strongly curved margin of the upper temporal fenestra. This bears a wide, oblique lateral surface for adductor muscle attachment, whereas the posterior border is incised by a deep lateral pocket for epaxial craniocervical muscles.

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

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

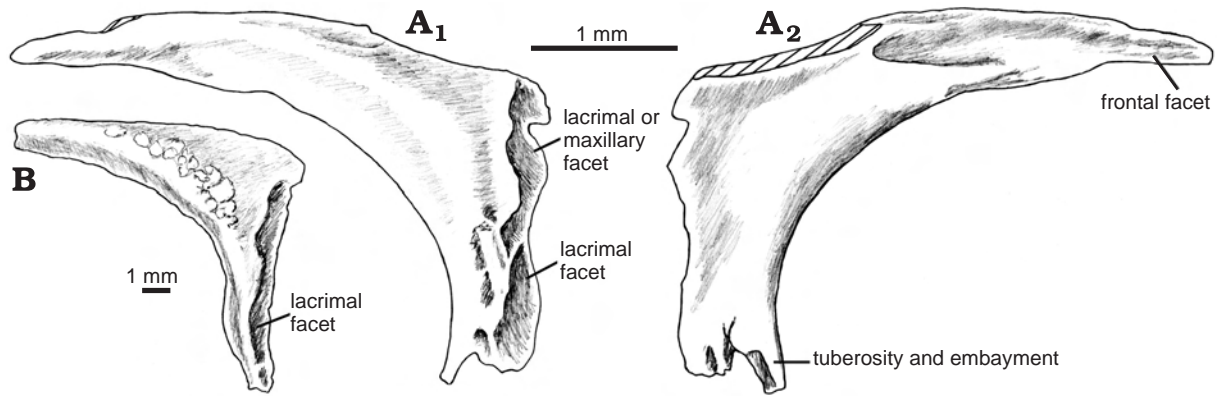


Fig. 9. **A.** *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Right prefrontal ZPAL RV 979, in lateral (A_1) and medial (A_2) views. **B.** *Kuehneosaurus*, Late Triassic, Emborough Quarry, England. Right prefrontal BMNH R.12866, in lateral view.

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

Prefrontal. — Prefrontals are well represented in the Czatkowice assemblage, but most are attributable to archosauromorphs or procolophonians. Of the two rarer types, only one (*e.g.*, ZPAL RV/979, 980, 1001, and 1002) bears a process that would fit against the facet on the *Pamelina* frontal (in being shallow, flat at its tip and then more L-shaped at the anterior point). This prefrontal type (Figs 9A, 10A) is limited to a narrow orbitonasal flange, and a narrow facial strip bordering a deep anterior facet. Only the posterior rim of the facet is ever preserved and it is not clear how much of the thin anterior portion has broken away. The facet is stepped. The lower part at least is interpreted as being for a lacrimal bone that formed much of the preorbital skull wall behind the facial process of the maxilla, but whether the maxilla contacted the prefrontal above the lacrimal is not clear. At the posteroventral edge of the facet there is typically a small low tuberosity or flange of uncertain function. In ZPAL RV/ 979 (Fig. 9A₂), the lower end of the orbitonasal flange is almost complete and is roughened, presumably for attachment (either directly or through soft tissue) to the palatine. A slight embayment in this margin might be associated with the infraorbital foramen (maxillary nerve).

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

Postfrontal. — The postfrontal (*e.g.*, ZPAL RV/1003, 1004, 1006, 1007) is attributed on the basis of fit (to the parietal and frontal), but also resembles other elements in being hollow rather than solid. The bone is the shape of a shallow right-angled triangle, with the hypotenuse forming the orbital margin (Figs 10C, 11A, B₁, B₂). In some specimens (*e.g.*, ZPAL RV/1003) this margin is ornamented by small tubercles (Fig. 11A₁). The longer of the remaining edges meets the frontal, its anterior tip fitting into a slight recess in that bone. The shorter, posterior edge of the postfrontal bears a grooved facet for the postorbital (Fig. 11A₂), although the posteromedial corner slotted into the anterolateral parietal recess (Fig. 11B₂, B₃). When articulated, the postorbital met the tip of the parietal wing to exclude the postfrontal from the margin of the upper temporal fenestra.

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

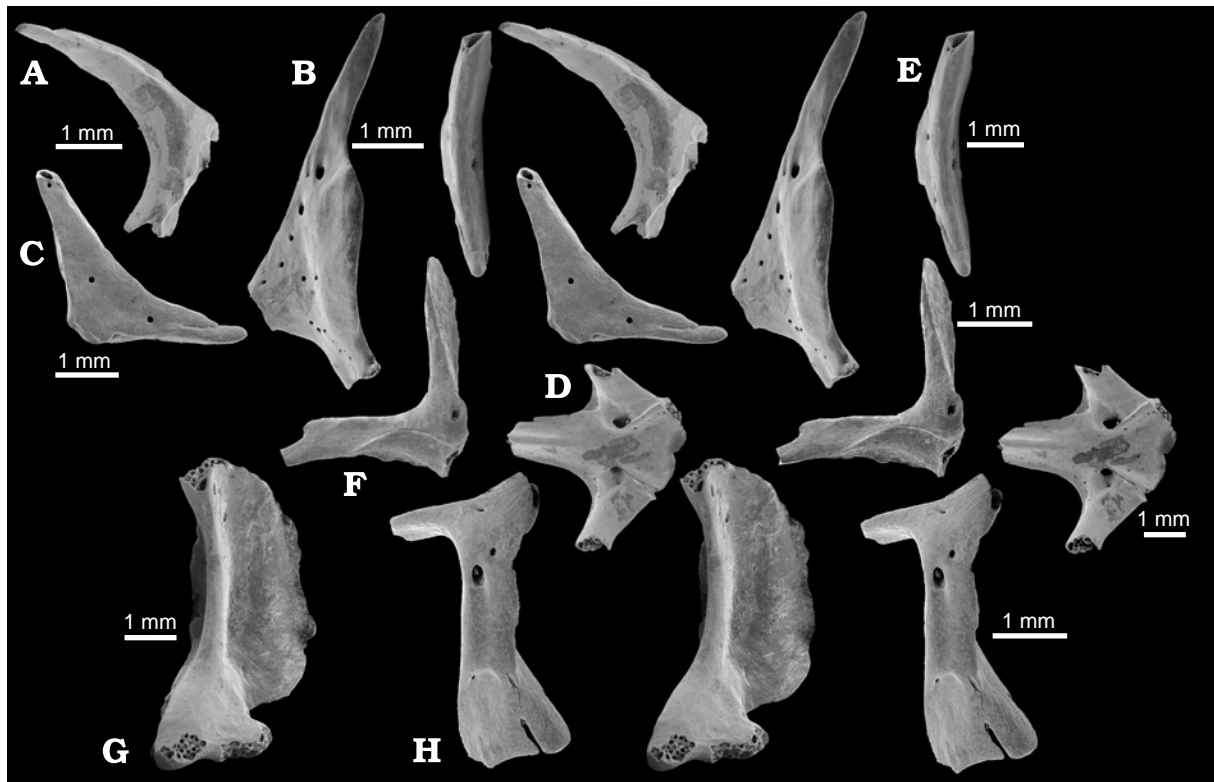


Fig. 10. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Skull bones. **A.** Right prefrontal ZPAL RV/979, stereopairs in posterodorsal view. **B.** Right postorbital ZPAL RV/1077, in lateral view. **C.** Right postfrontal ZPAL RV/1027, in dorsal view. **D.** Sphenoid ZPAL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

