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ARTICLE

A NEW LATE TRIASSIC VERTEBRATE FAUNA FROM POLAND WITH TURTLES, AETOSAURS, AND COELOPHYSOID DINOSAURS

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ABSTRACT—We report a new site with an occurrence of isolated bones of a *Palaeochersis*-like turtle in Norian-Rhaetian fluvial sediments from southern Poland. The turtle remains are associated with bones of a medium-sized aetosaur, a coelophysoid dinosaur, and a larger carnivorous archosaur, as well as a hybodontid shark, ganoid and dipnoan fishes, and a large temnospondyl.

INTRODUCTION

The Keuper strata (upper Middle and Upper Triassic in age) of southwestern Poland have produced a wealth of vertebrate remains since 1990 (Dzik et al., 2000, 2008a, 2008b; Dzik, 2001; Dzik and Sulej, 2007; Sulej et al., 2011a, 2011b; Niedźwiedzki et al., 2012). The vertebrate assemblages have a typical European Late Triassic composition (with some exceptions, see below) that includes large temnospondyl amphibians, phytosaurs, aetosaurs, other crurotarsans, small diapsid and archosauromorph reptiles, and rare ornithodirans (see Dzik and Sulej, 2007). The most famous of these localities, Krasiejów in the Opole Voivodeship, yields the tetrapod taxa *Cyclotosaurus intermedius* Sulej and Majer, 2005, *Metoposaurus diagnosticus krasiejowensis* Sulej, 2002, *Stagonolepis olenkae* Sulej, 2010, *Polonosuchus silesiacus* (Sulej, 2005), *Paleorhinus* sp., and *Silesaurus opolensis* Dzik, 2003. The occurrence of two characteristic species of conchostracans (Olempska, 2004; Kozur and Weems, 2010), the phytosaur *Paleorhinus*, and the temnospondyl *Metoposaurus* indicate that the Krasiejów assemblage is middle–late Carnian in age (Dzik and Sulej, 2007).

In 2006, a spectacular new locality (Lipie Śląskie-Lisowice) with vertebrate remains was discovered in the Silesian Voivodeship (Dzik et al., 2008a, 2008b) that yields partially articulated skeletons and isolated bones of a dicynodont (height 1.75 m). The dicynodont bones are associated with bones of two species of carnivorous archosaurs, small archosauromorphs, and pterosaurs, as well as capitosaurian and plagiosaurian temnospondyls (Niedźwiedzki et al., 2012). Two years after this discovery, more sites were found in the Silesian Voivodeship area. First, a site of middle–late Carnian age was discovered at Woźniki clay-pit, approximately 60 km eastward from Lipie Śląskie-Lisowice (Sulej et al., 2011a). In another old clay-pit at Miedary near Tarnowskie Góry, a new horizon with Middle Triassic (Ladinian) vertebrates was also identified (Sulej et al., 2011b). Isolated bones of supposed dicynodonts were also recently found in Upper Triassic deposits (probably Norian in age) cropping out at Marciszów-Zawiercie (Budziszewska-Karwowska et al., 2010; Racki, 2010).

In this paper we briefly describe the vertebrate fauna from the Poręba site, the fifth new locality to be discovered in the Polish Keuper. The strata exposed at Poręba (region of Jura Krakowsko-Częstochowska) belong to the upper part of the Keuper profile, and are known in lithostratigraphic schemes as the Zbąszynek Beds, deposits with many 'bone-breccia' horizons. The Zbąszynek Beds are correlated with the Upper Keuper formations (Arnstadt Formation and lowermost Exter Formation) from the Germanic Basin (see Bachmann and Kozur, 2004; Franz et al., 2007a, 2007b). These strata contain bone-bearing yellowish carbonitic conglomerates and gray fluvial carbonitic mudstones and claystones, interbedded with horizontally stratified yellowish or reddish sandstones. The whole observed stratigraphic section in this locality is at least 6 m thick and is partially exposed in the northern part of Poręba city, near the old waste dump (Fig. 1), about 4 km from Zawiercie, southern Poland (Szulc et al., 2006). Well-preserved, often eroded or rounded vertebrate bones or fragments of bones occur mainly in yellowish carbonate conglomerates; sometimes the bones are covered with a calcareous crust, rather than a more typical pyritic crust. Isolated and well-preserved bones were also found in gray mudstones and claystones. The newly discovered vertebrate assemblage is dominated by bones of a turtle (mainly shell fragments) and a coelophysoid theropod dinosaur (vertebrae, part of pelvis, and long bones). Bones of a large carnivorous archosaur and osteoderms of aetosaurs are very rare at this locality. Other vertebrate remains, including dipnoan teeth, hybodont shark fin spines, and ganoid skull elements and scales, are also rare.

These strata also contain numerous well-preserved micro- and macrofloral remains. The dominant plant species at Poręba is a conifer similar to *Brachyphyllum* sp. Fragments of branches with leaves and numerous fragments of charcoalized wood trunks, sometimes of large size, also occur (Fig. 2A, B). Abundant pollen of cf. *Classopollis* sp., which occur at Poręba in the gray facies, has elsewhere been associated with plants from the Cheirolepidiaceae (Reymanówna, 1992). The probable ginkgoalean palynomorph *Monosulcites* sp., as well as probable ginkgoalean leaves with perpendicular veins, were found but are too poorly preserved for detailed taxonomic descriptions. The liverwort spore *Ricciisporites tuberculatus* Lundblad, 1954, is also present at Poręba. These palynomorph taxa are known only from other central European sites believed to correspond to the late Norian and Rhaetian stages (Orłowska-Zwolińska, 1983; Schultz and

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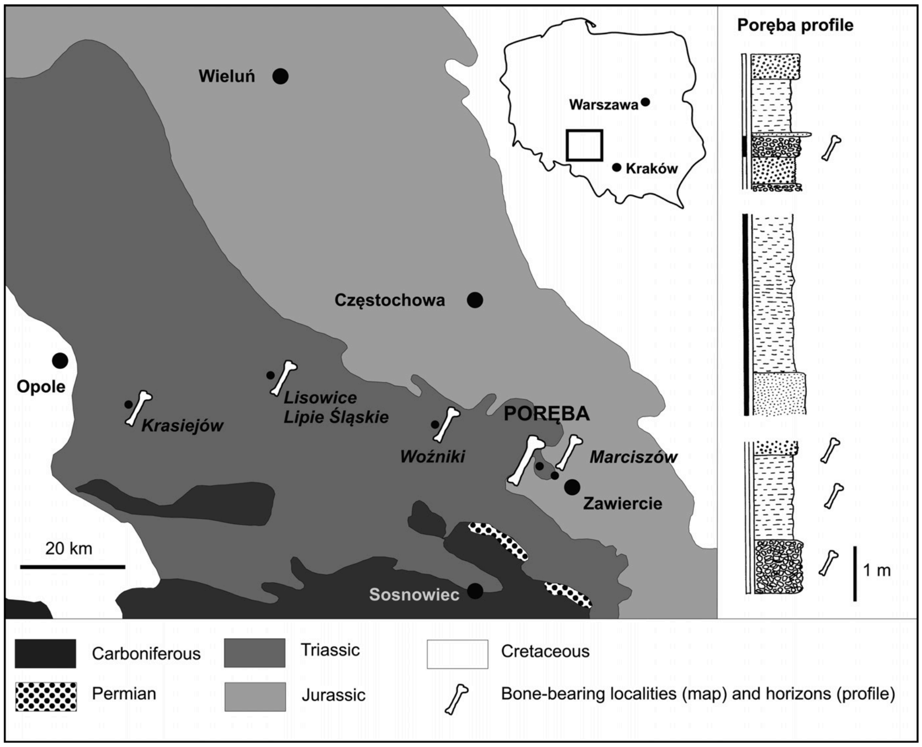

FIGURE 1. Location of the Poręba site in southern Poland (left) and geological profile visible in the artificial small outcrops (right).

