A microvertebrate assemblage from the Early Triassic of Poland

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The Early Triassic microvertebrate assemblage from karst deposits of Czatkowice quarry, Kraków Upland, Poland, has been dated as of latest Olenekian age at youngest. The assemblage contains mainly small reptiles: three to four possible genera of procolophonids, a small predatory archosaur of proterosuchid or pre-proterosuchid grade, a prolacertiform, and one or two genera attributable to Lepidosauromorpha, one of them, very small, being a possible stem-lepidosaurian. Furthermore there are some less numerous amphibians, including the first European salientian (stem-frog) – *Czatkobatrachus polonicus* Evans & Borsuk-Białynicka, 1998, as well as fishes. The bones are disarticulated but fairly well preserved. The assemblage provides a glimpse of the Early Triassic diversity of small taxa, otherwise poorly known, and has a considerable potential in highlighting the earliest phylogeny of such groups as lepidosauromorphs and salientians which are virtually unknown from other roughly contemporaneous horizons. The Czatkowice microvertebrate community appears to have lived under the mesic conditions of a freshwater oasis within the otherwise arid circumequatorial belt of Scythian Northern Pangea.

K e y   w o r d s : Archosauromorpha, Lepidosauromorpha, Lissamphibia, microvertebrates, Poland, Procolophonia, Scythian, Triassic.

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Introduction

The Early Triassic is an interesting epoch, witnessing a changeover from the archaic faunas of the Permian to those more typically associated with the Triassic and later Mesozoic. The end-Permian mass extinction resulted in the loss of some 85% of the marine biota and 70% of the terrestrial biota over a period of less than one million years (Bowring *et al.* 1998). This left vacant ecospace for the evolution and radiation of the survivors, mainly representatives of temnospondyl amphibians and amniotes of three phylogenetic lines: the synapsids, and the diapsid Archosauromorpha and Lepidosauromorpha, as well as the procolophonians. The result was the appearance of typical Triassic tetrapod groups such as herbivorous cynodonts, dicynodonts and rhynchosaurs, and the carnivorous or insectivorous archosaurs (Anderson & Anderson 1993a, b). Moreover, recent cladistic analyses predict that several extant tetrapod groups such as lissamphibians, turtles, crocodiles and lepidosaurs appeared about this time. The lissamphibian *Triadobatrachus* Piveteau, 1936, a primitive salientian from the Early Triassic of Madagascar (Rage & Roček 1989), and a possible lissamphibian larva from the Late Triassic of Kyrgyzstan, *Triassurus* Ivakhnenko, 1978, although poorly known, provide direct evidence of the earliest radiation of this group, probably as a part of the Griesbachian radiation of temnospondyls (Milner 1990). Squamates are unknown in the Triassic, but the presence of more than ten rhynchocephalian genera in Upper Triassic deposits, with two doubtful Early Triassic taxa (*Scharschengia* Huene, 1940, *Palacrodon* Broom, 1906), provides support for a Permo-Triassic origin and dichotomy of Lepidosauria.

In the Permian, the existence of the single Permian supercontinent Pangea allowed for the worldwide distribution of many groups. However, the degree of global faunal congruence decreased in the Induan because of the development of a broad circum-equatorial xeric belt partly separating Euramerica from Gondwana (Shishkin & Ochev 1993).

Early Triassic assemblages are known from several regions. There is a range of southern faunal assemblages from continental sedimentary basins in South Africa (Karroo), India, Australia, Antarctica, and from more coastal regions in Madagascar and Northwest Australia. Typically, these assemblages are dominated by synapsids (dicynodonts and therapsids), or by temnospondyl amphibians. The northern continental assemblages include those of the East European platform (Fig. 1, Table 1), North China, Mongolia and, in the boreal region, those of Greenland and Siberia. Again, temnospondyls and synapsids dominate. Most of these assemblages, both Laurasian and Gondwanan, represent a mix of mesic to semi-arid climatic conditions. Between them lay a central region representing more arid conditions. The Early Triassic and early Anisian Buntsandstein of Western Europe and the late Olenekian/early Anisian Moenkopi Formation of southern North America are typical of this belt (Anderson & Cruickshank 1978; Cooper 1982; Lozovsky 1993a; Ochev 1993; Shishkin & Ochev 1993). In all of these deposits, small tetrapods are relatively poorly known. The recovery of a bone breccia including a diverse microvertebrate assemblage of Early Triassic age at Czatkowice (Cracow Upland, Poland, Figs 1, 2B) is therefore of great interest.

Fig. 1. Generalized geographic map of Eastern Europe. The Czatkowice locality is marked by an asterisk.

The bone breccia of Czatkowice quarry was discovered in 1978, and then briefly studied by a team from the Institute of Geology of the Jagiellonian University (Paszkowski & Wieczorek 1982). The material was collected by one of us (T. Maryań-ska) and Prof. H. Osmólska (Institute of Paleobiology, Polish Academy of Sciences). Samples of the matrix were broken down in acetic acid. This time-consuming chemical preparation is still in progress. The bone material obtained is housed at the Institute of Paleobiology and the Museum of the Earth, Warsaw. Work on the assemblage is still at a preliminary stage, but it has revealed a diversity of small reptiles including archosauromorphs, lepidosauromorphs and procolophonids, as well as less numerous, but extremely interesting, amphibians and some fish. Most important, the assemblage includes two groups which are otherwise virtually unknown from this geological epoch – lepidosauromorphs and salientians (Evans & Borsuk-Białynicka 1998). The Czatkowice assemblage thus provides a glimpse of a mesic (at least locally) terrestrial small vertebrate community at the very beginning of the Mesozoic.

Institutional abbreviations: ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw; MZ, Museum of the Earth, Polish Academy of Sciences, Warsaw.
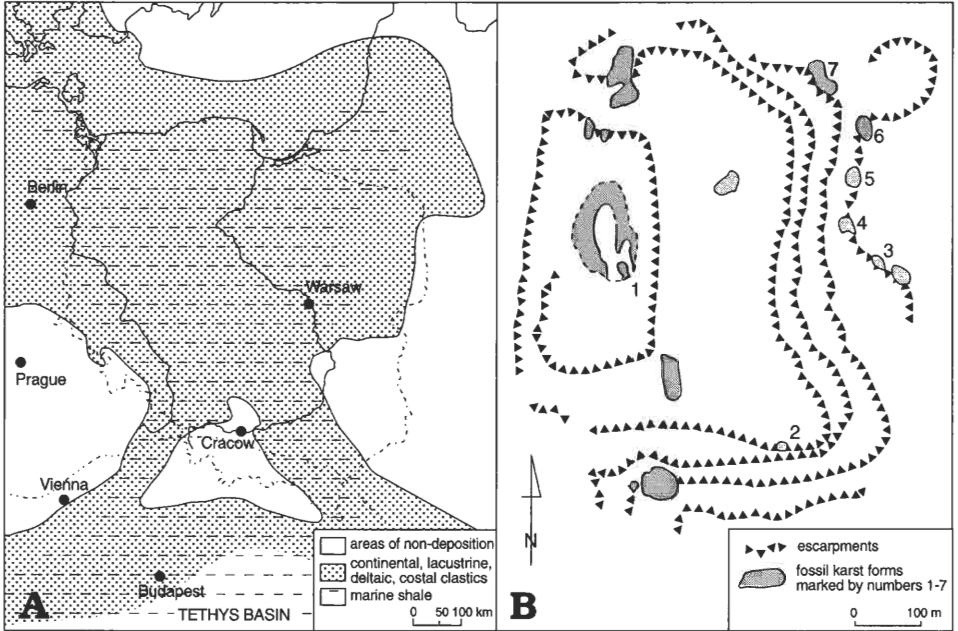
Fig. 2. **A**. Early Triassic palaeogeography of Eastern Europe, based on Ziegler (1990). **B**. Sketch map of the Czatkowice quarry in 1979, after Paszkowski & Wieczorek (1982).