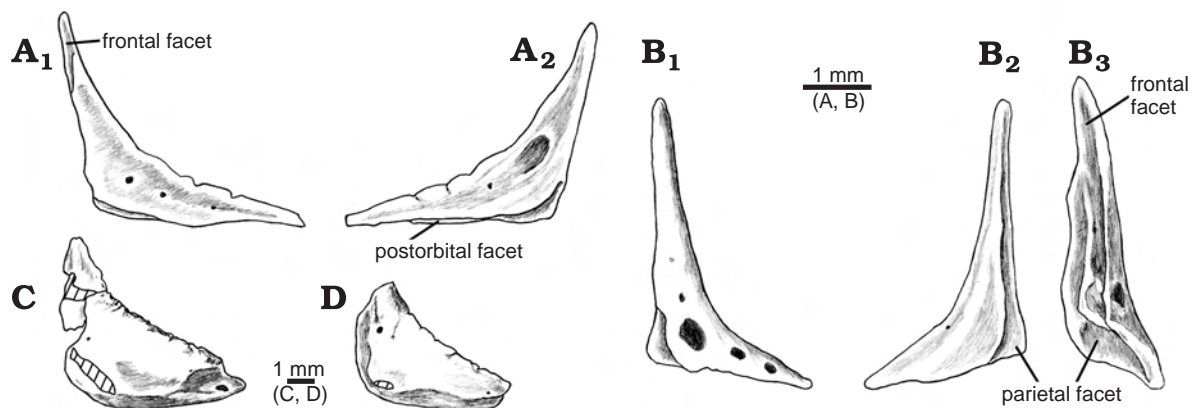


Fig. 11. **A, B.** *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A.** Right postfrontal ZPAL RV/1003, in dorsal (A_1) and ventral (A_2) views. **B.** Right postfrontal ZPAL RV/1004, in dorsal (B_1), ventral (B_2), and dorsomedial (B_3) views. **C, D.** *Kuehneosaurus*,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

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

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

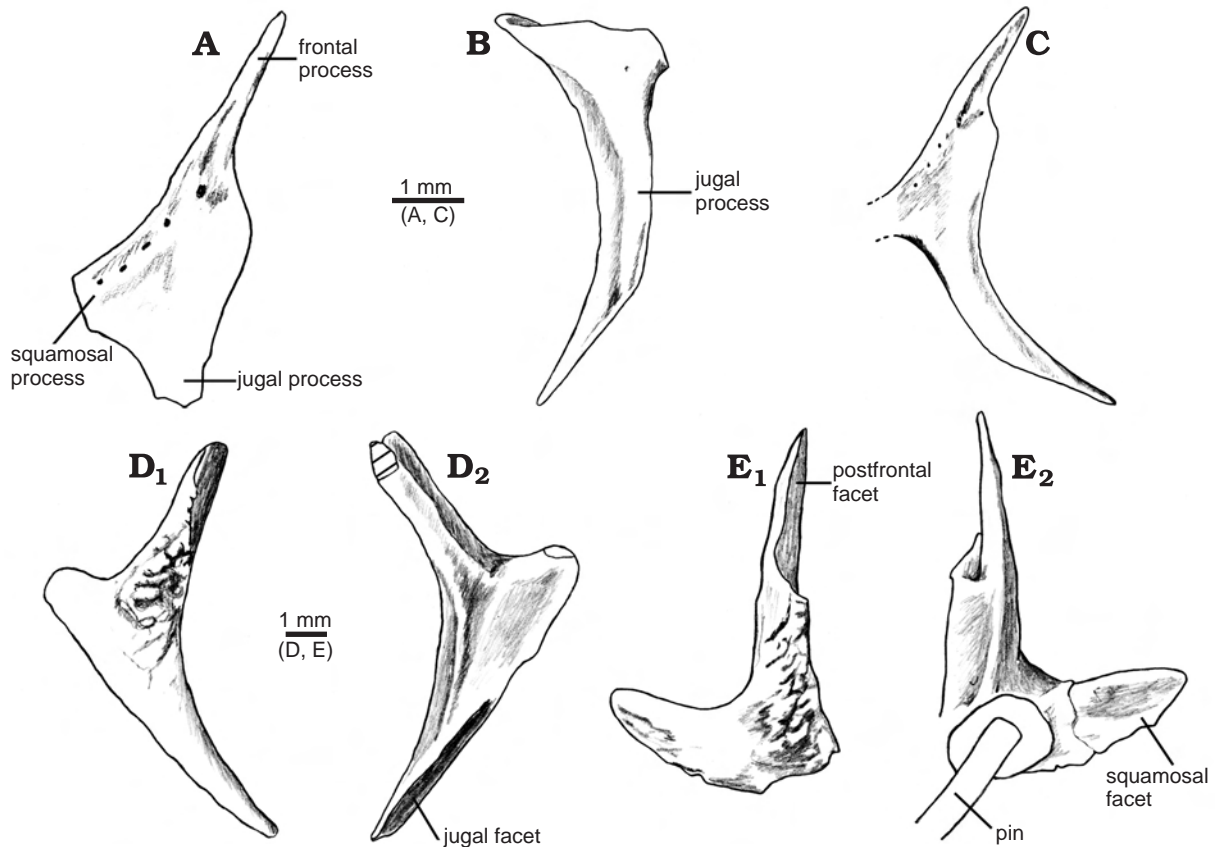


Fig. 12. **A–C.** *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland, postorbital. **A.** Right postorbital ZPAL RV/1077, in lateral view. **B.** Left postorbital ventral ramus ZPAL RV/1072, in lateral view. **C.** Partial reconstruction of right postorbital of *Pamelina*, in dorsolateral view. **D, E.** *Kuehneosaurus*, Late Triassic, Emborough Quarry, England. **D.** Right postfrontal BMNH R.12870, in dorsolateral (**D**₁) and ventromedial (**D**₂) views. **E.** Right postfrontal BMNH R.12871, in dorsolateral (**E**₁) and ventromedial (**E**₂) views (note that the specimen is attached to a museum pin that cannot be removed).

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

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

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

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

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

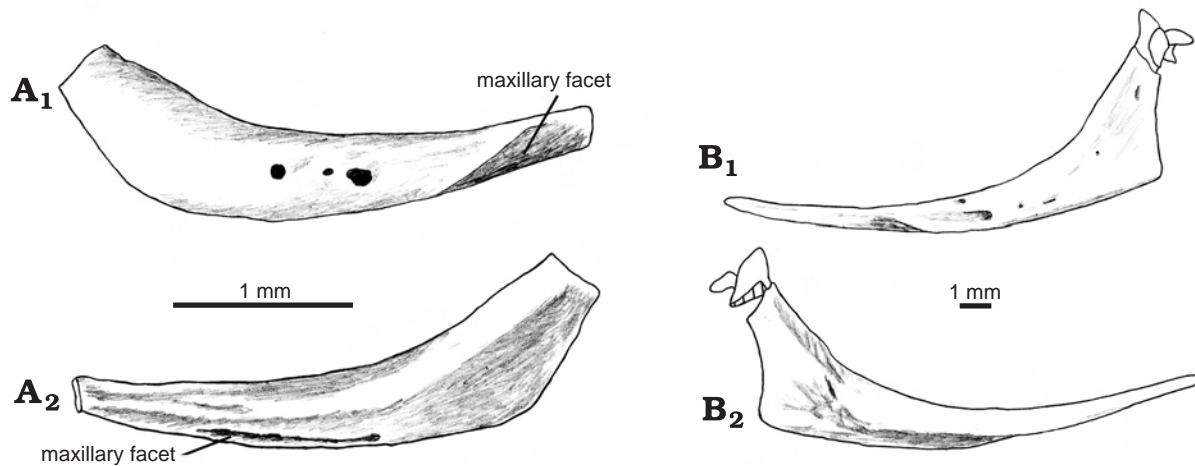


Fig. 13. **A.** *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Partial right jugal ZPAL RV/1008, in lateral (A₁) and medial (A₂) views. **B.** *Kuehneosaurus*, Late Triassic, Emborough Quarry, England. Left jugal BMNH R.12874, in lateral (B₁) and medial (B₂) views.

erally a slender lamina (short axis vertical, long axis horizontal), with a shallow terminal facet for the postorbital. Its slightly curved ventral border bears an articular cotyle for the quadrate, with the quadrate process overhanging posteriorly and presumably contributing to the frame for the tympanic membrane (Fig. 14C₂, D₂). The long dorsal parietal process makes an angle of nearly 90° with the body of the bone, and ascends medially and dorsally towards the skull roof (Fig. 14B₁, D₁). Its posteroventral surface is concave and fits around the anterodorsal surface of the postparietal process (e.g., ZPAL RV/147 fits closely onto parietal ZPAL RV/975), supporting the attribution of both elements to the same taxon. The closeness of fit also precludes the existence of an intervening supratemporal.