Heunisch, 2005). Well-preserved bivalve shells similar to freshwater unionids from Marciszów (Skawina and Dzik, 2011) were also recovered. Unidentified temnospondyl amphibians are represented by two large teeth, whereas two dental plate fragments belong to dipnoan fishes.

Institutional Abbreviation—ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

SYSTEMATIC PALEONTOLOGY

ELASMOBRANCHII Bonaparte, 1838
HYBODONTOIDEA Owen, 1846
LONCHIDIIDAE Herman, 1977
cf. *LISSODUS* Brough, 1935
(Fig. 3)

Material—We collected multiple fragments of dorsal fin spines ranging from ca. 10 to ca. 58 mm in length, representing different sections of the spines (Fig. 3). Each fragment is mediolaterally compressed and displays an oval cross-section. The lateral surfaces of the specimens are ornamented with longitudinal ridges or costae that tend to split into additional ridges towards the base of the spines. The costae are more tightly packed close to the posterior edge of each spine and the spacing between them increases towards the anterior edge. Small parts of the base of the spine, visible only in two specimens, are clearly distinguished from the remaining parts and are ornamented with very fine ridges. The unornamented posterior edges of the specimens are convex and display triangular denticles arranged in tightly spaced, alternate rows. Judging from the aforementioned characters present in the specimens from Poręba (costate ornamentation, posterior edge convex with denticles arranged in two alternating rows, and an oval cross-section; see Maisey, 1978, 1987), it is inferred that the fin spines belong to hybodont sharks (similar but more complete fin spines have been collected from the Lipie Śląskie-Lisowice locality of similar age; see Dzik et al., 2008a). The pattern of longitudinal costae and grooves also imply that the specimens may belong to the genus *Lissodus* or *Lonchidion* (the genera *Lissodus* and *Lonchidion* are considered synonyms by some authors but most probably they represent separate, closely related taxa; see Rees and Underwood, 2002; Heckert, 2004). Unfortunately, the lack of the shark teeth from Poręba makes more precise identifications impossible.

REPTILIA Linnaeus, 1758
TESTUDINATA Klein, 1760 (sensu Joyce et al., 2004)
cf. *PROTEROCHERSIS* Fraas, 1913
(Fig. 4)

Material—The whole shell and numerous bones of various sizes, diagnostic of Testudinata, are dispersed within a single layer. These bones include fragments of the carapace, plastron, scapula, femur (Fig. 4D), and humerus (Fig. 4A). One specimen (ZPAL V. 39/34) is a near-complete shell (Fig. 4E) that is broken and slightly compacted. The excellent preservation makes the reconstruction of the whole shell possible (Fig. 4B, C). On the carapace, a median ridge is present that is not observed in any other Triassic turtle (Fraas, 1913; Gaffney, 1990; Sterli et al., 2007). Three pairs of supramarginal scales are present in the carapace, situated at the level of the bridge. On the plastron, between the pectoral and femoral scutes, there are two abdominal scutes. In both characters the new taxon is similar to *Proterochersis robusta* (according to Fraas, 1913; Gaffney, 1990:fig.105G; W. Joyce, pers. comm., November 2011) from Germany. The region of the pygal notch is a little broken, but it appears that the notch is not as large as in *Proterochersis robusta* (W. Joyce, pers. comm., November 2011). The plastron is very unique. The anterior tip is smooth and lacks any specific structures on the ventral side, in contrast to all other Triassic turtles with various horns in this part of the plastron (Fraas, 1913; Gaffney, 1990; Sterli et al., 2007). On the dorsal side, a pair of posterodorsally directed epiplastral

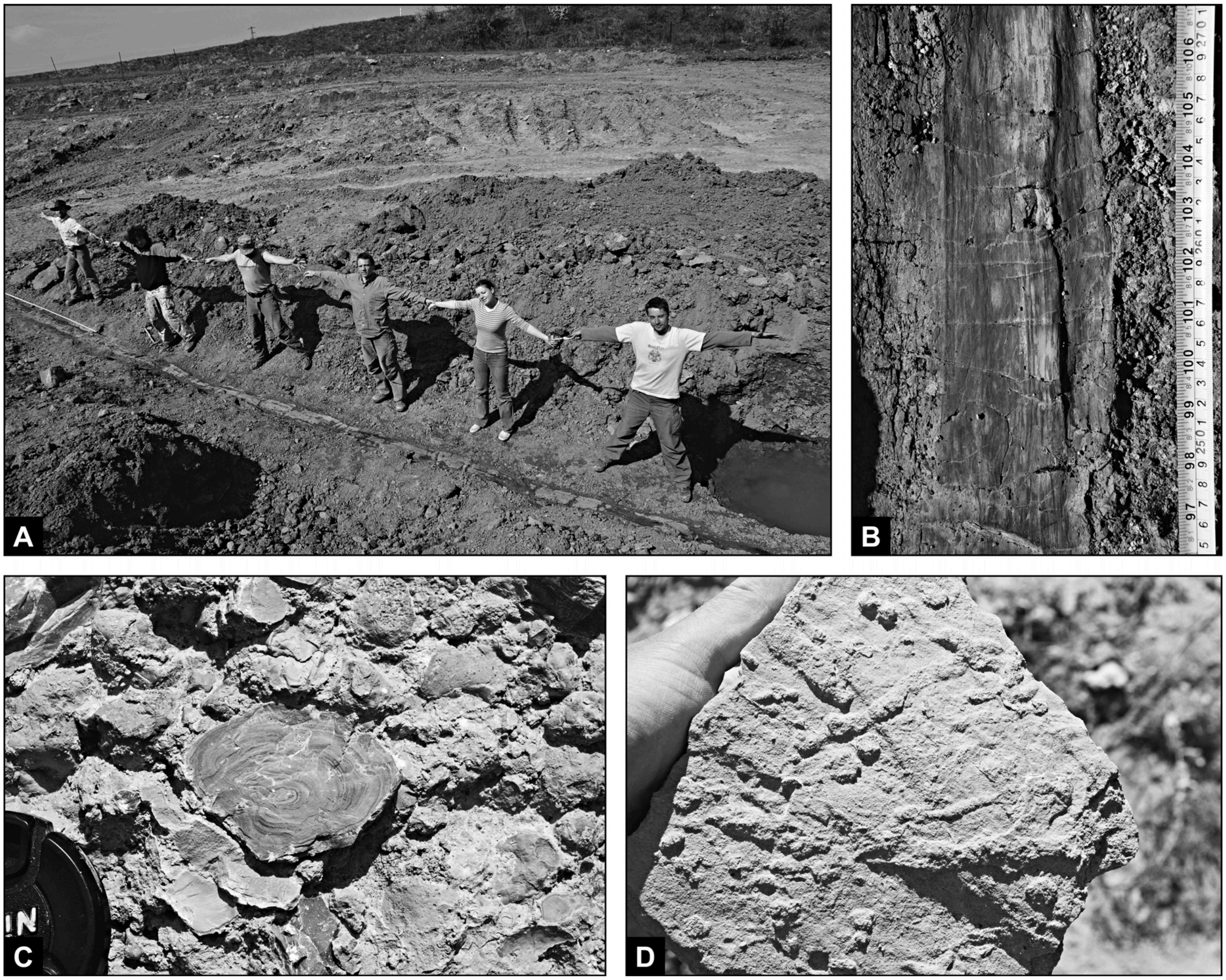

FIGURE 2. Plant, microbial, and invertebrate fossils from the Poręba site. **A** and **B**, large tree trunk, probably belonging to Coniferales; **C**, microbial concretion preserved in conglomerate; **D**, *Planolites* sp..isp., traces of worm-like animals.