Geological background

The Czatkowice quarry (Fig. 2) is the largest in the Cracow region and is still actively worked to extract the Lower Carboniferous limestone. The fissure/cave systems developed in the limestone include infillings of Early Triassic, Early Jurassic and Middle Jurassic age. The Triassic infillings are of a fine grained sandy yellow limestone with some calcite cement, and contain bones, occasional clasts and concretions (Mariusz Paszkowski, personal communication to S.E. and M.B-B in 1997). A few samples show evidence of sedimentary bedding and parallel orientation of the bones, but this is not generally the case. All the specimens described herein come from a single fissure exposure, Czatkowice 1 (Fig. 2B). The material is completely dissociated, and often broken, although at least some of the fragmentation probably occurs in preparation. The bones are mostly white, orange or dark brown, and are generally finely preserved, with relatively little abrasion or polishing. Many of the teeth retain details of fine structure (striations, facetting) under the Scanning Electron Microscope, and some very small delicate elements are preserved intact. Together this suggests rather gentle transport over a limited distance before deposition, although some specimens show evidence of reworking. Some size sorting may have occured, however, as all the skeletal remains are of small animals – one metre or less in size.

Fissure deposits are notoriously difficult to date but geological studies of the locality (Paszkowski & Wieczorek 1982) suggest the Czatkowice 1 material is of Scythian

age (i.e. around 245–242 Ma, Bowring *et al.* 1998; Gradsten *et al.* 1995). According to Paszkowski & Wieczorek (1982), the karstification phase during which the infillings of Czatkowice 1 were deposited may have lasted from the Late Permian to the Early Triassic. It ended before the Röt transgression which covered the region at the end of the Spathian. The transgressing sea came over a land surface of low relief and there was no high ground to form islands which could be subject to karstification. Thus the fissure infilling of Czatkowice 1 may be older than the latest Olenekian, but cannot be younger. It thus lies in the range of the Induan-Olenekian assemblages of the East European Platform and the *Lystrosaurus*–Lower *Cynognathus* zones of southern Africa.

In the Early Triassic, the Czatkowice region lay some 100 km inland and was a region of low upland (200 m). The water table was deep and there is evidence of hydrothermal vents. The environment would have been arid, with sparse vegetation, but with occasional pools (oases) large enough to have supported an aquatic community (fish and amphibians) as well as a small terrestrial tetrapod one around its shoreline. At times of heavy rain, flooding and surface run off would have washed animals and clays into the fissure system. Supporting evidence for this palaeoecological reconstruction comes from the Tumlin Sandstone (Buntsandstein) of Central Poland, which has yielded a few isolated tetrapod footprints and short trackways thought to have been made by a terrestrial reptile of *Chirotherium*-type. These trace fossils are associated with sedimentary structures indicative of ephemeral pools (Fuglewicz *et al.* 1990; Gradziński & Uchman 1994; Gradziński *et al.* 1979).

The Czatkowice assemblage

The material from Czatkowice is completely disarticulated but extensive experience at other microvertebrate localities by one of us (SE) has shown that it is possible to derive a considerable amount of information from such remains. Tooth-bearing elements (dentaries, premaxillae and maxillae) may first be associated on the basis of tooth implantation and tooth morphology (SEM studies). In addition to phylogenetically relevant information (pleurodonty, thecodonty, premaxillary and maxillary shape etc), the jaw material provides an indication of the number of taxa present, their relative sizes (or range of size), and whether they are common or rare. Attribution of other cranial and postcranial elements is more difficult but relies on a combination of size (and size distribution), robusticity, phylogenetically relevant characters, bone fit (based on facet shapes), sculpture patterns and numerical representation within the assemblage.

The assemblage contains fish, amphibians, procolophonids, and primitive lepidosauromorph and archosauromorph reptiles. Synapsids have never been found at Czatkowice 1, and a search for palynomorphs proved unsuccessful.

Fish (Fig. 3A, C, D). — Fish remains, like those of amphibians, form a relatively rare component of the Czatkowice 1 assemblage. They are represented by occasional fin spines and cranial elements, by small jaws bearing simple acrodont teeth (Fig. 3C, D), and by several jaws, premaxillae (Fig. 3A) and palatal elements with more gracile teeth.

Amphibians (Figs 3B, 8C). — Despite their rarity, amphibians are represented by several taxa. The largest, approaching the size of the small archosaur described below,
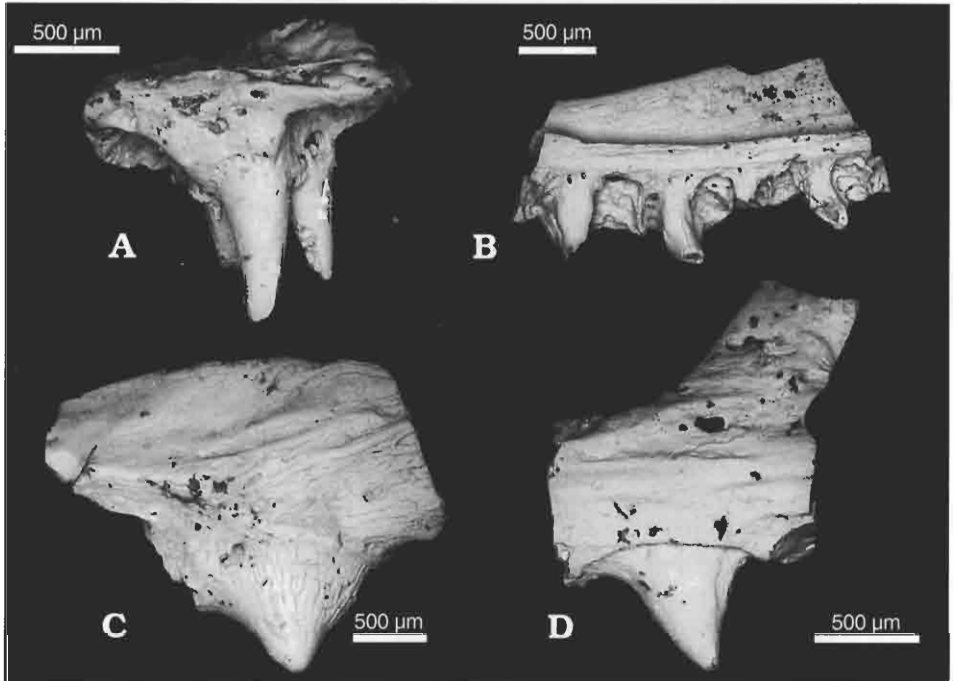
Fig. 3. Fish and amphibian toothed fragments from the Early Triassic of Czatkowice (Poland). **A, C, D**. Respectively ZPAL P.VII/1-3 – ? fish, toothed bones. **B**. ZPAL Ab.IV/51 – amphibian, fragment of maxilla in lingual view.

have sculptured jaw elements and conical teeth with a basal 'labyrinthodont' infolding. These jaw elements most closely resemble those of temnospondyls, but the striate sculpture suggests the material is juvenile (Andrew Milner, personal communication to SE 1998) making identification problematic. In addition, there are rare maxillae of at least two further amphibian taxa (one of them Fig. 3B), but neither shows any sign of pedicelly in the teeth.

In a terrestrial/aquatic assemblage of Early Triassic age, small temnospondyls are not unexpected. Rather less predictable was the recovery of bones of a small primitive salientian, broadly resembling *Triadobatrachus massinoti* Piveteau, 1936, a roughly contemporaneous stem-frog from the early Olenekian of Madagascar (Rage & Roček 1989; Shevyrev 1990). The Czatkowice animal, *Czatkobatrachus polonicus* Evans & Borsuk-Białynicka, 1998 is currently represented by vertebrae (e.g., Fig. 8C), limb bones and pelves, but further elements may be found. It resembles *Triadobatrachus* (Rage & Roček 1989) in the features of its pelvis and vertebral length, but is more derived in the form of the atlas, the humerus and the sacral and dorsal ribs.