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

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

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

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

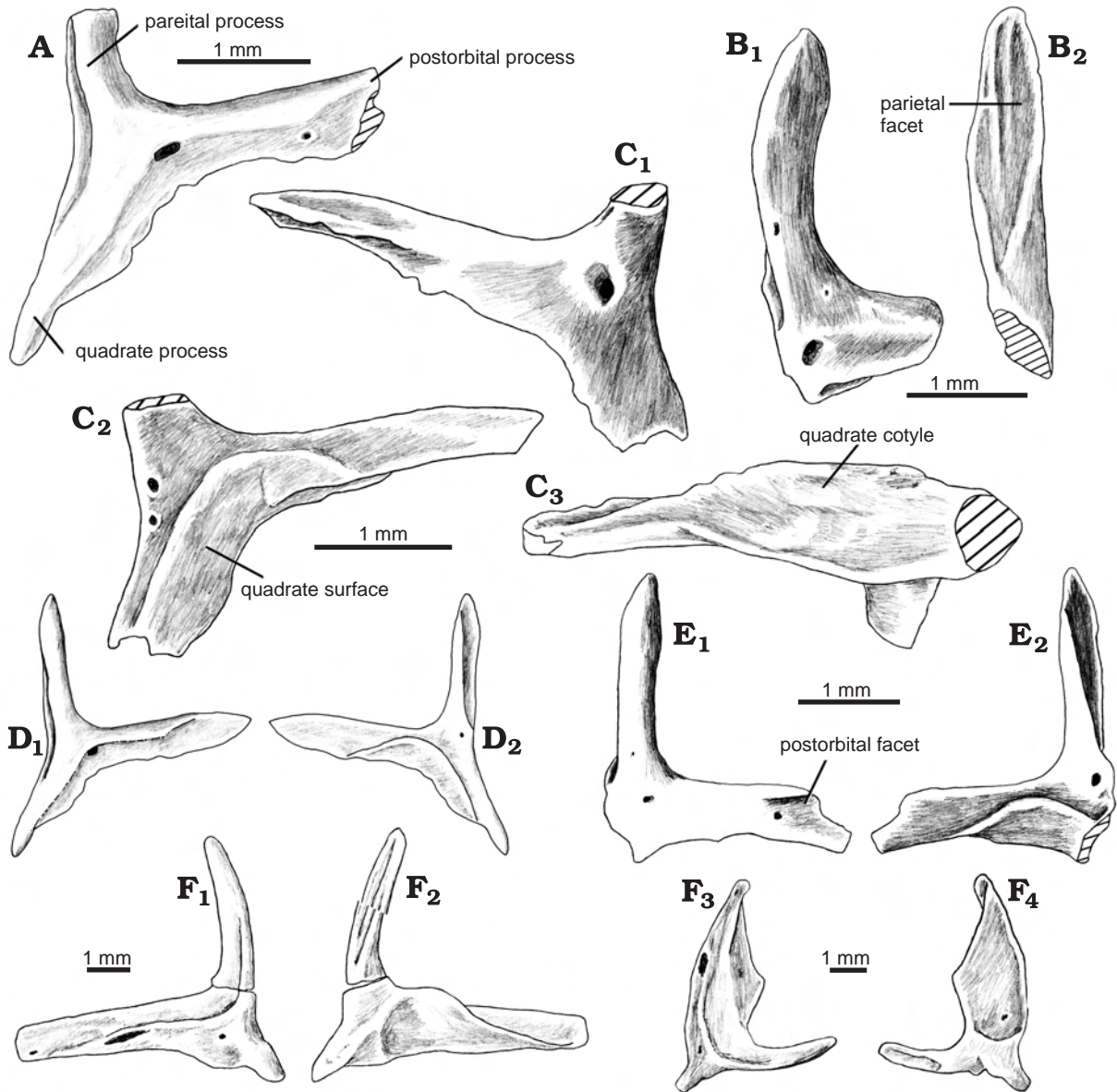


Fig. 14. A–E. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. A. Right squamosal ZPAL RV/1015, in dorsolateral view. B. Right squamosal dorsal parietal process ZPAL RV/1013, in dorsolateral (B₁) and posteromedial (B₂) views. C. Left squamosal ZPAL RV/1011, in dorsolateral (C₁), ventromedial (C₂), and ventral (C₃) views. D. Reconstruction of a right bone, in dorsolateral (D₁) and ventromedial (D₂) views; out of scale. E. Almost complete right bone ZPAL RV/147, in dorsolateral (E₁) and ventromedial (E₂) views. F. *Kuehneosaurus*, Late Triassic, Emborough Quarry, England. Left squamosal BMNH R.12877, in dorsolateral (F₁), ventromedial (F₂), dorsal (F₃), and ventral (F₄) views.

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

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

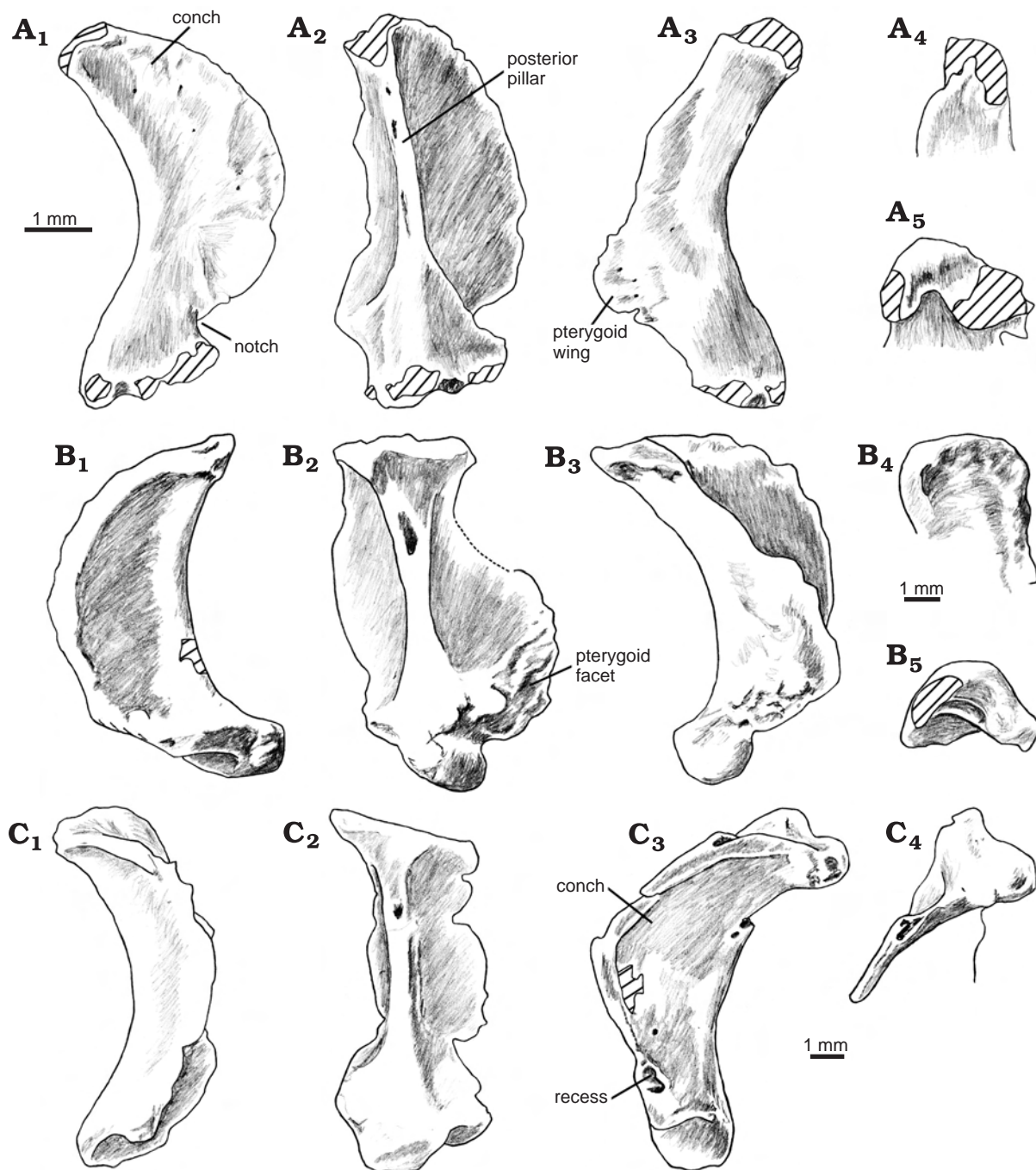


Fig. 15. **A.** *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Right quadrate ZPAL RV/1029, in lateral (A₁), posterior (A₂), medial (A₃), posterodorsal (A₄), and ventral (A₅) views. **B.** *Kuehneosaurus*, Late Triassic, Emborough Quarry, England. **B.** Left quadrate BMNH R.12894, in lateral (B₁), posterior (B₂), medial (B₃), posterodorsal (B₄), and ventral (B₅) views. **C.** Left quadrate BMNH R.12895, in medial (C₁), posterior (C₂), lateral (C₃), and dorsolateral (C₄) views.