processes are present that do not reach the carapace. Similar structures connected with the carapace were described by Gaffney (1990) for *Proganochelys quenstedti*. The limb bones of the turtle from Poręba are almost identical to those of *Proganochelys quenstedti* and *Palaeochersis talampayensis* (Gaffney, 1990; Sterli et al., 2007).

The study of the material is still preliminary but the structure of the shell indicates that this is a new taxon similar to *Proterochersis robusta*. The new material consists of multiple disarticulated remains (about 200 specimens) that were collected over the course of three field seasons. However, given that all fragments were collected from the same layer, consisting of about 20–45 cm of carbonate conglomerates with mudstone and sandstone intercalations, within less than 400 m^2, exhibit the same type of preservation, and are similar anatomically, all are confidently assigned to a single taxon in three different ontogenetic stages. The alternative would be the occurrence of two or three sympatric Triassic basal turtle species in a small, localized area that, in comparison with other localities from that time period and given the extreme scarcity of turtle material in those localities, seems unlikely. Historically, Triassic turtles were known only from Germany, but discoveries during the last 30 years have expanded their distribution to Thailand (de Broin et al., 1982), Greenland (Jenkins et al., 1994), Argentina (Rougier et al., 1995; Sterli et al., 2007), China (Li et al., 2008), and the U.S.A. (Joyce et al., 2009). The presence of a new testudinate from Central Europe adds further evidence that this group was at least moderately diverse and had a truly global distribution by the Late Triassic.

DINOSAURIA Owen, 1842
SAURISCHIA Seeley, 1887
THEROPODA Marsh, 1881
NEOTHEROPODA Bakker, 1986 (sensu Sereno, 1998)
COELOPHYSOIDEA Nopcsa, 1928 (sensu Sereno et al., 2005)
COELOPHYSOIDEA indet.
(Fig. 5)

Material—The central part of a pelvis (ZPAL V. 39/33), a partially preserved scapula (ZPAL V. 39/35), ungual phalanges from the pes (ZPAL V. 39/36), teeth (ZPAL V. 39/37), and caudal vertebrae with elongated centra (ZPAL V. 39/38) are also known from Poręba, and are similar in morphology to the Late Triassic *Liliensternus* (Huene, 1934; Cuny and Galton, 1993; Rauhut and Hungerbühler, 1998; Ezcurra and Cuny, 2007). The

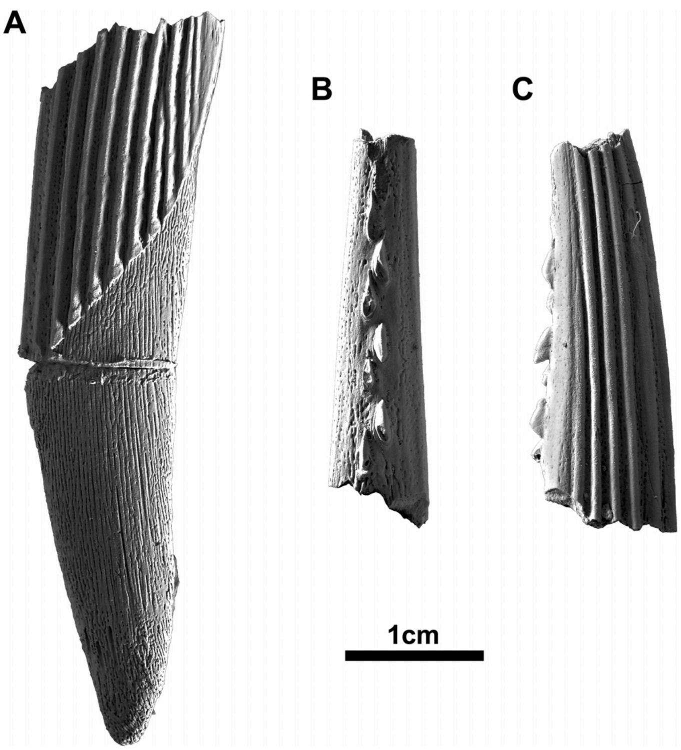

FIGURE 3. Chondrichthyan remains from the Poręba site, hybodont shark fin spine ZPAL V. 39/32. **A**, proximal part of spine; **B**, fragment of spine with denticles in posterior view; **C**, the same in lateral view.

coelophysoid neotheropods (e.g., *Coelophysis*, *Liliensternus*, and *Lophostropheus*, which may form either a clade or a grade of basal theropods; Nesbitt et al., 2009) were typical elements of the Norian and Rhaetian dinosaur communities of Europe (Rauhut and Hungerbühler, 1998; Ezcurra and Cuny, 2007; Brusatte et al., 2010). The earliest record of coelophysoid dinosaurs comes from early–middle Norian strata, as documented by the North American taxon *Camposaurus* (Hunt et al., 1998; Ezcurra and Brusatte, 2011; Irmis et al., 2011). During the Norian, a wide radiation of coelophysoid theropods is well documented around the world, with well-known taxa that include *Gojirasaurus*, *Zupaysaurus*, *Coelophysis*, *Liliensternus*, *Procompsognathus*, and *Lophostropheus* (Cuny and Galton, 1993; Rauhut and Hungerbühler, 1998; Ezcurra and Cuny, 2007; Nesbitt et al., 2007, 2009; Brusatte et al., 2010). The new material from Poręba is under study but preliminary results show that pelvis is very similar to that of *Liliensternus liliensterni* documented from only one site in the Germanic Basin. The supraacetabular crest is well developed above the entire length of the acetabulum of the new coelophysoid from Poland. In most neotheropods, this crest forms a rather continuous lamina with the lateral margin of the brevis shelf (Rauhut, 2003). In the ilium from Poręba, the supraacetabular crest is well separated from the lateral margin of the brevis shelf, a feature characteristic for basal Dinosauriformes (e.g., *Silesaurus*) and the earliest theropods (e.g., Herrerasauridae, *Guibasaurus*). A similar trait is present in *Liliensternus* (Ezcurra and Cuny, 2007) and this morphology differs from that of other coelophysoids (*Coelophysis*, *Lophostropheus*), where the supraacetabular crest is in contact with the lateral margin of the brevis fossa. The new find from Poland fills a geographical gap in the distribution of coelophysoid remains from the Upper Triassic of Europe.