Reptiles (Figs 4, 5–7, 8A, B, D–H). — The most common animal (around 80% of the preserved bone) is a small predatory archosaur which, at 4–5 cm skull length and probably 50–100 cm body length (roughly the size of a small monitor lizard), is one of the largest members of the assemblage. This archosaur is represented by almost all the
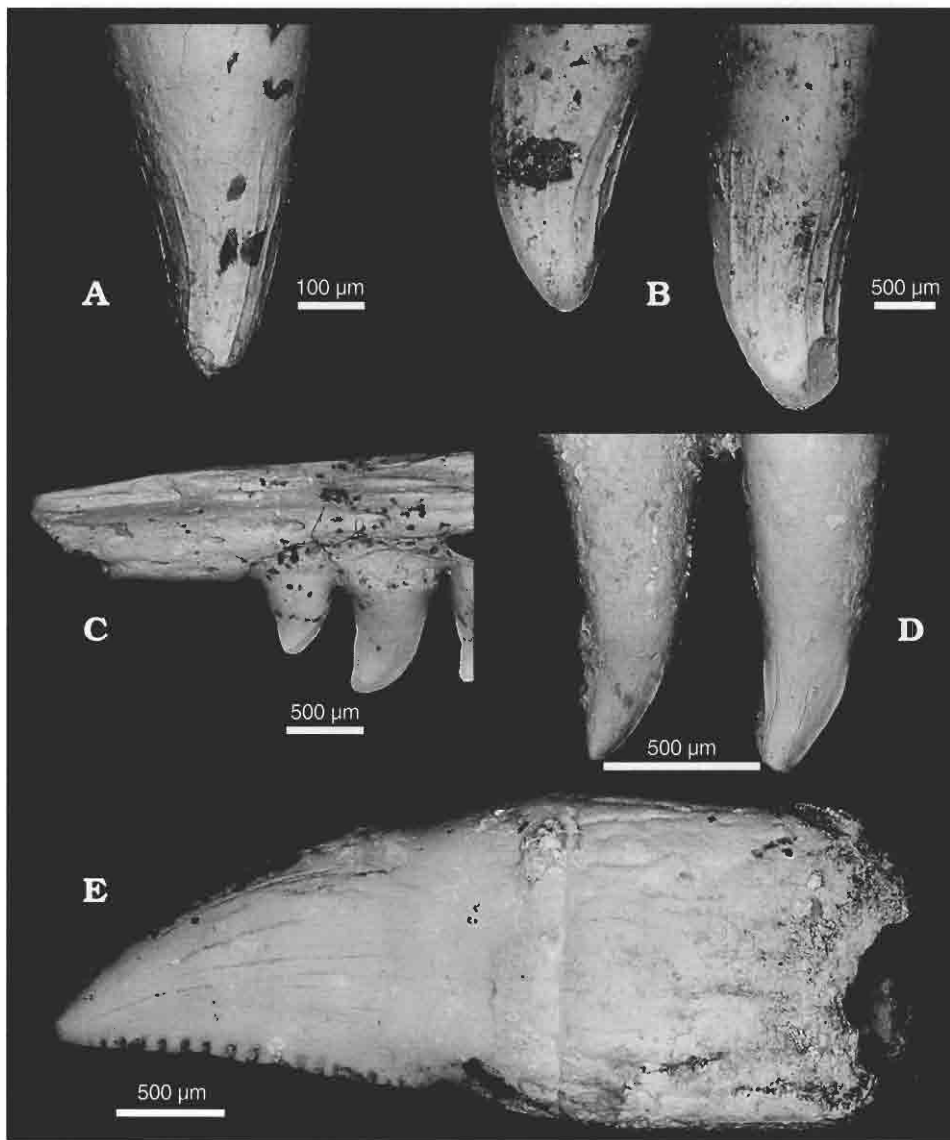
Fig. 4. Reptile teeth from the Early Triassic of Czatkowice (Poland). **A**. ZPAL R.V/1 – prolacertiform lower tooth in lingual view, reversed to add comparison. **B**. ZPAL R.V/5 – common lepidosauromorph lower teeth in lingual view. **C**. ZPAL R.V/2 – common lepidosauromorph, posterior part of maxilla with teeth in lingual view. **D**. ZPAL R.V/3 – small lepidosauromorph, two upper teeth, lingual view. **E**. ZPAL R.V/4 – archosaur, isolated tooth.

bones of the skull and postcranial skeleton (Figs 4E, 5D, 6D, F, 7A, 8G, H), and a partial reconstruction will be possible in the future, as well as a comprehensive discussion of its phylogenetic position. It has serrated, thecodont teeth and a large antorbital fenestra which is not recessed. It retains a partial palatal dentition and the premaxilla
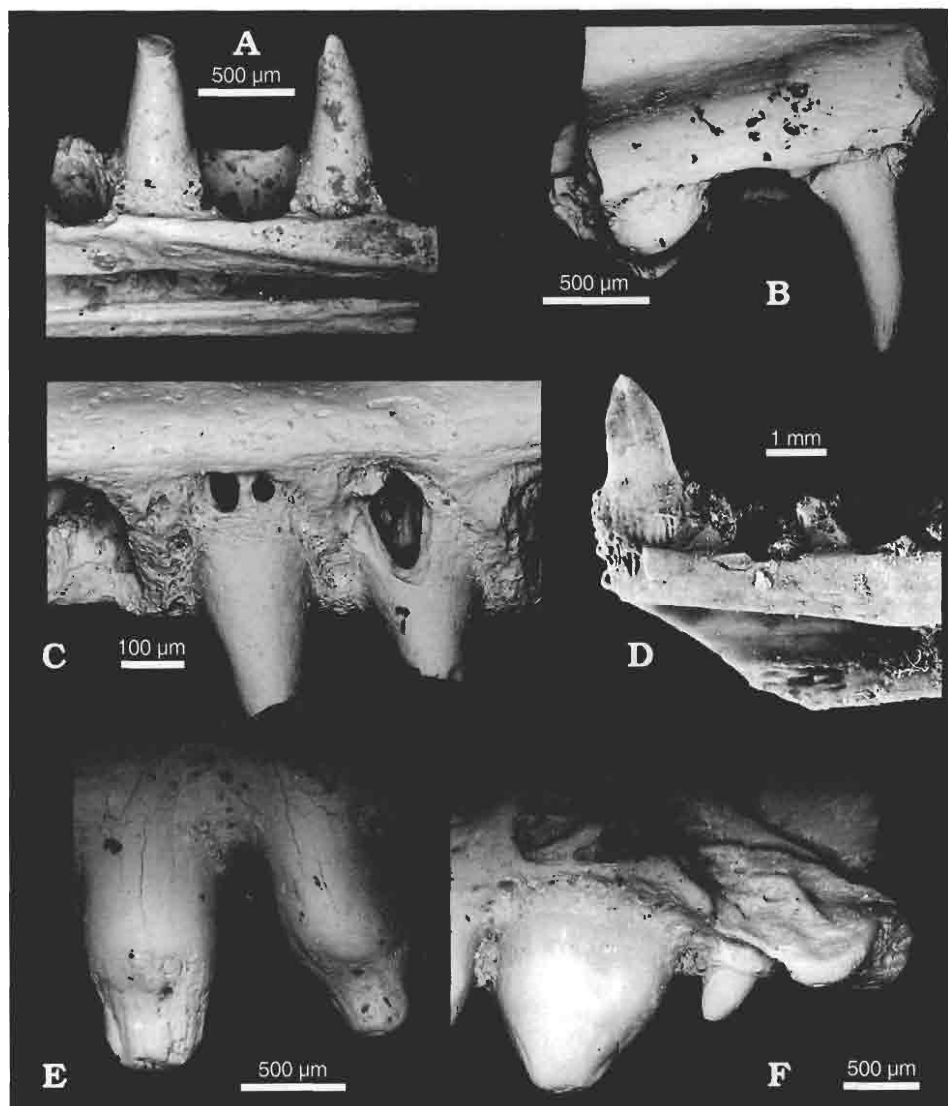
Fig. 5. Different types of tooth implantation in reptiles from the Early Triassic of Czatkowice (Poland). **A**, **D**. Dentary fragments. **B**, **C**, **F**. Maxillary fragments. **E**. Premaxillary fragment. **A**. MZ VIII VR 72 – common lepidosauromorph, weakly pleurodont implantation. **B**. ZPALR.V/6 – prolacertiform, subthecodont implantation. **C**. ZPAL R.V/7 – small lepidosauromorph, pleurodont implantation. **D**. ZPAL R.V/14 – archosaur, thecodont implantation. **E**. ZPAL R.V/51 – procolophonian type premaxillary teeth. **F**. ZPAL R.V/52 – procolophonian type posterior maxillary teeth.