15C₃) has a small deep recess on this edge that is very similar to that seen in juvenile specimens of *Gephyrosaurus* in which the rudimentary quadratojugal has been detached. It could be an attachment point for a quadratojugal or quadratomandibular ligament, but raises the possibility that *Kuehneosaurus* had incorporated a reduced quadratojugal into the ventral part of the conch.

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

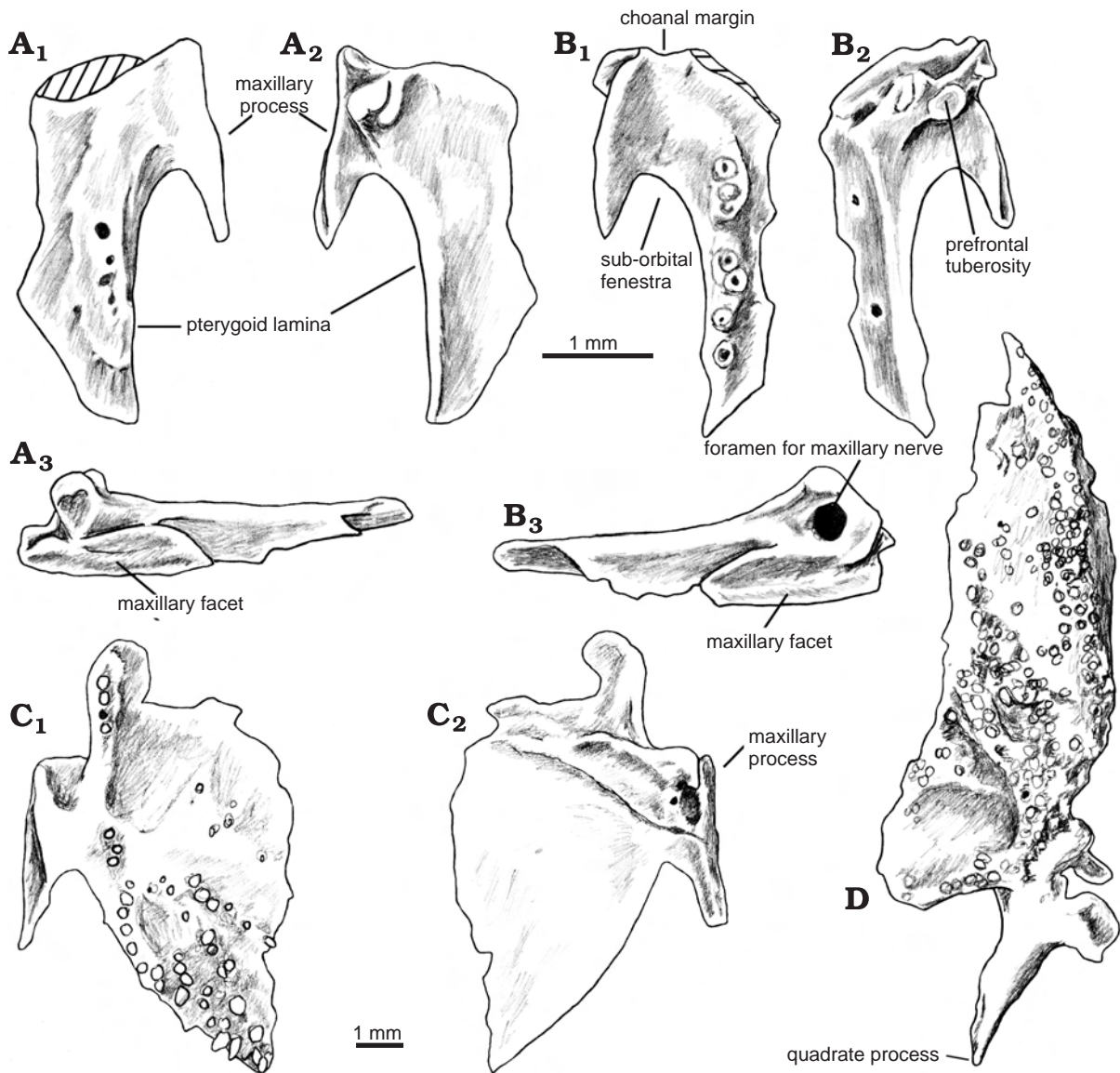


Fig. 16. **A, B.** Palatines tentatively attributed to *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A.** Left bone ZPAL RV/1066, in ventral (A_1), dorsal (A_2), and lateral (A_3) views. **B.** Right bone ZPAL RV/1067, in ventral (B_1), dorsal (B_2), and lateral (B_3)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

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

Palatine. — Palatine elements are surprisingly rare for the smaller Czatkowice reptiles. Fig. 16A, B shows two palatines (ZPAL RV/1066, 1067) that are very tentatively attributed to *Pamelina* on the basis of their size (smaller than the “protosaur”, larger than the second lepidosauromorph) and delicate construction (similar to the frontals and parietals). Only the stronger mid-section of the bone is preserved in each case, with the maxillary process separating a posterior embayment (the margin of the suborbital fenestra) from the curved anterior margin (marking the rear of the choana). The maxillary process is dorsoventrally flattened,

giving a narrow maxillary contact surface that is V-shaped in section and tapers posteriorly. Its dorsal surface bears an irregular rugosity for the prefrontal (either directly or through strong connective tissue, see also Prefrontal). Where complete, a thin bridge of bone links the anterolateral edge of the prefrontal rugosity to a small anteromedial shelf, thus enclosing a short canal for the maxillary nerve and blood vessels passing from the orbit to the maxilla. The pterygoid lamina extends backward almost parallel to the maxillary facet, leaving only a narrow gap for the suborbital fenestra. Dorsally the lamina is featureless; ventrally its lateral edge bears a tooth row. This is bordered medially and posteriorly by the pterygoid facet. Without further specimens, the presence or absence of additional tooth rows remains unknown.

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

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

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

Sphenoid. — The most common sphenoid elements in the Czatkowice collection are attributed to *Osmolskina* and the “protorosaur”; only rare representatives of other types have been found. One morphotype is represented by several specimens (e.g., ZPAL RV/1048–1050), but none is complete. They are attributed to *Pamelina* on the basis of size (too large to fit the pterygoids of the small lepidosauromorph) and morphology (the sphenoids of the procolophonids have a distinct form with anteriorly directed basiptyergoid processes). In ventral view (Figs 10D, 17A₁, B₂), the bones appear pentaradiate, with a broad-based anterior parasphenoid rostrum, relatively slender basiptyergoid processes that are directed laterally with only a slight anterior curvature, and a flared posterior parasphenoid plate. There are no denticles. The borders of the parasphenoid are clearly visible anteriorly as raised crests, but become less distinct at the base of the rostrum in large individuals. There was no enclosed vidian canal and the internal carotid foramina are clearly visible perforating the bone at the level of the basiptyergoid processes. Dorsally (Fig. 17A₂, B₂), the foramina open into the posterolateral margins of an elongated, but shallow, hypophysial fossa. The dorsum sellae is weakly developed as a short horizontal plate with shallow lateral concavities for the retractor bulbi eye muscles, separated in the midline by a slight ridge. There are no abducens foramina or grooves for these nerves, and they presumably passed through soft tissue dorsal to the bone. Bilaterally, each basiptyergoid process is subdivided by a strong crest into a flattened anterior region and a deeply posterior concavity that extends along the posterolateral margin of the bone.