ARCHOSAURIA Cope, 1869
AETOSAURIA Marsh, 1884

AETOSAURIA indet.
(Fig. 6)

Material—Until recently, aetosaurian remains from Poland were reported only from the Krasiejów locality (middle–late Carnian), consisting of numerous osteoderms and other bones representing the whole skeleton of a new species of *Stagonolepis* (Dzik and Sulej, 2007; Sulej, 2010). New finds of aetosaurs at Poręba are represented by skeletal elements collected during multiple excavations including one spine, a dorsal vertebra, and multiple fragments of osteoderms. The lateral plate ZPAL V. 39/30 (Fig. 6F, G) has a dorsal eminence that projects slightly beyond the posterior edge of the osteoderm. The dorsal surface possesses radiating sculpture consisting of pits and grooves. An anterior bar occurs on the dorsal surface. The lateral surface of the osteoderm is curved strongly ventrally, and its sculpture is formed by grooves. The ventral osteoderm ZPAL V. 39/41 (Fig. 6D) is flat and the whole ventral side is covered by sculpture consisting of pits in the center and short ridges in the marginal regions. The spike (or dorsal eminence, ZPAL V. 39/31) is an approximately 2 cm long projection that is subtriangular in lateral view (Fig. 6E). One side of the eminence (because of the lack of the rest of the plate and uncertainties as to the exact arrangement of the body armor of the taxon the spike belongs to, we do not use exact positional terms to describe the specimen) is inclined at an angle of ~45° and the opposite side is almost straight along its entire length. The dorsal eminence ends in a rounded, slightly bent, blunt tip. The surface of the spike is covered with small pits indicating the presence of a horny sheath during life. Around the base of the spike, remnants of the remaining parts of the osteoderm are present. The surface of the specimen in this region is sculpted with pits and anastomosing robust ridges indicating ornamentation on the dorsal aspect of the plate. Additional osteoderms from Poręba are too fragmentary to allow the reconstruction of the exact shape of each specimen and the whole carapace. Nevertheless, the dorsal

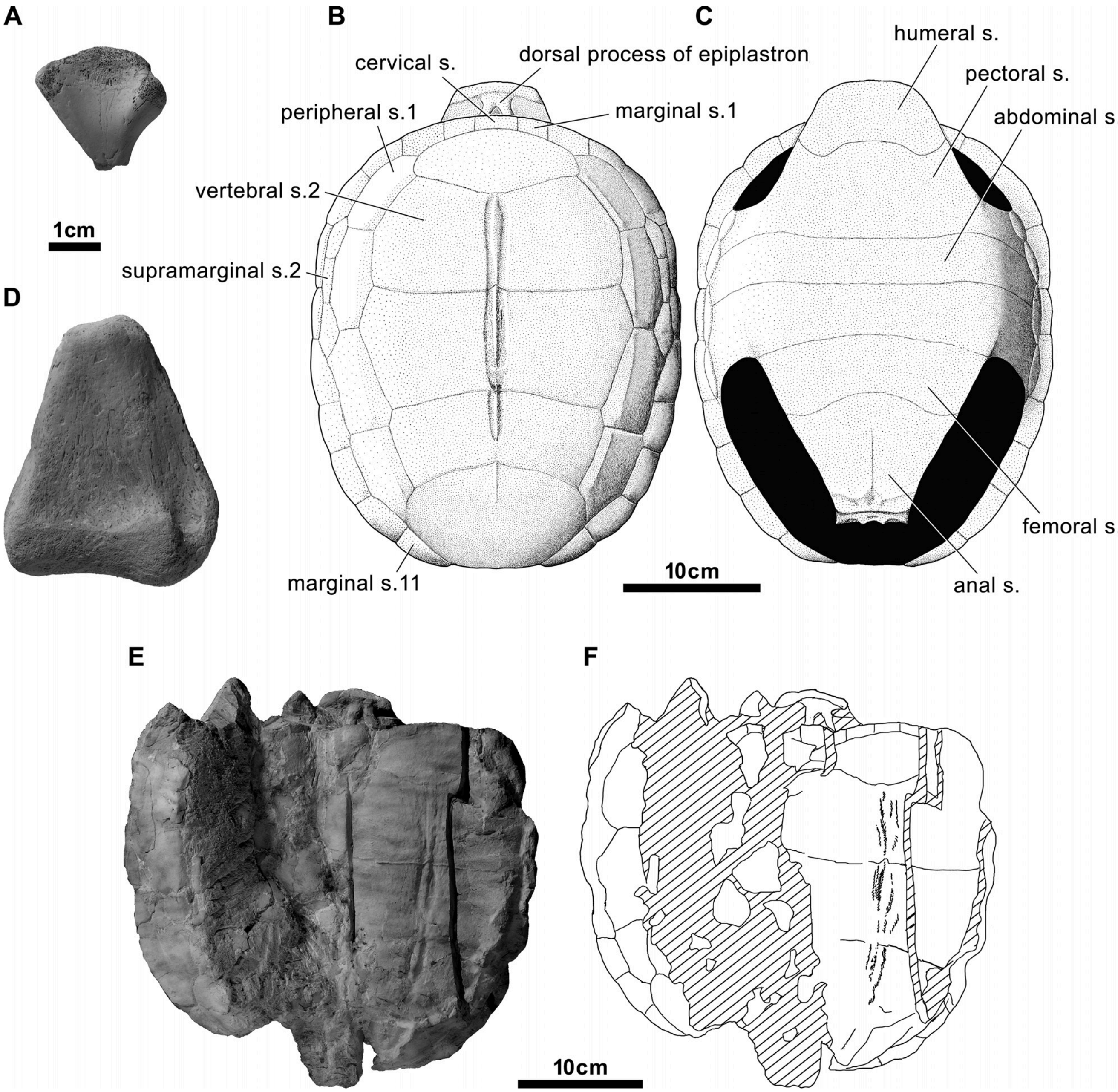

FIGURE 4. The new turtle from Poręba. **A**, proximal head of humerus ZPAL V. 39/25 in posterior view; **B**, reconstruction of the shell in dorsal view; **C**, reconstruction of the shell in ventral view; **D**, distal end of femur ZPAL V. 39/26 in posterior view; **E**, reconstruction of the shell in ventral view; **F**, explanatory drawing of the shell ZPAL V. 39/34 in dorsal view.

ornamentation formed of anastomosing robust ridges clearly indicates their aetosaurian affinities (Long and Ballew, 1985; Long and Murry, 1995; Parker, 2007).