may have been down-curved like that of *Proterosuchus* Broom, 1903. Braincase elements are relatively well preserved and, by comparison with roughly contemporaneous taxa (Gower & Sennikov 1997), appear to represent a rather primitive construction. The neck vertebrae are short and the ilium lacks a strong anterior process. This
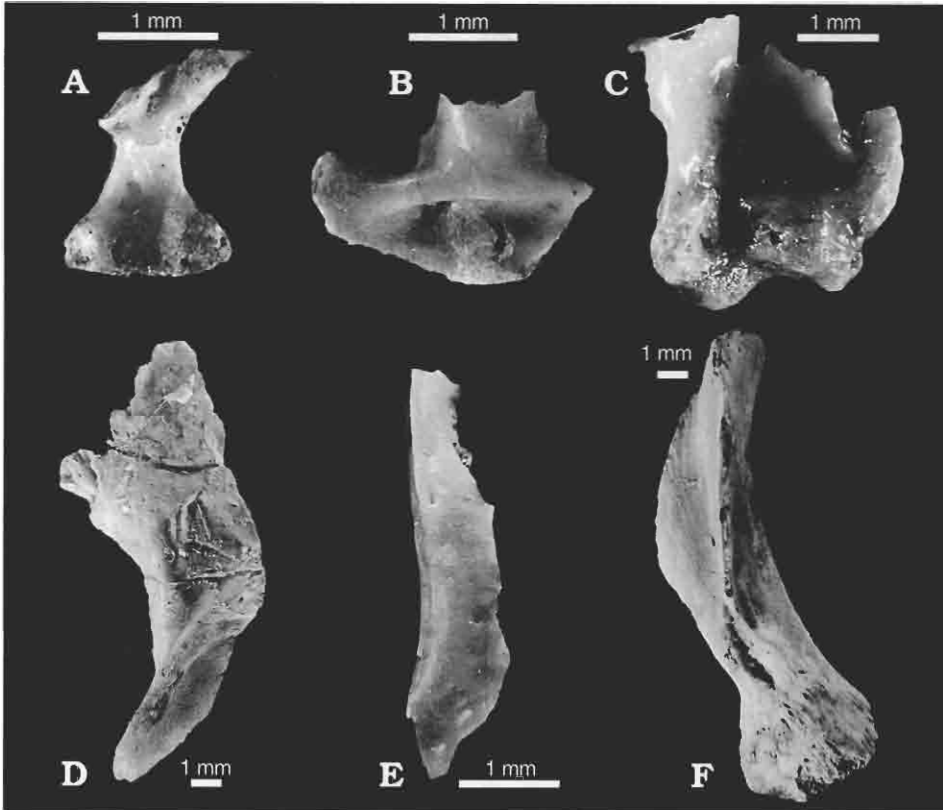
Fig. 6. Skull bones of reptiles from the Early Triassic of Czatkowice (Poland). **A**. ZPAL R.V/20 – right exoccipital in lateral view. **B**. ZPAL R.V/26 – left prootic in lateral view. **C**. ZPAL R.V/13 – partial left quadrate with quadratojugal in anterior view. **D**. ZPAL R.V/17 – archosaur left parietal in dorsal view. **E**. ZPAL R.V/18 – left frontal in dorsal view. **F**. ZPAL R.V/19 – archosaur left quadrate in lateral view.

and other features are indicative of a primitive archosaurian, either of proterosuchid (*sensu* Gower & Sennikov 1997), or pre-proterosuchid grade.

In addition to the archosaur, the assemblage contains remains of at least three further diapsids, all of which are of small size and have long slender pleurodont, sub-pleurodont or sub-thecodont teeth showing some measure of posterior curvature. The tooth-bearing elements are complemented by a number of skull and postcranial bones which permit a tentative attribution of these three taxa to group.

All skull roofing elements are paired and unsculptured. Temporal bones include several distinct types of jugal (e.g., Fig. 7A, B) and quadrate (Fig. 6C). Each of the jugal types lacks a full quadratojugal process, indicating that the lower temporal bar was incomplete in all three genera – a conclusion supported by the structure of isolated quadrates.

The first of the small diapsids is the rarest, has confluent nares, a posterolateral process on the premaxilla, and subthecodont teeth (Figs 4A, 5B), rounded in cross-section and with striae. The posterolateral process of the premaxilla could place it with archosauromorphs or with lepidosauromorph kuehneosaurs, while the confluent nares
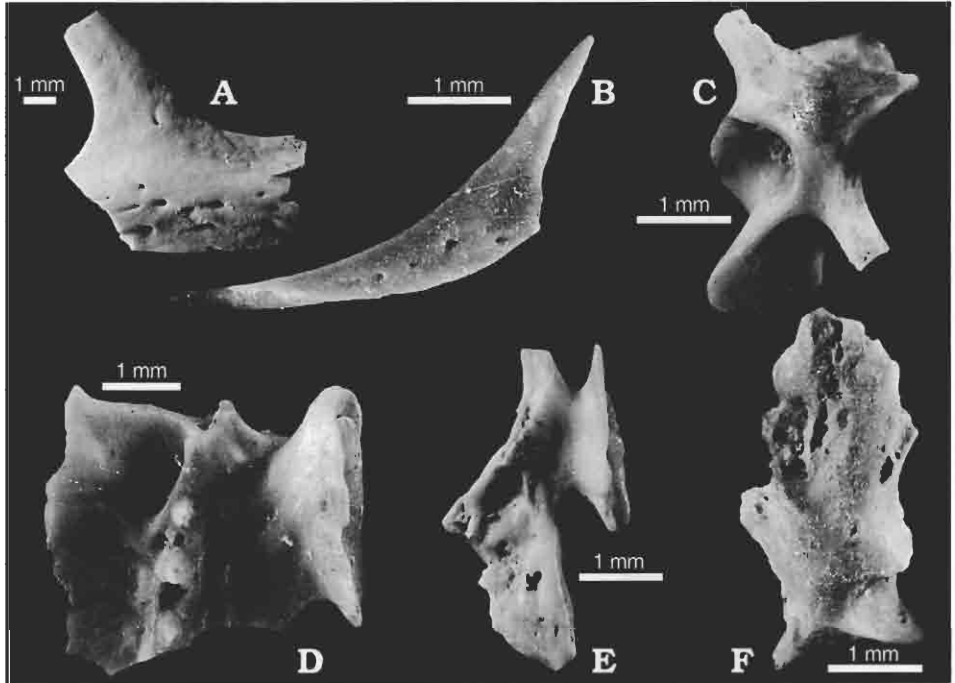
Fig. 7. Skull bones of reptiles from the Early Triassic of Czatkowice (Poland). **A**, **B**. Fragments of two types of jugal in lateral view: ZPAL R.V/9 – archosaur, right lateral view (**A**) and ZPAL R.V/10 – small lepidosauromorph type, left lateral view (**B**). **C**, **F**. Fragments of two types of pterygoid: ZPAL R.V/11 – procolophonid left basipterygoid region in palatal view (**C**) and ZPAL R.V/16 – small diapsid reptile type in palatal view (**F**). **D**, **E**. Two types of palatine in palatal view: ZPAL R.V/12 – small reptile left palatine, type 1 (**D**) and ZPAL R.V/15 – small reptile left palatine, type 2 (**E**).

more closely resemble the condition in the latter. Amongst the preserved parietals and postfrontals is a set which demonstrates the exclusion of the postfrontal from the margin of the upper temporal fenestra – a feature of prolacertiforms, kuehneosaurs and some other primitive small diapsids. However, the tooth replacement (small tooth erupting into an empty alveolus) is more like that of *Prolacerta* Parrington, 1935 than of *Kuehneosaurus* Robinson, 1962 (SE personal observations). This is supported by a number of elongated cervical vertebrae (Fig. 8A) with double-headed rib facets and long low neural spines. In general form, these cervicals match those of prolacertiforms described from Permian and Triassic deposits, and correspond in size to the jaw elements with subthecodont teeth. The small Czatkowice subthecodont diapsid is thus provisionally attributed to the Prolacertiformes.