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

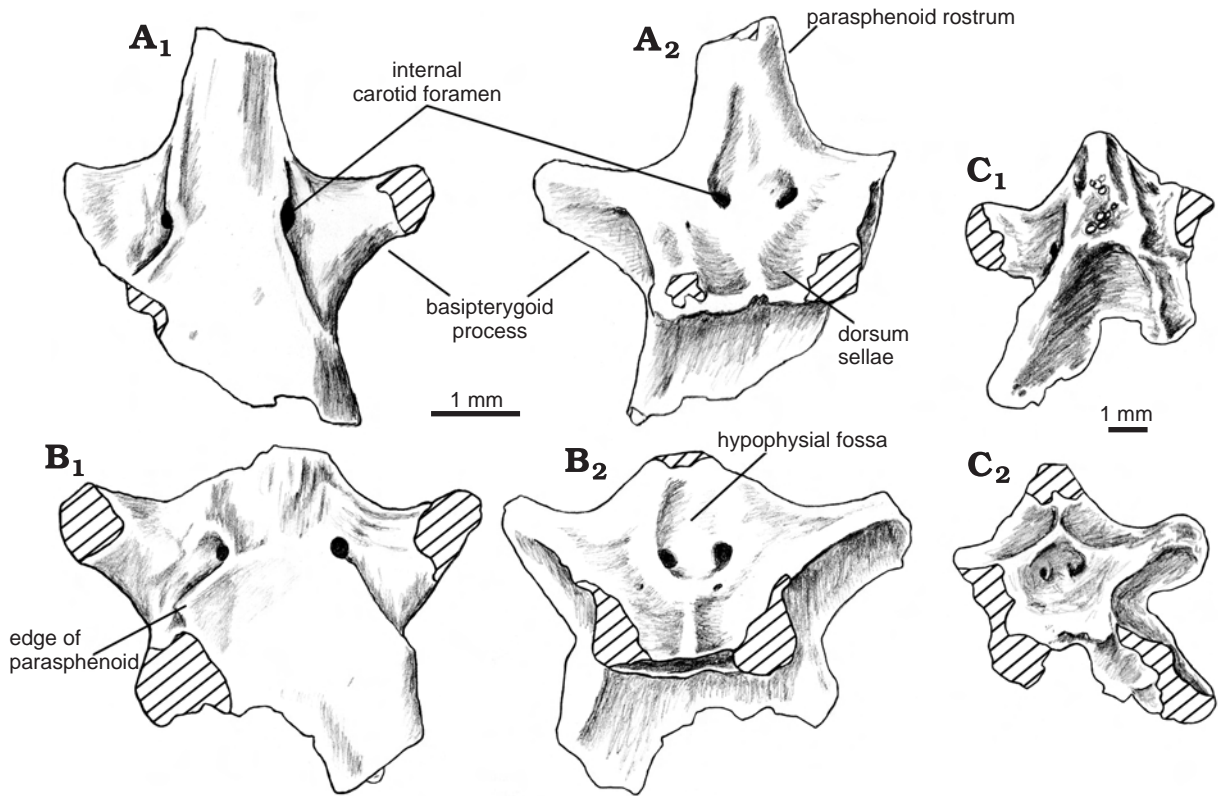


Fig. 17. **A, B.** *Pamelina polonica* gen. et sp. n. **A.** ZPAL RV/1048, in ventral (A₁) and dorsal (A₂) views. **B.** ZPAL RV/1049, in ventral (B₁) and ventral (B₂) views. **C.** *Kuehneosaurus*, Late Triassic, Emborough Quarry, England. Sphenoid BMNH R12647, in ventral (C₁) and dorsal (C₂) views.

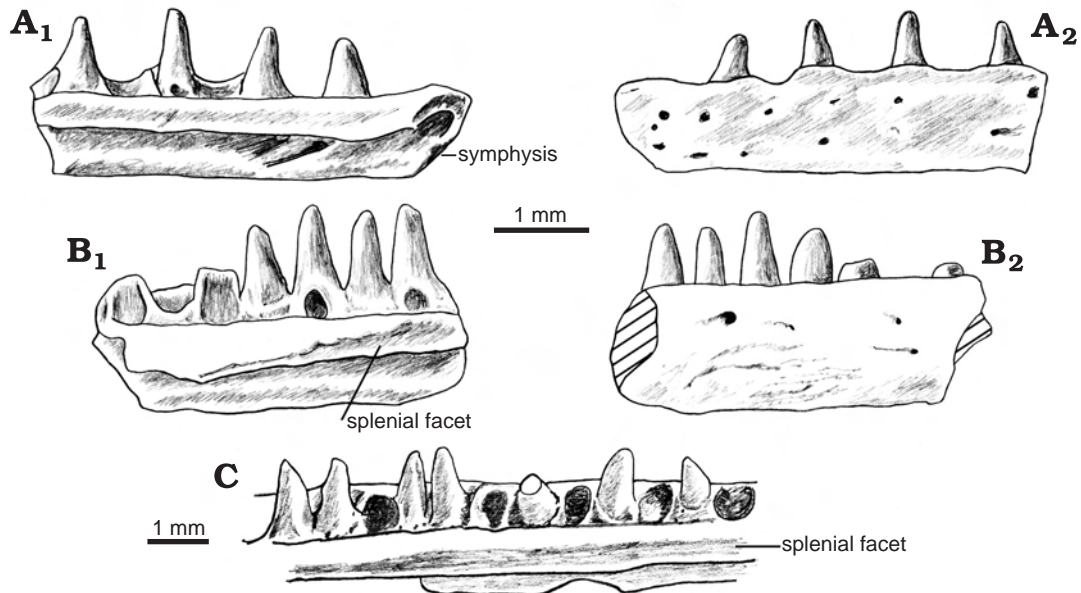


Fig. 18. **A, B.** *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice I, Poland. **A.** Symphyseal region of a left dentary ZPAL RV/1047, in medial (A₁) and lateral (A₂) views. **B.** Mid-section of a right dentary ZPAL RV/1046, in medial (B₁) and lateral (B₂) views. **C.** *Kuehneosaurus*, Late Triassic, Emborough Quarry, England. Section of a larger right dentary BMNH R.12904, in dorsomedial view.

ther differs in that the posteromedial part of the bone bears a deep concavity, bordered anteriorly by a ridge. The other striking difference is the presence of a small cluster of denticles at the base of the parasphenoid rostrum in both *Kuehneosaurus* and *Icarosaurus* (Colbert 1970) but not *Pamelina*. If the attribution of these

bones is correct, it suggests that this apparently primitive feature of the Late Triassic genera is a reacquisition, perhaps related to prey handling in the mouth just prior to swallowing (see above).

Dentary. — The dentary is a long shallow bone with parallel dorsal and ventral margins (no curvature of the ventral margin) and a shallow subdental ridge (Figs 2F, G, 18A₁, B₁). An estimated 25–30 dentary teeth were present. The symphysis is terminal and is divided between the upper and lower margins of the Meckelian fossa (ZPAL RV/1047). A facet on the subdental ridge shows that the splenial did not reach the symphysis, leaving the Meckelian fossa open for a short distance. The entry foramen for the inferior alveolar canal lies towards the back of the jaw. ZPAL RV/1046 (Fig. 18B₁) is a partial left dentary of *Pamelina* showing a clear pattern of alternate tooth replacement.