The axial skeleton is represented by a single dorsal vertebra ZPAL V. 39/29 (Fig. 6C). No suture is visible between the centrum and neural arch, indicating an adult or subadult age for the specimen. The anterior articular surface of the centrum is broken. The posterior surface is gently concave and has a clearly marked, beveled edge. Judging from the overall shape of the specimen, the centrum was constricted at mid-length, anteroposteriorly short, dorsoventrally compressed, and wider than tall. On the dorsal surface of the centrum, between the neural arch, there is a deep groove forming the ventral part of the neural canal (which is taller than wide). The neural arch is not complete and lacks the lateral parts of the transverse processes, especially on the left side, and probably half of the spine. Thin laminae running from the bases of the postzygapophyses to the bases of the transverse processes are visible, similar to those described for other aetosaurs (Walker, 1961; Parker, 2008). The postzygapophyses have their posterior edges straight in lateral (elongated into a hyposphene) and dorsal views, similar to those described for *Desmatosuchus spurensis* (Parker, 2008). Although the anterior edge of the prezygapophyses is a little broken, its shape suggests that their anterior edges were straight and perpendicular to the long axis of the

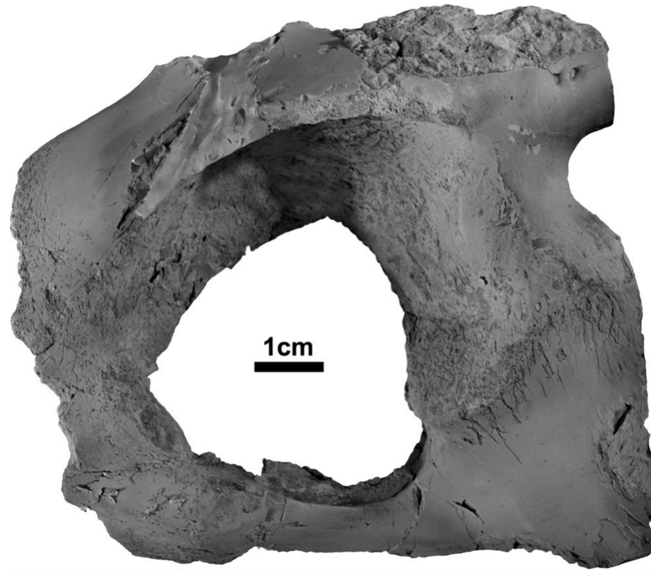

FIGURE 5. Partial coelophysoid dinosaur pelvis ZPAL V. 39/33 in lateral view (anterior on the left).

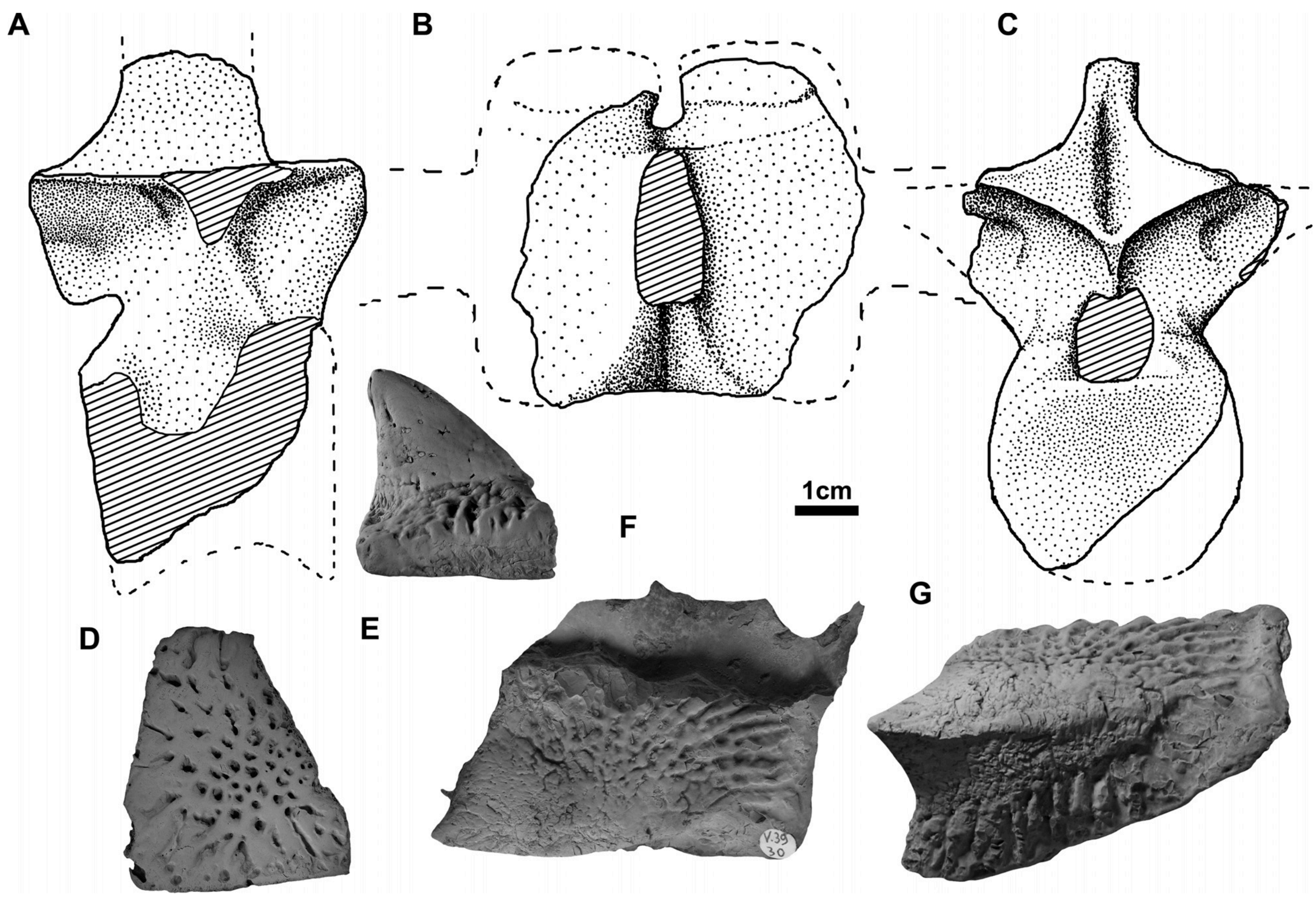

FIGURE 6. Aetosaur vertebra and osteoderms from Poręba. **A**, dorsal vertebra ZPAL V. 39/29 in right lateral view; **B**, the same in dorsal view; **C**, the same in posterior view; **D**, ventral osteoderm ZPAL V. 39/41; **E**, osteoderm spike ZPAL V. 39/31; **F**, paramedial osteoderm with spine ZPAL V. 39/30 in dorsal view; **G**, the same in lateral view.

vertebrae in dorsal view. The combination of the above-described characters indicates that this vertebra is from the dorsal region, most probably from a position anterior to the seventh dorsal (Walker, 1961; Desojo and Báez, 2005; Parker, 2008).

DIAPSIDA Osborn, 1903
ARCHOSAUROMORPHA Huene, 1946
ARCHOSAURIA Cope, 1869
ARCHOSAURIA indet.

Material—Two teeth (ZPAL V. 39/39 and ZPAL V. 39/40) from a large predatory archosaur (larger and more robust than any known coelophysoid from Europe and probably similar in size to *Gojirasaurus*, a large coelophysoid from the Upper Triassic of New Mexico; Carpenter, 1997; Nesbitt et al., 2007) and a fragment of a femoral shaft with a large marrow cavity were found. The tooth size and morphology (with characteristic serrations and enamel wrinkles on the external crown surfaces), the size of the femoral shaft fragment, and also the microstructure of this bone are similar to those of ZPAL V. 33/50, V. 33/51, and V. 33/52 from Lipie Śląskie-Lisowice (Niedźwiedzki et al., 2012). The remains from these two localities probably belong to the same, or very closely related, taxon of large carnivorous archosaur from the late Norian–early Rhaetian (Dzik et al., 2008a; Niedźwiedzki et al., 2012).