By far the commonest of the non-archosaurian diapsids is a reptile whose jaw elements range in size from very small juveniles to adults which overlap the lower size range of the archosaur. The natural size range suggests the animal was a common component of the local fauna. It has weakly pleurodont teeth (under the definition that the labial wall is higher than the lingual wall as seen in lingual view – but not by much, Fig. 5A), which are normally striated but striae may be lost with age of wear. The main fea-
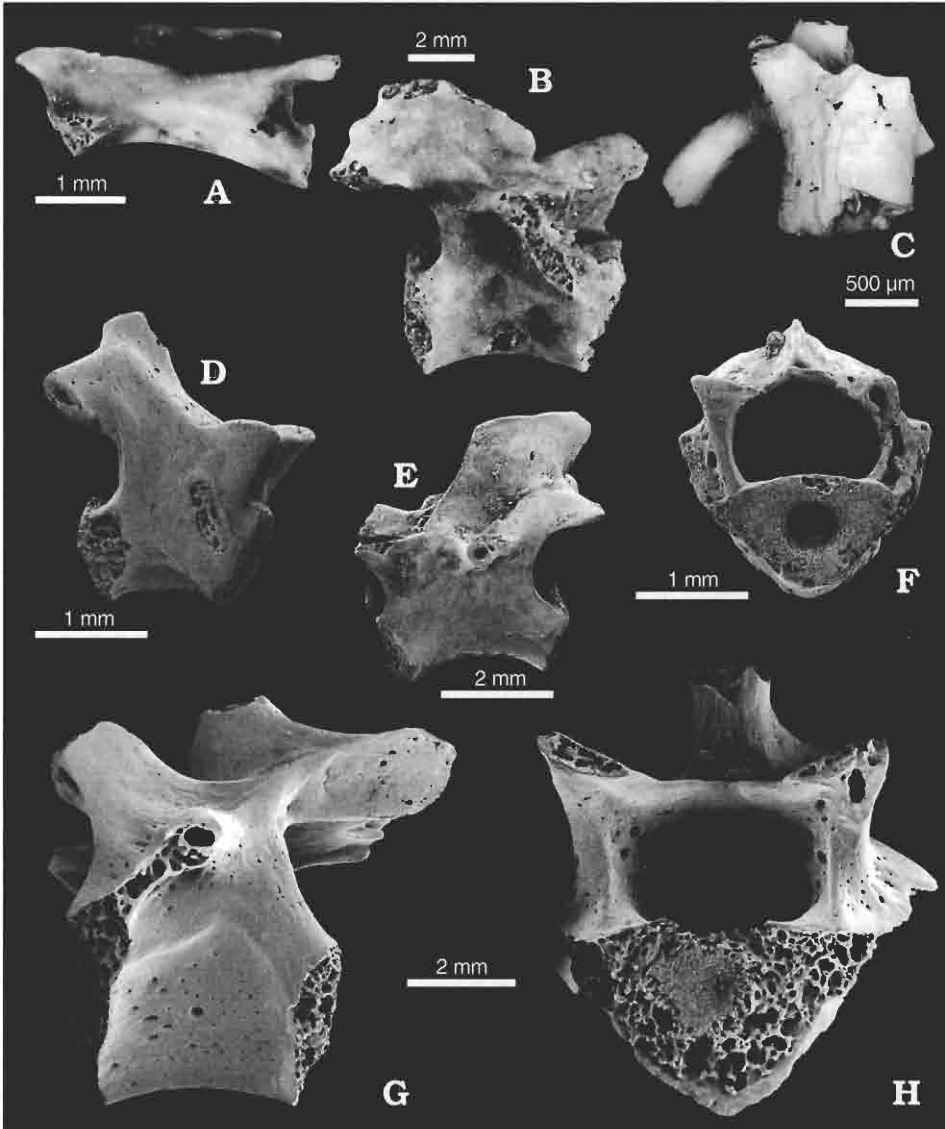
Fig. 8. Tetrapod vertebrae from the Early Triassic of Czatkowice (Poland). **A**. ZPAL R.V/21 – prola-certiform cervical vertebra in left lateral view. **B, D–H**. Dorsal vertebrae. **B**. ZPAL R.V/22 – pro-colophonian type in right lateral view. **D, F**. ZPAL R.V/23 – small lepidosauromorph type in left lateral view (**D**); the same in anterior view (**F**). **E**. ZPAL R.V/23 – common lepidosauromorph type in left lateral view. **G**. ZPAL R.V/24 – archosaurian type in left lateral view, **H** the same in anterior view. **C**. ZPAL Ab.IV/10 salientian *Czatkobatrachus polonicus* Evans & Borsuk-Białynicka, 1998, sacral vertebra in dorsal view.

ture is a short deep groove on the posterior aspect of the tooth (Fig. 4B). The maxilla has a long anterior maxillary process which underlay the nares and met one of a pair of premaxillae each carrying 4–5 teeth. Strong dorsal premaxillary processes met the nasals

and divided the nares. Several skull bones can be attributed to this form on the basis of relative abundance, and, more importantly, the range of size (but common morphology) from very small to relatively large. The animal has paired skull roofing bones, an incomplete lower temporal arcade, and an extensive palatal dentition. In the braincase, the metotic fissure was small and undivided and the basicranium has a basically primitive morphology although the dorsum sellae is sufficiently well developed to have abducens foramina (unlike Late Triassic *Kuehneosaurus* for example). A series of common vertebrae attributed to this form have a characteristic morphology. They are of rather similar length throughout the vertebral column with all vertebrae except sacrals bearing very thin dorsally placed transverse processes. Cervical vertebrae, identified by their ventral keels, have an additional rib facet placed at the extreme anteroventral margin of the centrum. This facet is not obvious in more posterior vertebrae and the parapophysis may have been on an intercentrum. A small number of two-headed (Y shaped) ribs probably belong to this form. The neurocentral sutures are closed in all except the very smallest specimens, and the sacral ribs are fused but the line of suture is still visible. This common form appears to be a primitive lepidosauromorph (tooth implantation, skull structure) but further work is needed to establish its phylogenetic position with more clarity. No known taxon is directly comparable.

The last of the small diapsids is represented only by very small specimens which appear to be adult. It is not the juvenile form of largest non-archosaurian diapsid described above because the teeth are more deeply pleurodont (Fig. 5C) and of a different form, and the anterior maxillary process is vertical, not horizontally oriented. The teeth are, at most, only weakly striated with delicate compressed tips and anterior and posterior keels (Fig. 4D). Typically there is a build up of bone of attachment around the tooth base. Amongst the smallest bones from Czatkowice 1 are short notochordal vertebrae without transverse processes and with single-headed rib facets (Fig. 8D, F), and small skull bones which show the presence of a quadrate conch, an incomplete lower temporal bar (jugal Fig. 7B), and a postfrontal which enters the margins of the upper temporal fenestra. These features suggest a derived lepidosauromorph close to the base of Lepidosauria. However, the apparent absence of both a thyroid fenestra in the pelvis and separate epiphyses on the limb bones preclude inclusion within the crown--group.