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

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

POSTCRANIAL SKELETON

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

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

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

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

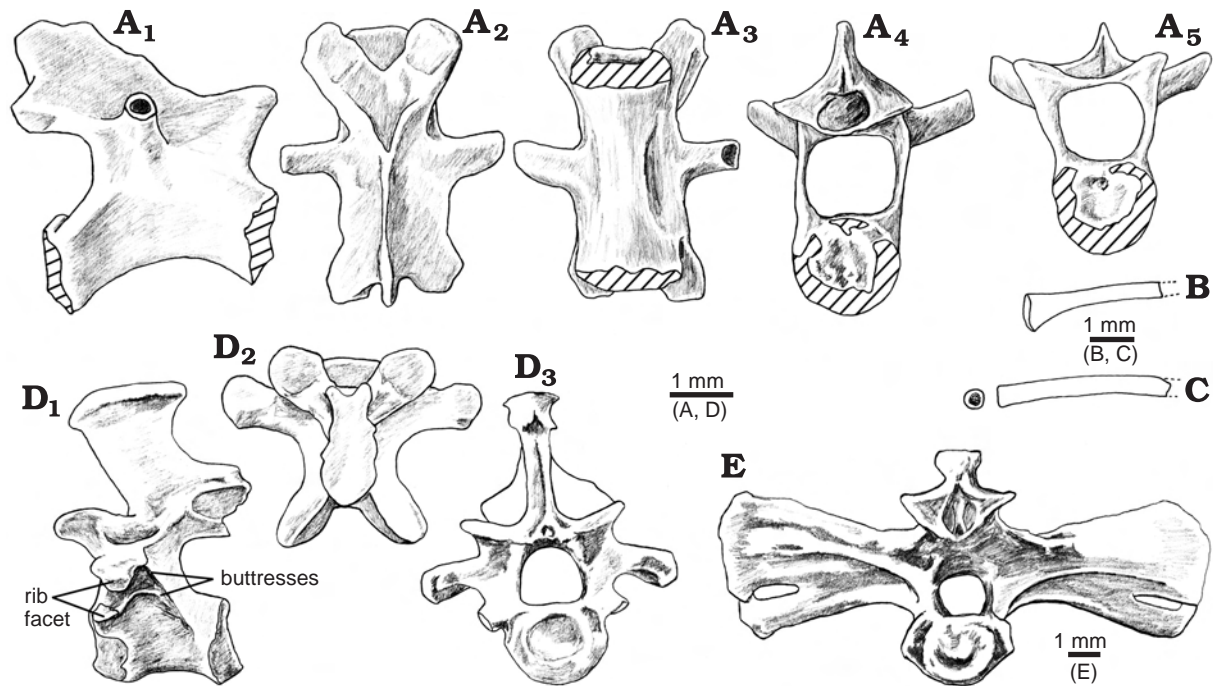


Fig. 19. A–C. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. A. Posterior dorsal vertebra ZPAL RV/1199, in right lateral (A₁), dorsal (A₂), ventral, (A₃), posterior (A₄), and anterior (A₅) views. B, C. Dorsal rib fragments attributed to *Pamelina*. B. ZPAL RV/1214, in side view. C. ZPAL RV/1211, in terminal and side views. D, E. *Kuehneosaurus*, Late Triassic, Emborough Quarry, England. D. Cervicodorsal vertebra BMNH R/12983, in left lateral (D₁), dorsal (D₂), and anterior (D₃) views. E. Anterior dorsal vertebra BMNH R.12991, in posterior view, showing the depth of the transverse process (with diapophysis and parapophysis merging) and posterior pocket between zygapophyses.

keel. In lateral view, the ventral margin of the centrum is distinctly concave. The transverse process is small in cross-section and is directed dorsolaterally. There is also a parapophysis that gradually ascends from the anterior edge of the centrum towards the transverse process. ZPAL RV/1194–1197 characterise this vertebral region (Figs 20A, 22A). In ZPAL RV/1196 and 1197 the parapophysis is still at the anterior edge of the centrum, but a ridge may connect it to the transverse process (ZPAL RV/1197, Fig. 21A). In ZPAL RV/1194, a more posterior vertebra, the parapophysis has moved away from the edge and the transverse process is buttressed by anterior and posterior ridges (Fig. 22B₁). In the more fragmentary ZPAL RV/1195 (not figured), the parapophyses are in different positions on the two sides, low on the left and close to the transverse process on the right. Cervical vertebrae are not very numerous in the Czatkowice collection and *Pamelina* may have had a rather short neck.

ZPAL RV/612 (Fig. 21B) and ZPAL RV/1203 (Fig. 22C) are dorsal vertebrae with a centrum that is rounded in cross-section. The transverse process has a larger diameter and is more laterally directed, and the neural spine is longer. By comparison with other reptiles, this vertebral type is likely to be transitional between the cervicals and more typical dorsals (*i.e.*, an anterior dorsal) since the strongest ribs and processes are generally those that relate to the pectoral girdle (muscle attachments), and both centrum length and cross-section (wider than deep) are intermediate between those of the cervical and dorsal series. ZPAL RV/1204 (Figs 20E, 22D) is a vertebra of similar type to ZPAL RV/1203 with a stout transverse process to which is fused the proximal end of a rib that is directed straight laterally (Figs 21E, 22D₂–D₅). This fusion of the rib to the vertebra is unusual and, if not pathological, suggests rib fixation at the level of the neck-trunk boundary (see below).

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

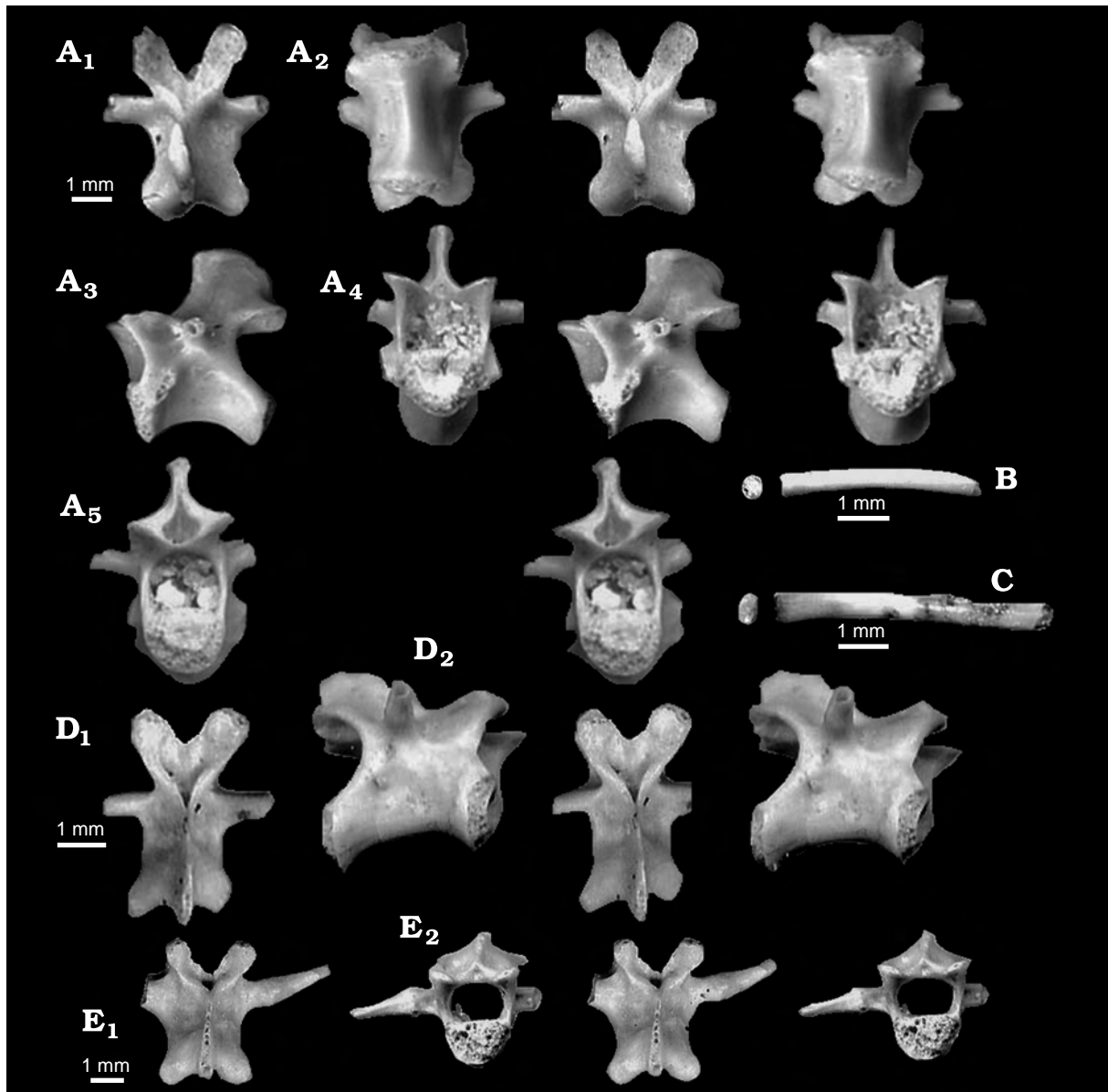


Fig. 20. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Vertebrae and ribs. A. Cervical vertebra ZPAL RV/1194, in dorsal (A₁), ventral (A₂), left lateral (A₃), anterior (A₄), and posterior (A₅) views. B. Attributed dorsal rib ZPAL RV/1211, in terminal and side views. C. Attributed dorsal rib ZPAL RV/1215, in terminal and side views. D. Posterior dorsal vertebra ZPAL RV/1199, in dorsal (D₁) and right lateral (D₂) views. E. Anterior dorsal vertebra with fused rib ZPAL RV/1204, in dorsal (E₁) and anterior (E₂) views. SEM micrographs; all but B, C stereo-pairs.