DISCUSSION

In both Poręba, described herein, and Lisowice, described previously by Dzik et al. (2008a, 2008b), the fin spines of hybodont sharks and the teeth of dipnoan fishes co-occur with the remains of two archosaurs, one small and the other much larger. The differences between these localities include the absence of dicynodonts and the presence of aetosaurs and turtles in Poręba, in contrast to the Lisowice locality that has yielded dicynodonts, but not aetosaurs or turtles (Dzik et al., 2008a, 2008b). This difference might be environmental, or could result from taphonomic bias or incomplete sampling. In Lisowice, the mudstones and sandstones suggest a low-energy river, which was an environment favorable for large dicynodonts (Dzik et al., 2008a; Sulej et al., 2011a). Instead, the presence of conglomerates in Poręba indicates deposition in a high-energy fluvial system (although there is no evidence that this was the environment of the turtles, they could have been transported from a different area). The oldest known turtles in the fossil record inhabited marginal areas of the sea or river deltas (Li et al., 2008).

The new turtle material from Poręba is still being collected, but what is currently available is representative enough to demonstrate the presence of a new taxon of Triassic European turtle, the third one discovered to date. This indicates that turtles were already diverse in the Late Triassic, and probably originated prior to the Carnian. The origin of turtles is still being debated (molecular data: Lee, 2001; Lyson et al., in press; paleontological data: Gaffney et al., 1987; Rieppel, 2000; Joyce, 2007; Li et al., 2008; Lyson et al., 2010) and questions regarding the early evolution of the shell remain unresolved. The material from Poręba, although still very fragmentary, consists of the fragments of shells of early and late ontogenetic stages. After collecting more material, the study of ontogeny of the 'first turtles' may therefore be possible. According to Joyce and Gauthier (2004), Scheyer and Sander (2007), Lyson et al. (2010), and Benson et al. (2011), both *Proganochelys quenstedti* and *Palaeochersis talampayensis* were definitely not marine, but it is not possible to determine out if they were lentic, lotic, or terrestrial. Because of the similarity between the limb bones from the Poręba turtle and *Proganochelys* and *Palaeochersis*, the same is probably true of this new taxon.

The aetosaur material extends the occurrence of medium-sized representatives (length of 2–4 m) of this group in Europe up to the upper Norian–Rhaetian. Osteoderms of a very small aetosaur from Trossingen (upper Norian) were mentioned by Seegis (2005) and their identity confirmed by Matzke and Maisch (2011). The whole undescribed skeleton of a paratypothoracisin aetosaur was found in Stubensandstein (Norian) sediments in Germany and is currently being studied in Stuttgart (R. Schoch, pers. comm.). Our new finds, and the new German paratypothoracicin, may clarify similarities and differences between these European aetosaurs and those of North America. In Western European faunas of similar age, namely those of Trossingen (Germany; Seegis, 2005) and Greenland (Jenkins et al., 1994), turtles, aetosaurs, and coelophysoids co-occur with *Plateosaurus*-like basal sauropodomorphs ('prosauropods'), in contrast to the Poręba assemblage. The Poręba assemblage also differs from that from Trossingen (Sander, 1992; Seegis, 2005) in the lack of phytosaurs.

CONCLUSIONS

The new locality in Poręba yields three very rare Late Triassic European vertebrates. The turtle probably represents a new taxon similar to *Proterochersis robusta* and is sufficiently distinct to indicate the presence of a third species of turtle in Europe. The new material of the coelophysoid dinosaur expands the range of this group in the Germanic Basin. The aetosaur material broadens the occurrence of forms with spines on the osteoderms, which are very rare in the latest Triassic record. Poręba is the second site from south Poland with terrestrial vertebrates where aetosaurs occur but bones of dicynodonts are lacking. This discrepancy suggests potentially large environmental differences between these localities, but an exact understanding of this disparity demands more study.

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LITERATURE CITED

Bachmann, G. H., and H. W. Kozur. 2004. The Germanic Triassic: correlations with the international scale, numerical ages and Milankovitch cyclicity. Hallesches Jahrbuch für Geowissenschaften B 26:17–62.

Bakker, R. T. 1986. The Dinosaur Heresies: New Theories Unlocking the Dinosaurs and Their Extinction. William Morrow and Company, New York, 481 pp.

Benson, R. B. J., G. Domokos, P. L. Várkonyi, and R. R. Reisz. 2011. Shell geometry and habitat determination in extinct and extant turtles (Reptilia: Testudinata). Paleobiology 37:547–562.

Bonaparte, C. L. 1838. Synopsis vertebratorum systematis. Nuovi Annali delle Science Naturali (Bologna), Series 1 2:10–133.

de Broin, F., R. Ingavat, J. Janvier, and N. Sattayarak, 1982. Triassic turtle remains from northeastern Thailand. Journal of Vertebrate Paleontology 2:41–46.

Brough, J. 1935. On the structure and relationships of the hybodont sharks. Memoirs and Proceedings of the Manchester Literary and Philosophical Society 79:35–50.

Brusatte, S. L., S. J. Nesbitt, R. B. Irmis, R. J. Butler, M. J. Benton, and M. A. Norell. 2010. The origin and early radiation of dinosaurs. Earth Science Reviews 101:68–100.

Budziszewska-Karwowska, E., A. Bujok, and G. Sadlok. 2010. Bite marks on an Upper Triassic dicynodontid tibia from Zawiercie, Kraków-Częstochowa Upland, southern Poland. Palaios 25: 415–421.

Carpenter, K. 1997. A giant coelophysoid (Ceratosauria) theropod from the Upper Triassic of New Mexico. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 205:189–208.

Cope, E. D. 1869. Synopsis of the extinct Batrachia, Reptilia and Aves of North America. Transactions of the American Philosophical Society, New Series 14:1–252.

Cuny, G., and P. M. Galton. 1993. Revision of the Airel theropod dinosaur from the Triassic-Jurassic boundary (Normany, France). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 187:261–288.

Desojo, J. B., and A. M. Báez. 2005. The postcranial skeleton of *Neoaetosauroides* (Archosauria: Aetosauria) from the Upper Triassic of west-central Argentina. Ameghiniana 41:115–126.

Dzik, J. 2001. A new *Paleorhinus* fauna in the early Late Triassic of Poland. Journal of Vertebrate Paleontology 21:625–627.

Dzik, J. 2003. A beaked herbivorous archosaur with dinosaur affinities from the early Late Triassic of Poland. Journal of Vertebrate Paleontology 23:556–574.

Dzik, J., and T. Sulej. 2007. A review of the early Late Triassic biota from Silesia, Poland. Palaentologia Polonica 64:3–27.

Dzik, J., G. Niedźwiedzki and T. Sulej. 2008b. Zaskakujące uwieńczenie ery gadów ssakokształtnych. Ewolucja 3:2–21.

Dzik, J., T. Sulej, and G. Niedźwiedzki. 2008a. A dicynodont-theropod association in the latest Triassic of Poland. Acta Palaeontologica Polonica 53:733–738.

Dzik, J., T. Sulej, A. Kaim, and R. Niedźwiedzki. 2000. Późnotriasowe cmentarzysko kręgowców lądowych w Krasiejowie na Śląsku Opolskim. Przegląd Geologiczny 48:226–235.