In addition to diapsid reptiles, the assemblage contains several types of procolophonids (Figs 5E, F, 7C) represented by jaw, palate and skull roof material, as well as rarer vertebrae (Fig. 8B). They are of small body size (perhaps juvenile) but show considerable variability in their dentition (in terms of tooth number, degree of heterodonty, degree of mesiodistal flattening, crown proportions).

With one rare exception, all the Czatkowice procolophonids have single-cusped teeth. In some taxa, this is probably a primitive character; in others it may simply be the juvenile state (Li 1983), and this complicates comparison and classification.

Of four dentary types, one resembles the genus *Burtensia* Ivakhnenko, 1975 from the Early Triassic (late Olenekian) of Russia in terms of tooth form and the number of incisiviform teeth; a second shows similarities with *Kapes* Ivakhnenko, 1975, in terms of the increase in size of the molariform teeth along the jaw and the presence of one tooth significantly larger than the others (Fig. 5F); while a third is of rather more primitive form in having little tooth differentiation along the jaw and shows a closer resem-

blance to the genus *Contritosaurus* Ivakhnenko, 1974 from the early Olenekian. A fourth type shows greatly enlarged molariform teeth which match no previous descriptions. In addition, one very fragmentary specimen has bicuspid teeth more like those of later (Middle–Late Triassic) procolophonids.

Comparison with contemporaneous assemblages

Early Triassic assemblages of the East European Platform

Currently, the best known and most complete profiles of Lower Triassic continental deposits are those of the East European Platform (Ochev & Shishkin 1989; Shishkin & Ochev 1993). The area in question (Fig. 1) extends from the Ural Mountains over the whole East European Platform in the broadest sense, including the southern marginal part of the southern Cis-Ural Trough. Two principal biostratigraphical complexes have been distinguished in the Lower Triassic faunal sequence on the basis of temnospondyl assemblages. These are (Table 1) the *Benthosuchus–Wetlugasaurus* (= neorhachitomous) and *Parotosuchus* faunistic complexes (Ochev & Shishkin 1989; Shishkin 1995). The former includes three subzones: *Tupilakosaurus*, Rybinskian (*Benthosuchus*), Sludkian (*Wetlugasaurus*). The *Parotosuchus* fauna of the Yarenskian is characterised by the appearance of the new trematosaurid families, the Trematosauridae (*Trematosaurus*) and Yarengidae (*Yarengia*).

By comparison with assemblages elsewhere, the *Tupilakosaurus* complex is estimated to be of Induan (= Griesbachian + Dienerian) age; the *Benthosuchus–Wetlugasaurus* complex of early Olenekian age; and the *Parotosuchus* faunal complex of late Olenekian (= Spathian) age. All of these assemblages include temnospondyls, procolophonids and primitive archosaurs. Other small diapsids are rarer. Interestingly, the therapsids, the dominant group in the Triassic of Gondwana, are practically absent from the East European Scythian, except perhaps for the earliest Induan (= Griesbachian) (for the discussion see Shishkin *et al.* 1995). The exceptions include one genus, *Scalopognathus*, from the early Olenekian and another, *Silphedosuchus*, from the late Olenekian when the potential for exchange between the Gondwanan and Laurasian parts of Pangea had been restored (Shishkin *et al.* 1995).

Spanning the time of the neorhachitomous and *Parotosuchus* faunas, the proterosuchian epoch (Induan plus Olenekian time, Ochev & Shishkin 1989) is marked by a dominance of primitive archosaurians. Sennikov (1995) has named numerous archosaurian genera of proterosuchid grade. According to this author, the genus *Chasmatosuchus* occurs from the Induan through the early Olenekian. In the Induan, it is accompanied by representatives of *Vonhuenia*, and in the Yarenskian by the poorly known genus *Gamosaurus*. According to Gower & Sennikov (1997), all these genera are of doubtful validity because of the extremely fragmentary nature of the material on which they are based. However, they suggest that proterosuchid grade archosaurs were present in the East European region from the Permian (*Archosaurus*, see Tatarinov 1960) until the Middle Triassic (*Sarmatosuchus*, see Gower & Sennikov 1997).

The Erythrosuchidae are another widely distributed primitive archosaurian group, but appear slightly later in the record and include large-sized taxa. In the East European Platform, they are represented in the late Olenekian by two species of *Garjainia*

and the poorly known *Jaikosuchus*. The more derived, globally distributed, Rauisuchidae (Sennikov 1995) are represented on the Russian Platform by *Tsylmosuchus*, known from the early to late Olenekian.

Two other groups of small diapsid reptiles, are poorly (Prolacertiformes) or questionably (Lepidosauromorpha) represented in the Triassic deposits of the East European Platform. In fact, only four genera have been named: *Microcnemus* (Huene 1940) a supposed prolacertiform represented by isolated fragments throughout the Induan and early Olenekian; *Boreopricea* (Tatarinov 1979; Benton & Allen 1997), a second prolacertiform represented by a partial skeleton of possible early Olenekian age; *Blomosaurus* (Tatarinov 1979), an isolated skull from the Induan (Shishkin *et al.* 1995) which has been tentatively referred to the Lepidosauromorpha; and *Scharschengia*, a possible rhynchocephalian known from fragmentary postcranial material throughout the Wetlugian (Shishkin *et al.* 1995).

Unlike small diapsids, procolophonids are relatively well-represented in the East European Scythian (Table 1).

According to Shishkin *et al.* (1995), the genera *Contritosaurus* and *Phantosaurus* (subfamily Spondylolestinae) are characteristic of the Induan (Vokhmian). A second subfamily, the Procolophoninae, appears in the early Olenekian (Novikov 1993b), with the genus *Tichvinskia*, which is then a consistent element of the Scythian fauna, typically present in the early Olenekian. In the Olenekian, *Tichvinskia* is accompanied by *Orenburgia*. Other genera have a more limited stratigraphic range, for example *Insulophon*, *Timanophon* and *Samaria* from the early Olenekian, *Vitalia* and *Burtensia* from the beginning of the late Olenekian, and *Kapes* and *Macrophon* from later horizons (Ivakhnenko *et al.* 1997).

Procolophonids have been widely used in biostratigraphic correlation in the Triassic (Shishkin *et al.* 1995). However, according to Ivakhnenko (1979), their value as biostratigraphic indicators is reduced by the fact that evolution of particular lineages proceeded in parallel at different rates. Nonetheless, they may have some value in the comparison of geographically adjacent regions.

Early Triassic assemblages of Laurasia beyond the East European Platform

Apart from the assemblages of the East European Platform, the principal Early Triassic faunas of Laurasia are those from the Torrey and Wutpaiki Formations of the Moenkopi Formation of Southwestern North America (Morales 1987); from the Germanic Basin, and from China (Lucas 1993; Li & Cheng 1995), although newer assemblages are emerging from other regions, e.g. Greenland (Clemmenson 1979). Of these, the Buntsandstein assemblages of the Germanic Basin are probably the most relevant to the current discussion since they extend into Poland.