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

Vertebrae have been identified from both proximal and distal parts of the tail. ZPAL RV/1206 is a rather short (even allowing for breakage) postsacral vertebra with transverse processes that are arched posteriorly. ZPAL RV/627 and RV/1207–1209 are more typical anterior caudals that show some elongation of the neural arch and long transverse processes that may be recurved (ZPAL RV/1207, 1208, Fig. 22F₂, F₃) or straight (ZPAL RV/627, Fig. 21C). Ventrally, these vertebrae lack a groove for the caudal blood vessels. ZPAL RV/1210 (not shown) is a more distal caudal in which the transverse processes have been reduced to a short lateral ridge. Further posteriorly, this ridge disappears and the vertebrae elongate further with the development of a ventral groove for the caudal blood vessels. No caudal vertebra shows any trace of an autotomy septum.

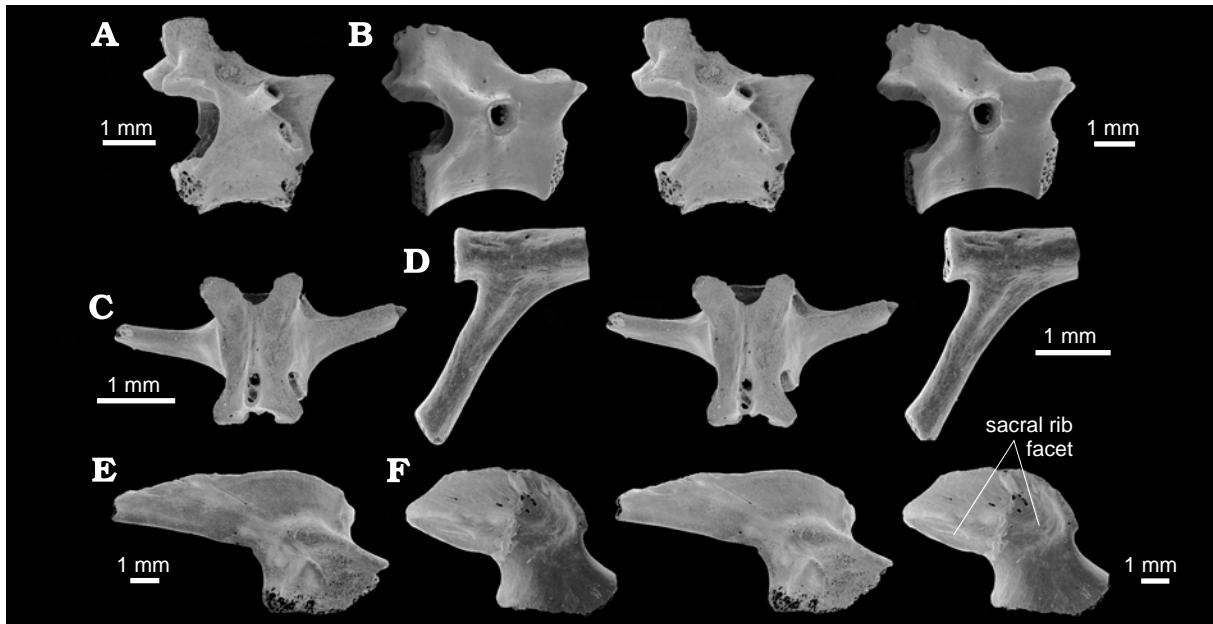


Fig. 21. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Postcranial bones. A. Cervical vertebra with double rib facet ZPAL RV/617, in right lateral view. B. Anterior dorsal vertebra ZPAL RV/612, in right lateral view. C. Anterior caudal vertebra ZPAL RV/627, in dorsal view. D. Possible posterior cervical rib ZPAL RV/936. E. Right ilium ZPAL RV/981, in lateral view. F. Left ilium ZPAL RV/555, in medial view. SEM stereo-pairs.

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

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

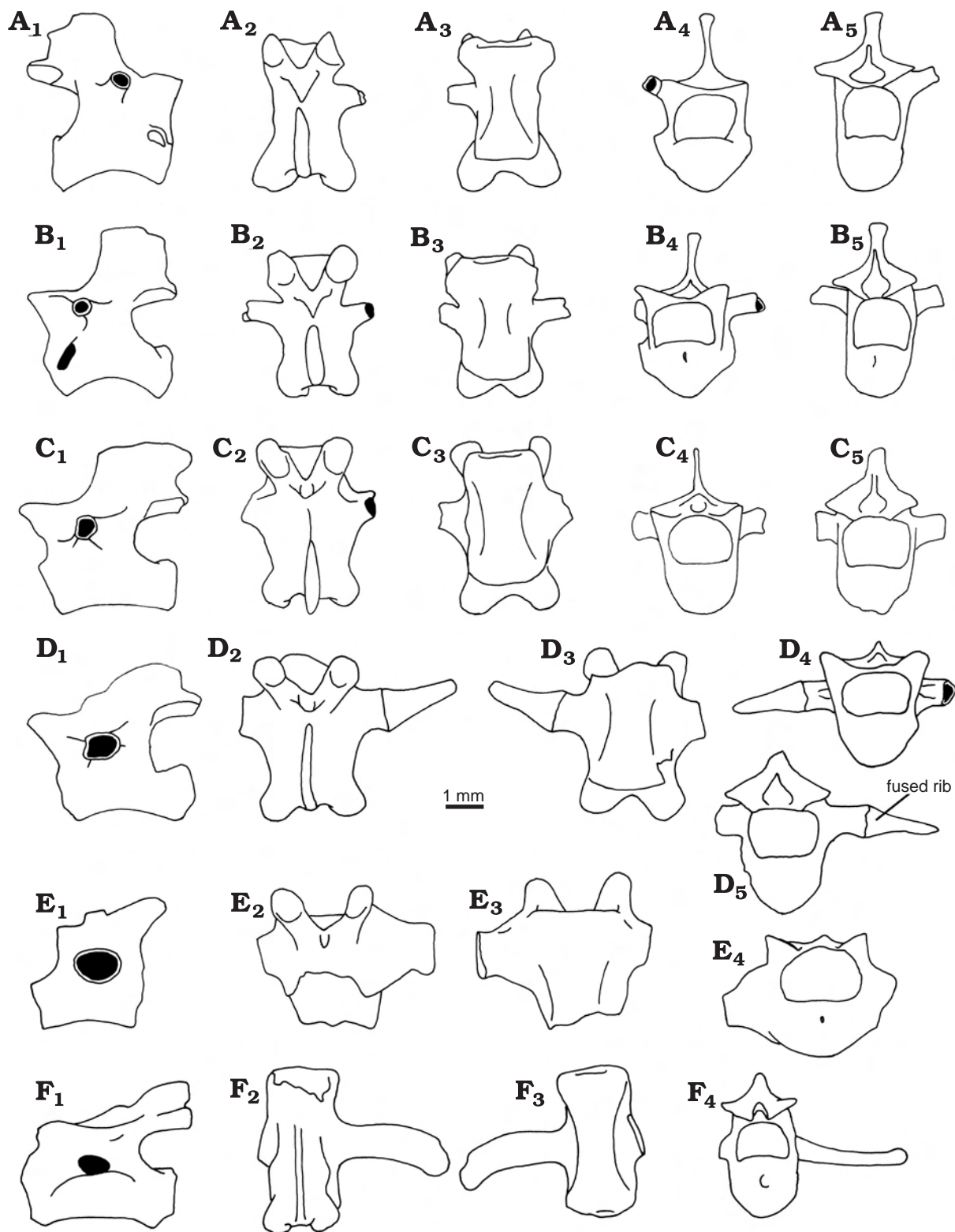


Fig. 22. *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A.** Anterior cervical vertebra ZPAL RV/1197, in right lateral (A₁), dorsal (A₂), ventral (A₃), anterior (A₄), and posterior (A₅) views. **B.** Posterior cervical vertebra ZPAL RV/1194, in left lateral (B₁), dorsal (B₂), ventral (B₃), anterior (B₄), and posterior (B₅) views. **C.** Anterior dorsal vertebra ZPAL RV/1203, in left lateral (C₁), dorsal (C₂), ventral (C₃), anterior (C₄), and posterior (C₅) views. **D.** Anterior dorsal vertebra with broken rib attached on right side ZPAL RV/1204, in left lateral (D₁), dorsal (D₂), ventral (D₃), anterior (A₄), and posterior (D₅) views. **E.** Partial sacral vertebra ZPAL RV/1205, in right lateral (E₁), dorsal (E₂), ventral (E₃), and anterior (E₄) views. **F.** Anterior caudal vertebra ZPAL RV/1208, in left lateral (F₁), dorsal (F₂), ventral (F₃), posterior (F₄) views.