Ezcurra, M. D., and S. L. Brusatte. 2011. Taxonomic and phylogenetic reassessment of the early neotheropod dinosaur *Camposaurus arizonensis* from the Late Triassic of North America. Palaeontology 54:763–772.

Ezcurra, M. D., and G. Cuny. 2007. The coelophysoid *Lophostropheus airelensis*, gen. nov.: a review of the systematics of "*Liliensternus*" *airelensis* from the Triassic-Jurassic boundary outcrops of Normandy (France). Journal of Vertebrate Paleontology 27:73–86.

Fraas,E. 1913. Proterochersis, eine pleurodire Schildkröte aus dem Keuper. Jahreshefte des Vereins für Vaterländische Naturkunde in Württemberg 69:13–90.

Franz, M., G. H. Bachmann, and G. Beutler. 2007a. Retyk *sensu polonico* versus Rhaet *sensu germanico*—new results. Schriftenreihe der Deutschen Gesellschaft für Geowissenschaften 53: 99–100.

Franz, M., G. H. Bachmann, and G. Beutler. 2007b. Sedimentology and facies of the Polish Retyk and the German Arnstadt and Exter Formations (Norian, Rhaetian) in the eastern Central European Basin (CEB). Schriftenreihe der Deutschen Gesellschaft für Geowissenschaften 53:101.

Gaffney, E. S. 1990. The comparative osteology of the Triassic turtle *Proganochelys*. Bulletin of the American Museum of Natural History. 194:1–163.

Gaffney, E., H. Hutchinson, F. Jenkins, and L. Meeker. 1987. Modern turtle origins; the oldest known cryptodire. Science 237:289–291.

Heckert, A. B. 2004. Late Triassic microvertebrates from the Lower Chinle Group (Otischalkian-Adamanian: Carnian), southwestern U.S.A. New Mexico Museum of Natural History and Science Bulletin 27:1–170.

Heckert, A. B., S. G. Lucas, L. F. Rinehart, M. D. Celeskey, J. A. Spielmann, and A. P. Hunt. 2010. Articulated skeletons of the aetosaur *Typothorax coccinarum* Cope (Archosauria: Stagonolepididae) from the Upper Triassic Bull Canyon Formation (Revueltian: Early-Mid Norian), Eastern New Mexico, USA. Journal of Vertebrate Paleontology 30:619–642.

Herman, J. 1977. Les Sélaciens des terrains néocrétacés & paléocènes de Belgique & des contreés limitrophes. Eléments d'une biostratigraphie intercontinentale. Mémoires pour servir à l'explication de Cartes Géologiques et Minières de la Belgique. Service Géologique de Belgique 15:1–401.

Huene, F. von. 1934. Ein neuer Coelurosaurier in der thüringischen Trias. Palaeontologische Zeitschrift 16:145–170.

Huene, F. von. 1946. Die grossen Stamme der Tetrapoden in den geologischen Zeiten. Biologisches Zentralblatt 65:266–275.

Hunt, A. P., A. B. Heckert, R. M. Sullivan, and M. G. Lockley. 1998. Late Triassic dinosaurs from the western United States. Geobios 31:511–531.

Irmis, R. B., R. Mundil, J. W. Martz, and W. G. Parker. 2011. High-resolution U-Pb ages from the Upper Triassic Chinle Formation (New Mexico, USA) support a diachronous rise of dinosaurs. Earth and Planetary Science Letters 309:258–267.

Jenkins, F. A., Jr., N. H. Shubin, W. W. Amaral, S. M. Gatesy, C. R. Schaff, L. B. Clemmensen, W. R. Downs, A. R. Davidson, N. Bonde, and F. F. Osbaeck. 1994. Late Triassic continental vertebrates and depositional environments of the Fleming Fjord Formation, Jameson Land, East Greenland. Meddelelser om Grønland, Geoscience 32:1–25.

Joyce, W. G. 2007. Phylogenetic relationships of Mesozoic turtles. Bulletin of the Peabody Museum of Natural History 48:3–102.

Joyce,W. G., and J.Gauthier. 2004. Paleoecology of Triassic stem turtles sheds new light on turtle origins. Transactions of Royal Society of London B 271:1–5.

Joyce, W. G., J. F. Parham, and J. A. Gauthier. 2004. Developing a protocol for the conversion of rank-based taxon names to phylogenetically defined clade names, as exemplified by turtles. Journal of Paleontology 78:989–1013.

Joyce, W. G., S. G. Lucas, T. M. Scheyer, A. B. Heckert, and A. P. Hunt. 2009. A thin-shelled reptile from the Late Triassic of North America and the origin of the turtle shell. Proceedings of the Royal Society of London B 276:507–513.

Klein, I. T. 1760. Klassification und kurze Geschichte der vierfüßigen Thiere. Jonas Schmidt, Lübeck, Germany, 381 pp.

Kozur, H. W., and R. E. Weems. 2010. The biostratigraphic importance of conchostracans in the continental Triassic of the northern hemisphere; pp. 315–417 in S. G. Lucas (ed.), The Triassic Timescale. Special Publication of the Geological Society of London 334.

Lee, M. S. Y. 2001. Molecules, morphology, and the monophyly of diapsid reptiles. Contributions to Zoology 70:121–138.

Li, C., X.-C. Wu, O. C. Rieppel, L.-T. Wang, and L.-J. Zhao. 2008. An ancestral turtle from the Late Triassic of southwestern China. Nature 456:497–501.

Linnaeus, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Volume 1. Laurentii Salvii, Holmiae, 828 pp.

Long, R. A., and K. L. Ballew. 1985. Aetosaur dermal armour from the southwestern of North America, with special reference to material from the Chinle Formation of Petrified Forest National Park. Museum of Northern Arizona Bulletin 47:45–68.

Long, R. A., and P. A. Murry. 1995. Late Triassic (Carnian and Norian) tetrapods from the southwestern United States. New Mexico Museum of Natural History and Science, Bulletin 4:1–254.

Lundblad, B. 1954. Contributions to the geological history of the Hepaticae. Fossil Marchantiales from the Rhaetic-Liassic coalmines of Skromberga (prov. of Scania), Sweden. Svensk Botanisk Tidskrift 48:381–417.

Lyson, T. R., G. S. Bever, B. A. Bhullar, W. G. Joyce, and J. A. Gauthier. 2010. Transitional fossils and the origin of turtles. Biology Letters 6:830–833.

Lyson, T. R., E. A. Sperling, A. M. Heimberg, J. A. Gauthier, B. L. King, and K. J. Peterson. In press. MicroRNAs support a turtle + lizard clade. Biology Letters. doi: 10.1098/rsbl.2011.0477.

Maisey, J. G. 1978. Growth and form of finspines in hybodont sharks. Palaeontology 21:657–666.

Maisey, J. G. 1987. Cranial anatomy of the Lower Jurassic shark *Hybodus reticulates* (Chondrichtyes: Elasmobranchii), with comments on hybodontid systematics. American Museum Novitates 2878:1–39.

Marsh, O. C. 1881. Classification of the Dinosauria. American Journal of Science, Series 3 23:81–86.

Marsh, O. C. 1884. The classification and affinities of dinosaurian reptiles. Nature 31:68–69.

Matzke, A. T., and M. W. Maisch. 2011. The first aetosaurid archosaur from the Trossingen *Plateosaurus* Quarry (Upper Triassic, Germany). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 262:354–357. doi: 10.1127/0077–7749/2011/0203.