The Buntsandstein of Middle Europe is a continental red bed sequence of alternating mudstones and sandstones deposited under mostly fluvial conditions, but with some aeolian imput (Mader 1984). The general environment is thought to have been arid to semi-arid, but with larger areas of standing freshwater towards the later parts of the series (Mader 1984). The Germanic Buntsandstein is divided into three parts – Lower (roughly equivalent to Induan), Middle (roughly Olenekian) and Upper (mostly Middle Triassic but its lowermost horizon may be latest Olenekian). The Buntsandstein fossil record is divided between a varied ichnofauna and much more limited

Table 1. Some elements of Early to Middle Triassic tetrapod faunas of Europe compared with those of Gondwana

BUNTSANDSTEIN				Early Anisian	Stages	STRATIGRAPHIC SUBDIVISIONS		
SCYTHIAN								
Induan	Early Olenekian		Late Olenekian	Röt				
Gries-bachian	Diener-ian	Smithian	Spathian					
Vokhmian	Rybin-skian	Sludkian	Fedorov-skian / Gamskian					
VETLUGIAN Neorhachitomous fauna			YARENSKIAN Parotosuchus fauna		Series			

East European Platform

TEMNOSPONDYLI
- Benthosuchus, Thoosuchus
- Tupilakosaurus
- *Angusaurus*
- Wetlugasaurus
- Luzocephalus
- trematosaurids, yarenskids
- capitosaurids
- Kapes

PROCOLOPHONIA
- Phantosaurus
- Contritosaurus
- Samaria, Timanophon, Lestanshoria, Insulophon, Tichvinskia, Orenburgia
- Burtensia, Tichvinskia, Vitalia
- Kapes, Orenburgia, Macrophon
- Kapes

ARCHOSAURIA
- PROTEROSUCHIAN EPOCH
- *Chasmatosuchus*
- Vonhuenia
- *Tsylmosuchus*
- Gamosaurus
- erythrosuchids
- Sarmatosuchus

Non-archosaurian diapsids
- Scharschengia
- Microcnemus
- Blomosaurus
- Boreopricea

THERAPSIDA
- Scalopognathus
- Lystrosaurus
- Silphedosuchus
- kannemeyerids

WESTERN EUROPE — TETRAPODA
- trematosaurids
- capitosaurids
- Basileosaurus
- Koiloskiosaurus
- Anomoiodon
- Trachelosaurus
- Ctenosauriscus
- Macrocnemus, Tanystropheus (Middle Cynognathus Zone)

GONDWANA — TETRAPODA
- Lystrosaurus Zone
- Rhinesuchidae
- Lydekkerinidae therapsids
- Proterosuchus
- Procolophon
- Paliguana
- Prolacerta
- Noteosuchus
- Kadimakara
- Triadobatrachus
- Lower Cynognathus Zone
- capitosaurids
- trematosaurids
- therapsids
- erythrosuchids
- procolophonids

Time Ma	248.2	244.8	243.0	241.7	249.0

body fossil assemblages. That of the Middle Buntsandstein includes a range of temnospondyl amphibians (Morales & Kamphausen 1984; Kamphausen & Keller 1986; Wagner 1925; Wepfer 1923) – the aberrant *Sclerothorax, Trematosaurus*, and the capitosauroids *Parotosuchus* and *Odenwaldia* (Parotosuchidae), *Meyerosuchus* (Stenotosauridae), and *Heptosaurus* (Mastodonsauridae), procolophonids (*Basileosaurus, Koiloskiosaurus* and *Anomoiodon*); *Sclerosaurus* (described by several authors, e.g., Krebs 1969, as a procolophonid, but Lee 1993 considers it to be a sister taxon of pareiasaurs + chelonians); the possible prolacertiform *Trachelosaurus* see Broili & Fischer 1916); and the abberant long-spined archosaur *Ctenosauriscus* (Krebs 1969). Krebs (1969) added the phytosaur '*Mesorhinus*' (= *Palaeorhinus*, see Hunt & Lucas 1991), but there are problems with the age of the original material since all other phytosaurs are of Late Triassic age (Hunt & Lucas 1996).

Overlying Upper Buntsandstein deposits also yield temnospondyls – further material of the mastodonsaurid *Heptosaurus*, the stenotosaurid *Stenotosaurus*, and the more derived heylerosaurid *Eocyclotosaurus* (Kamphausen 1989), as well as the procolophonid *Anomoiodon*, prolacertiforms *Macrocnemus* and *Tanystropheus*, the enigmatic *Eifelosaurus*, and laterally compressed recurved teeth attributable to archosaurs.

Early Triassic assemblages of Gondwana

The only other Early Triassic assemblages of comparable diversity are those of Gondwana – notably those of southern Africa (*Lystrosaurus* and *Cynognathus* zones), Antarctica (Lower Fremouw Formation), India (Panchet Formation) and Australia (Arcadia Formation). With respect to Czatkowice, the assemblages of South Africa and Australia are the most relevant (in containing small diapsids in addition to procolophonids and proterosuchid archosaurs). The early Olenekian horizon (Shevyrev 1990) in Madagascar which yielded the early salientian *Triadobatrachus* (Rage & Roček 1989) is also important.

In the southern African Karroo, the *Lystrosaurus* and *Cynognathus* zones are famous for their richness of vertebrate fossils, although – once again, the microvertebrate content is very poorly known. The Gondwanan *Lystrosaurus* fauna is thought to represent an Induan–early Olenekian time period (Shishkin *et al.* 1995). This is in contrast to the situation on the East European Platform where the *Lystrosaurus* fauna is thought to be indicative only of the Induan. Apart from its eponymous dicynodont and other synapsids (e.g. *Thrinaxodon*), the assemblage includes rhinesuchid and lydekkerinid temnospondyls, the procolophonid *Procolophon*, and several diapsids including a possible lepidosauromorph, *Paliguana*, and the archosauromorphs *Prolacerta* and *Proterosuchus*. The age of the *Cynognathus* zone has also been much debated. Shishkin (1995) recognizes three subzones, the lowermost of which is thought to be of late Early Triassic age (Spathian), and equivalent to the latest Olenekian of the East European Platform. Representatives of the trematosaurids (*Trematosuchus* of South Africa and *Trematosaurus* of the Germanic Basin) and capitosaurids (*Kestrosaurus* of South Africa and *Parotosuchus* of Russia), as well as of erythrosuchid archosaurians, indicate that the interconnection between both faunal realms (i.e. northern and southern), interrupted in the middle Scythian, had been reestablished.

The Early Triassic terrestrial/freshwater assemblages of Australia (Queensland, Western Australia; Perth Basin, Tasmania – Howie 1972; Thulborn 1983, 1984), are notable for their abundance of amphibians and their rarity of therapsids (Bartholomai & Howie 1970; Thulborn 1984). The Arcadia Formation of Queensland is the richest of all Australian Triassic tetrapod localities. It includes the only known scraps of therapsids as well as procolophonids, proterosuchians (*Kalisuchus*, Thulborn 1979), several small diapsids of which two, *Kadimakara*, a possible prolacertiform (Bartolomai 1979) and *Kudnu*, a proposed lepidosauromorph (Bartholomai 1979), have been named. A proterosuchid has also been recorded from the Knocklofty Formation of Tasmania, the only horizon to produce unquestionable lydekkerinid material.

The age of the Czatkowice assemblage

The geological evidence outlined in the opening sections provides a clear indication of an Early Triasic age for the Czatkowice assemblage, but cannot, as yet, provide a more precise dating. Biostratigraphic dating is widely applied in such situations, but must be used with caution. Independently dated deposits show that some lower vertebrate taxa have relatively long stratigraphic ranges and this reduces their usefulness in dating. The problem is compounded at Czatkowice by the absence of large temnospondyls and of therapsids.

The review of Early Triassic global fauna presented above shows that, despite obvious regional and facies differences in faunal composition, there is a broadly similar Early Triassic assemblage, dominated either by synapsids (e.g. in South Africa and Antarctica) or temnospondyls (e.g. in East European Platform and Australia), and including prolacertiforms, primitive (proterosuchid grade) archosaurs, and procolophonids with unicuspid teeth. Primitive lepidosauromorphs and protofrogs are very rare, but they too are found in deposits of this age. Thus, Czatkowice fits the general pattern.