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

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

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

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

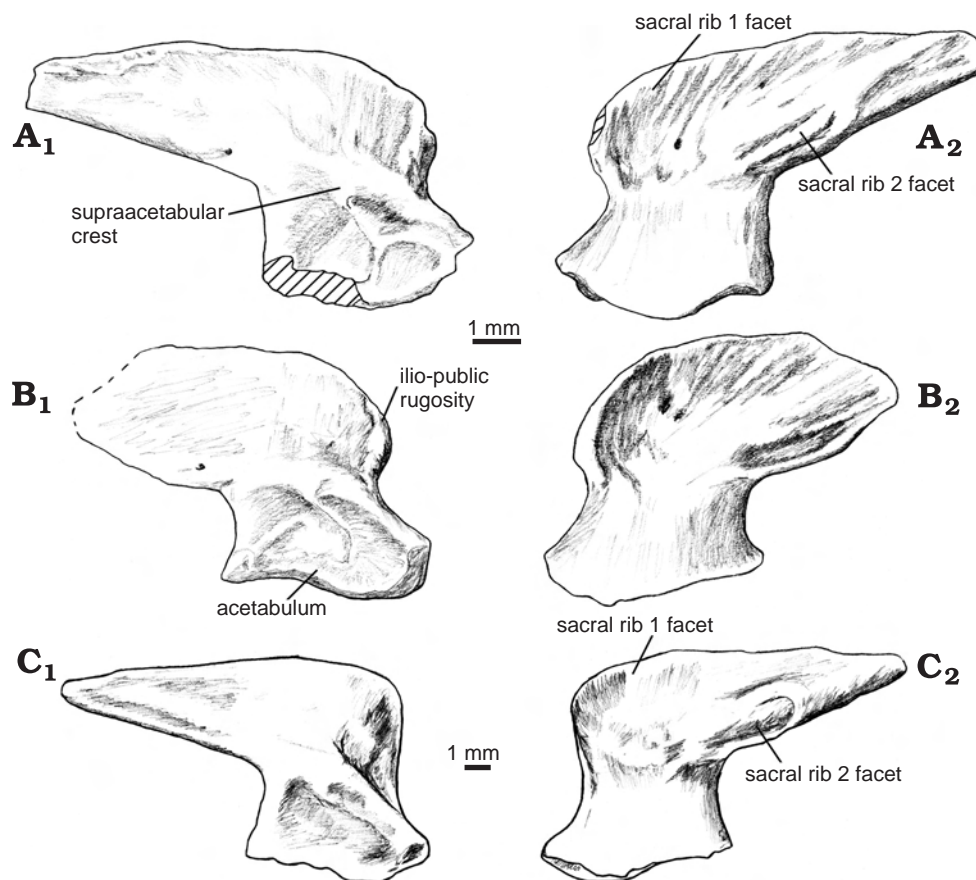


Fig. 23. **A, B.** *Pamelina polonica* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A.** Right ilium ZPAL RV/981, in lateral (A_1) and medial (A_2) views. **B.** Left ilium ZPAL RV/555, in lateral (B_1) and medial (B_2) views. **C.** *Kuehneosaurus*, Late Triassic, Emborough Quarry, England.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

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

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

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

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

DISCUSSION

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

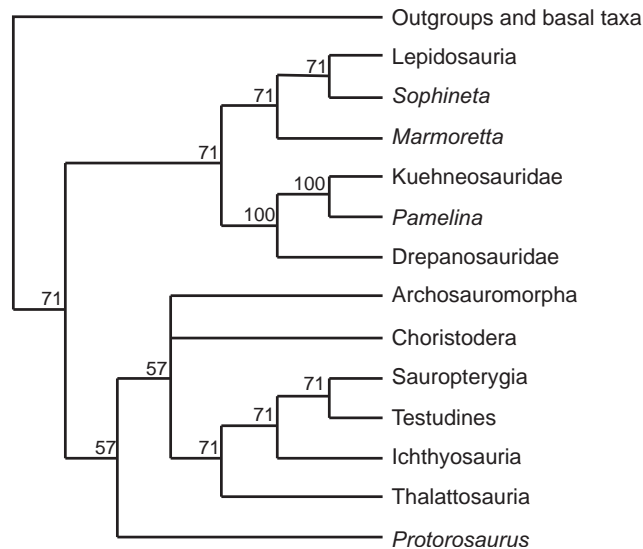


Fig. 24. 50% Majority Rule consensus of seven equally parsimonious trees obtained from a heuristic search using the diapsid data set from Müller (2004) with some character codings added or updated (note that although all the taxa from the original matrix were included in the analyses, they have been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

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

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

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

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

CONCLUSIONS

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

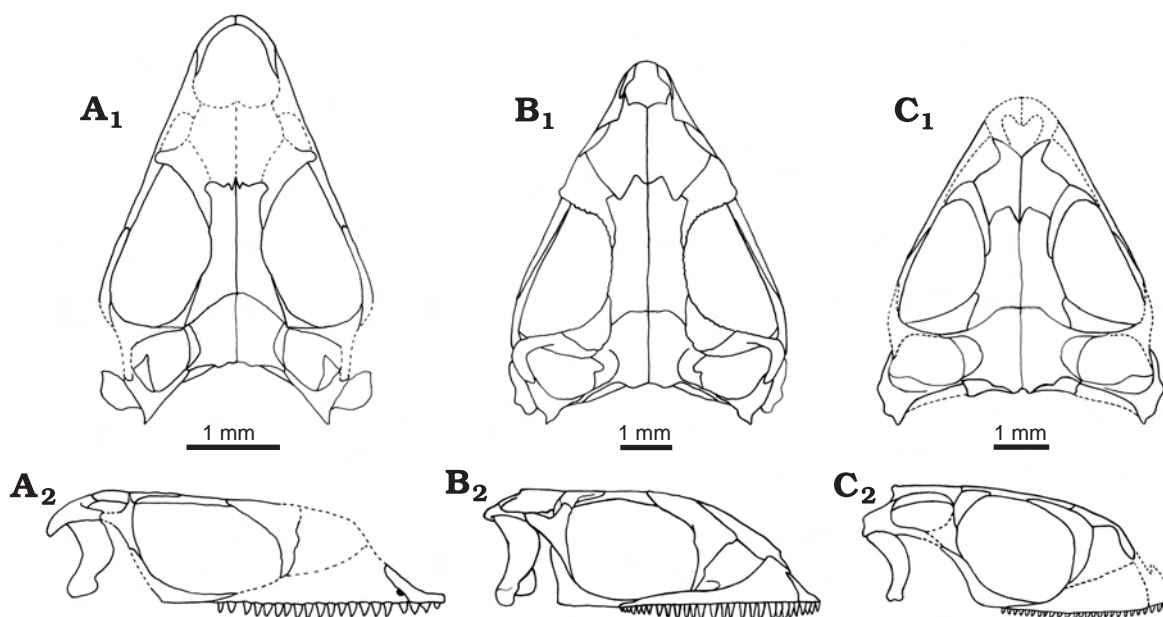


Fig. 25. Comparison of the skulls of *Pamelina* (A), *Kuehneosaurus* (B), and *Icarosaurus* (C), in dorsal (A₁, B₁, C₁) and lateral (A₂, B₂, C₂) views.

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

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

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APPENDIX 1

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

<i>Pamelina</i>	01000 10011 02011 022?1 10??? 1111? 10001 01011 0??00 111?1 ????? ????? ????? ????? ????? ????? 20011 00010 200?? 1??00 ??02? 10??? ???23 00??? ?0?00 101?0 00??? ???20 ????? ?????? ?0001 11??? ?1?0 ????1? ??0? ?0000 10?1
Kuehneosauridae	01000 10011 02011 02201 10101 11110 10001 0?011 0110? 11?01 11101 00000 00121 00112 011?1 ???10 00011 0?010 200?? 00000 10020 11?00 00003 00010 ?0000 10100 00??0 1??10 ??0?? 00?10 ?0000 1100? 00100 01?10 00?00 20000 1011

APPENDIX 2

Müller (2004) characters emended

Rhynchocephalia

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

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

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

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

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

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

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

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

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

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

10/184 — 5.4%

Squamata

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

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

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

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

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

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

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

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

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

9/184 — 5%