Nesbitt, S. J., R. B. Irmis, and W. Parker. 2007. A critical re-evaluation of the Late Triassic dinosaur taxa of North America. Journal of Systematic Palaeontology 5:209–243.

Nesbitt, S. J., N. D. Smith, R. B. Irmis, A. H. Turner, A. Downs, and M. A. Norell. 2009. A complete skeleton of a Late Triassic saurischian and the early evolution of dinosaurs. Science 326:1530–1533.

Niedźwiedzki, G., T. Sulej, and J. Dzik. 2012. A large predatory archosaur from the Late Triassic of Poland. Acta Palaeontologica Polonica 57:267–276.

Nopcsa, F. 1928. The genera of reptiles. Palaeobiologica 1:163–188.

Olempska,E. 2004. Late Triassic spinicaudatan crustaceans from southwestern Poland. Acta Palaeontologica Polonica 49:429–442.

Orłowska-Zwolińska, T. 1983. Palinostratygrafia epikontynentalnych osadów wyższego triasu w Polsce. Prace Instytutu Geologicznego 104:1–88.

Osborn, H. F. 1903. On the primary division of the Reptilia into two subclasses, Synapsida and Diapsida. Science 17:275–276.

Owen, R. 1842. Report on British fossil reptiles. Part II. Reports of the British Association for the Advancement of Science 1841:60–294.

Owen, R. 1846. Lectures on the Comparative Anatomy and Physiology of the Vertebrate Animals, Delivered at the Royal College of Surgeons of England in 1844 and 1846. Part 1. Fishes. Longman, London, 308 pp.

Parker, W. G. 2007. Reassessment of the aetosaur '*Desmatosuchus*' *chamaensis* with a reanalysis of the phylogeny of the Aetosauria (Archosauria: Pseudosuchia). Journal of Systematic Palaeontology 5:41–68.

Parker, W. G. 2008. Description of new material of aetosaur *Desmatosuchus spurensis* (Archosauria: Suchia) from the Chinle Formation of Arizona and a revision of the genus *Desmatosuchus*. PaleoBios 28:1–40.

Parker, W. G., and J. W. Martz. 2010. Using positional homology in aetosaur (Archosauria: Pseudosuchia) osteoderms to evaluate the taxonomic status of *Lucasuchus hunti*. Journal of Vertebrate Paleontology 30:1100–1108.

Racki, G. 2010. Ewolucja środowisk lądowych kajpru Górnego Śląska jako biotopów kręgowców–nowy projekt badawczy. Przegląd Geologiczny 58:124–126.

Rauhut, O. W. M., and A. Hungerbühler. 2002. A review of European Triassic theropods. Gaia 15:75–88.

Rees, J., and C. J. Underwood. 2002. The status of the shark genus *Lissodus* Brough, 1935, and the position of nominal *Lissodus* species within the Hybodontoidea (Selachii). Journal of Vertebrate Paleontology 23:471–479.

Reymanówna, M. 1992. Two conifers from the Liassic flora of Odrowaz in Poland; pp. 307–311 in J. Kovar-Eder (ed.), Palaeovegetational Development in Europe and Regions Relevant to its Palaeofloristic Evolution: Proceedings of the Pan-European Palaeobotanical Conference, Vienna, 19–23 September 1991. Museum of Natural History, Vienna.

Rieppel, O. 2000. Turtles as diapsid reptiles. Zoologica Scripta 29: 199–212.

Rougier, G. W., M. S. de la Fuente, and A. B. Arcucci. 1995. Late Triassic turtles from South America. Science 268:855–858.

Sander, P. M. 1992. The Norian *Plateosaurus* Bonebeds of central Europe and their taphonomy. Palaeogeography, Palaeoclimatology, Palaeoecology 93:255–299.

Scheyer,T., and P. M.Sander. 2007. *Shell bone histology indicates terrestrial palaeoecology* of *basal turtles*. Proceedings of the Royal Society B 274:1884–1893.

Schultz, E., and C. Heunisch. 2005. Palynostratigraphische Gliederungsmöglichkeiten des deutschen Keupers; pp. 43–49 in G. Beutler (ed.), Stratigraphie von Deutschland. IV Keuper. Courier Forschungsinstitut Senckenberg 253.

Seegis, D. 2005. Tetrapoden; p. 296 in Deutsche Stratigraphische Kommission (ed.), Stratigraphie von Deutschland IV Keuper. Courier Forschungsinstitut Senckenberg 253.

Seeley, H. G. 1887. On the classification of the fossil animals commonly named Dinosauria. Proceedings of the Royal Society of London 43:165–171.

Sereno, P. C. 1998. A rationale for phylogenetic definitions, with application to the higher-level taxonomy of Dinosauria. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 210:41–83.

Sereno, P. C., S. Mcallister, and S. L. Brusatte. 2005. Taxon-Search: a relational database for suprageneric taxa and phylogenetic definitions. PhyloInformatics 8:1–21.

Skawina, A., and J. Dzik. 2011. Umbonal musculature and relationships of the Late Triassic filibranch unionoid bivalves. Zoological Journal of the Linnean Society 163:863–883.

Sterli, J., M. S. de la Fuente, and G. W. Rougier. 2007. Anatomy and relationships of *Palaeochersis talampayensis*, a Late Triassic turtle from Argentina. Palaeontographica, Abteilung A 281:1–61.

Sulej, T. 2002. Species discrimination of the Late Triassic labyrinthodont *Metoposaurus diagnosticus*. Acta Paleontologica Polonica 47: 535–546.

Sulej, T. 2005. A new rauisuchian reptile (Diapsida: Archosauria) from the Late Triassic of Poland. Journal of Vertebrate Paleontology 25:78–86.

Sulej, T. 2010. The skull of an early Late Triassic aetosaur and the evolution of the stagonolepidid archosaurian reptiles. Zoological Journal of the Linnean Society 158:860–881.

Sulej, T., and F. Majer. 2005. The temnospondyl amphibian *Cyclotosaurus* from the Upper Triassic of Poland. Palaeontology 48:157–170.

Sulej, T., R. Bronowicz, M. Tałanda, and G. Niedźwiedzki. 2011a. A new dicynodont-archosaur assemblage from the Late Triassic (Carnian) of Poland. Earth and Environmental Science Transactions of The Royal Society of Edinburgh 101:261–269.

Sulej, T., G. Niedźwiedzki, R. Niedźwiedzki, D. Surmik, and M. Stachacz. 2011b. New vertebrate assemblage from the marginal-marine and land Lower Keuper strata (Ladinian, Middle Triassic) of Miedary, Silesia, SW Poland. Przegląd Geologiczny 59:426–430.

Szulc, J., M. Gradziński, A. Lewandowska, and C. Heunisch. 2006. The Upper Triassic crenogenic limestones in Upper Silesia (southern Poland) and their paleoenvironmental context; pp. 133–151 in A. M. Alonso-Zarza and L. H. Tanner (eds.), Paleoenvironmental Record and Applications of Calcretes and Palustrine Carbonates. Geological Society of American Special Paper 416.

Walker, A. D. 1961. Triassic reptiles from the Elgin area: *Stagonolepis*, *Dasygnathus* and their allies. Philosophical Transactions of the Royal Society of London, Series B 244:103–204.

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