The resemblance of two Czatkowice procolophonid genera to *Burtensia* and *Kapes* of the late Olenekian East European Platform, and the presence of a single fragment of a more derived bicuspid dentition, provide some support for a late Olenekian age of Czatkowice assemblage. The Czatkowice archosaur is much smaller than the taxa described from other localities and has a morphology (e.g., unrecessed antorbital fenestra, primitive braincase, simple ilium) suggestive of primitive proterosuchid or pre-proterosuchid grade. It resembles the Middle Buntsandstein *Ctenosauriscus* (Krebs 1969) in having short vertebral centra, but differs in the absence of the hypertrophied dorsal spines. The apparently downturned premaxilla is reminiscent of the condition in the South African *Proterosuchus*, but the two differ in the length of the neck vertebrae (short in the Czatkowice form, long in *Proterosuchus*). Short neck vertebrae are also present in the East European Platform proterosuchid *Sarmatosuchus* (Gower & Sennikov 1997), and this could be related to the Czatkowice archosaur, although not congeneric. *Sarmatosuchus* is roughly twice the size of Czatkowice animal and some individual elements (squamosals, braincase, scapula) show distinctive differences. A closer comparison will be needed when the Polish form is fully described. *Sarmatosuchus* comes from deposits dated as middle Triassic (Gower & Sennikov 1997), and thus could support a late rather than early Olenekian age for the Czatkowice form. Prolacertiforms are known from the

Late Permian to the Late Triassic, but the early record is very fragmentary. The most complete specimen is the partial skeleton of *Boreopricea* from the early Olenekian of the East European Platform (Tatarinov 1979; Benton & Allen 1997). Unfortunately, comparable parts of the skull of the Czatkowice prolacertiform (premaxilla, parietal) are not preserved in *Boreopricea*. The cervical vertebrae, however, differ significantly. Those of the Czatkowice form are proportionally much longer and lower than those of *Boreopricea*, and the two are clearly not congeneric. In fact, in their length and low neural spines, the cervicals of the Polish prolacertiform more closely resemble those of the Upper Buntsandstein *Tanystropheus*, although the Czatkowice animal is much smaller and the vertebral elongation is less extreme.

Thus the procolophonids support a late Olenekian age for the Czatkowice assemblage, and neither the archosaur nor the prolacertiform contradict it. The lepidosauromorphs and salientians are more problematic, since their Early Triassic record is poor. Cladistic analysis predicts that Lepidosauria *sensu stricto* had originated by at least the end of the Early Triassic but there are no unequivocal records. The status of *Scharschengia* and *Blomosaurus* are unresolved, while the South African *Paliguana* may be a lepidosauromorph but shows no conclusively lepidosaurian character states. The fragmentary *Kudnu* (Bartholomai 1979) from Australia needs reexamination, while the South African *Palacrodon* may be a procolophonid. The relatively derived condition of the small Czatkowice lepidosauromorph (close to the base of Lepidosauria) adds some support for a late rather than early Olenekian age, although at our present state of knowledge of the early history of this group, this is very speculative.

A Triassic salientian is known from only one locality other than Czatkowice, and that is in Madagascar. The deposits yielding the single specimen of *Triadobatrachus* were thought to be of Induan age (Rage & Roček 1989), but are now known to be equivalent to early Olenekian based on the presence of ammonites representative of the Flemingianus Zone (Shevyrev 1990). *Czatkobatrachus* (Evans & Borsuk-Białynicka 1998) resembles *Triadobatrachus* in its general level of organisation and in the form of its ilium and vertebrae, but differs (and is more derived) in the structure of the atlas, the humerus, and the transverse processes of the presacral vertebrae. A middle to late Olenekian age for the Czatkowice assemblage would again be consistent.

Conclusion

The new microvertebrate assemblage from Czatkowice 1 is broadly comparable to other Early Triassic assemblages around the world in its combination of procolophonids with unicuspid dentitions, prolacertiforms, primitive archosaurs and temnospondyls. It is rendered unique, however, by the small size of the individual taxa (thus providing a glimpse of another level of Early Triassic diversity), by the preservation of groups (lepidosauromorphs, lissamphibians) virtually unknown in other roughly contemporaneous horizons, and by abundance and exquisite three-dimensional preservation of its bones, despite the disarticulation and fragmentation. In association with the geological evidence (Mariusz Paszkowski, personal communication to MB-B and SE 1997), the presence of fish and amphibians suggests the primary deposition was in small shallow freshwater pool which formed an oasis in an otherwise rather arid Cen-

tral European Scythian environment, typical of the xeric circumequatorial belt of Northern Pangea (Otchev 1993; Shishkin & Otchev 1993). The absence of synapsids would be consistent with this xeric (in general) paleoenvironmental reconstruction.

Acknowledgements

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Zespół małych kręgowców z wczesnego triasu Polski

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Streszczenie

Praca obejmuje wstępne opracowanie zespołu małych kręgowców z wczesnotriasowych
utworów krasowych stanowiska Czatkowice k/Krakowa, z leja krasowego Czatkowice 1,
na tle porównywalnych zespołów faunistycznych z terenu Pangei. Na podstawie sytuacji
geologicznej Paszkowski i Wieczorek (1982) datują utwory Czatkowic 1 na scytyk.
Według tych autorów sedymentacja Czatkowic 1 mogła rozpocząć się w późnym permie,
lecz musiała zakończyć się z transgresją retu, która zalała ten rejon całkowicie.

Opracowany zespół kręgowcow obejmuje jeden rodzaj archozaura, przypuszczalnie
poziomu ewolucyjnego proterosuchidowego, dwa rodzaje Lepidosauromorpha, jeden
rodzaj Prolacertiformes, kilku przedstwicieli Procolophonia oraz wczesnego przed-
stawiciela Salientia, bliskiego płazom bezogonowym (*Czatkobatrachus polonicus* Evans
& Borsuk-Białynicka, 1998), a także niewielką domieszkę szczątków rybich. Zespół ten
potwierdza wczesnotriasowy wiek utworów, sugerując późną część tej epoki. Wskazuje
na to pewne podobieństwo niektórych przedstawicieli fauny Czatkowic do rodzajów
znanych z triasowych utworów wschodniej Europy. Obecne tu prokolofony wykazują
podobieństwo do rodzajów *Burtensia* i *Kapes* z późnego oleneku, zaś archozaur do
Ctenosauriscus ze środkowego pstrego piaskowca oraz do nieco młodszego, środkowo-
triasowego rodzaju *Sarmatosuchus*. Także przedstawiciel Prolacertiformes nawiązuje do
późnego oleneku przypominając wydłużeniem kręgów szyjnych rodzaj *Tanystropheus*
z górnego pstrego piaskowca Europy zachodniej, a *Czatkobatrachus* przypomina *Tria-
dobatrachus* z wczesnego oleneku (Shevyrev 1990) Madagaskaru, jest jednak bardziej
nowoczesny niż ten ostatni. Jednak wobec ubóstwa szczątków Lepidosauromorpha
i Salientia w utworach dolnego triasu odkrycie przedstawicieli tych grup w faunie
czatkowickiej ma przede wszystkim znaczenie filogenetyczne, ponieważ na wczesny
trias przypada najprawdopodobniej moment powstania linii ewolucyjnej płazów bez-
ogonowych (Anura), których dotychczasowa dokumentacja kopalna sięga tylko wczes-
nej jury, a także gadów łuskonośnych (Lepidosauria).

Opracowany zespół fauny występował w obrębie równoleżnikowego pasa klimatu
suchego, który we wczesnym triasie rozdzielał strefy Pangei o bardziej zróżnicowanym
klimacie, położone na północ i na południe od niego. Najbardziej typowe dla tego pasa są
utwory pstrego piaskowca Europy zachodniej i formacja Moenkopi Ameryki Pn. (m.in.
Shishkin & Ochev 1993). Zespół Czatkowic 1 musiał powstać w warunkach oazy,
w sąsiedztwie zbiornika słodkowodnego. Unikalność zespołu polega na selektywnym
zachowaniu kręgowców o bardzo małych rozmiarach, nadzwyczaj słabo poznanych
skądinąd. Brak dużych temnospondyli i gadów ssakokształtnych utrudnia porównania
z faunami równowiekowymi.