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Authors: Dzik, Jerzy, Sulej, Tomasz, and Niedźwiedzki, Grzegorz

Source: Acta Palaeontologica Polonica, 53(4) : 733-738

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.2008.0415

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Brief report Acta Palaeontologica Polonica 53 (4): 733–738, 2008

A dicynodont-theropod association in the latest Triassic of Poland

JERZY DZIK, TOMASZ SULEJ, and GRZEGORZ NIEDŹWIEDZKI

It is generally accepted that during the Triassic the composition of tetrapod faunas underwent a series of fundamental transformations, mainly as a result of diversification of archosaurs and decline of therapsids (Benton 1994, 2004, 2006). The last herbivorous basal synapsids, dicynodonts, disappeared from the record in the early Norian of the Americas, about 220 Ma (Langer et al. 2007), being unknown from the Late Triassic of Europe. Here, we report a partially articulated skeleton and isolated bones of a giant rhino-size dicynodont in the Upper Triassic fluvial sediments at Lisowice (Lipie Śląskie clay-pit) in southern Poland. Paleobotanical data indicate an early Rhaetian age for the fauna (Dzik et al. 2008; Niedźwiedzki and Sulej 2008). The dicynodont bones are associated with bones of carnivorous dinosaurs, pterosaurs, as well as capitosaur and plagiosaur amphibians. Dicynodonts were represented in the Germanic Basin throughout the Late Triassic, as proven by findings of smaller dicynodonts in older deposits in the same area, associated there with temnospondyl amphibians. It appears, thus, that the fossil record of tetrapod succession in the Late Triassic was strongly controlled by ecological factors and biased by uneven representation of particular environments. The Lisowice assemblage proves that faunas dominated by dicynodonts did not entirely disappear at least until the end of the Triassic.

Introduction

Bone-bearing greenish, reddish, and grey fluvial mudstones and siltstones, interbedded with cross- or horizontally-stratified greywacke sandstones (the whole stratigraphic section is aproximately 12 meters thick) are exposed in the Lipie Śląskie clay-pit (Fig. 1) at Lisowice village, near the town Lubliniec in southern Poland (Szulc et al. 2006). Well-preserved vertebrate bones occur in a lenticular body of grey mudstone and claystone in the northern part of the Lipie Śląskie clay-pit, mostly covered with calcareous and pyritic crust or preserved within limestone concretions. The vertebrate assemblage is dominated by bones of a giant dicynodont, as well as large theropod bones. Other vertebrate remains, including a coelophysoid dinosaur, pterosaur, large capitosaur, and small plagiosaur, as well as dipnoan teeth, hybodont shark fin spines, and ganoid skull elements and scales, are rare. About 150 m below this fossil-bearing greenish-gray sequence, playa and fluvial reddish mudstones of the Keuper occur, lithostratigraphically correlatable with the Late Carnian strata of Krasiejów containing *Paleorhinus* and *Metoposaurus*, located about 25 km to east (Dzik et al. 2000; Dzik 2001, 2003; Dzik and Sulej 2007; Sulej 2005). The fresh-water hybodont sharks elsewhere tend to be especially abundant in times of global sea level rise. Their presence in Lisowice and absence in Krasiejów may thus be meaningful.

In these bone-bearing strata numerous well-preserved micro- and macrofloral remains were found. The dominant plant species at Lisowice is a conifer similar to *Hirmeriella muensteri* (Schenk, 1867), as is the case with the Rhaetian and earliest Liassic floras of the region (Clement-Westerhof and Van Konijnenburg-Van Cittert 1991; Reymanówna 1992), although its twigs (in ZPAL V33/212) are more robust than in Jurassic specimens. Abundant pollen of *Classopollis* morphology occurring there is elsewhere associated with this species (Reymanówna 1992). The second most common plant species is represented by twigs (ZPAL V33/213) similar to *Stachyotaxus septentrionalis* (Agardh, 1823) from the Rhaetian of Greenland and Scania (Harris 1932; Arndt 2002). Associated seed scales (ZPAL V33/214), with no signs of separate bract and scale being present, have entire margins and apparently supported two ovules. Unlike *S. septentrionalis*, as interpreted by Arndt (2002), the scale apex is blunt, resembling instead cone scales of the south-Gondwanan Jurassic *Mataia* (Townrow 1967). *Stachyotaxus* produced spherical wingless pollen (Harris 1931; Stewart and Rothwell 1993), which could be represented by *Brachysaccus neomundus* (Leschik, 1955) at Lisowice. The probable gingkoalean pollen *Monosulcites* cf. *M. minimus* Cookson, 1947 (leaves—ZPAL V33/215 similar to *Schmeissneria* are associated) and the liverwort spores *Ricciisporites* cf. *R. tuberculatus* Lundblad, 1954 are present at Lisowice; these taxa are known only from other central European sites believed to correspond to late Norian and early Rhaetian (Orłowska-Zwolińska 1983; Schultz and Heunisch 2005). Well preserved cuticule fragments of typical Rhaetian seed-fern, *Lepidopteris* cf. *L. ottonis* were also described from the Lisowice site (Staneczko 2007). The dipteridacean fern *Clathropteris*, a member of a generally Jurassic flora of SE Asian origin, which entered Europe and Greenland in the Rhaetian (Harris 1937; Lundblad 1950; Mader 1995; Czier 1998), was reported from a carbonate facies which overlies the clastic strata in this region (Roemer 1867), although Ash (2005) claimed presence of *Clathropteris* in the early Norian of western North America.

Among probable isoëtalean macrospores from Lisowice, *Trileites* cf. *T. pinguis* (Harris, 1935) is common in the Rhaetian of central Europe, although it is also known from the late Norian of Germany and Poland. *Horstisporites bertelseni* Fuglewicz, 1977 has at least a close relative in the Rhaetian of the core Rødby N. 1 in southern Denmark (Fuglewicz 1977; Fuglewicz and Śnieżek

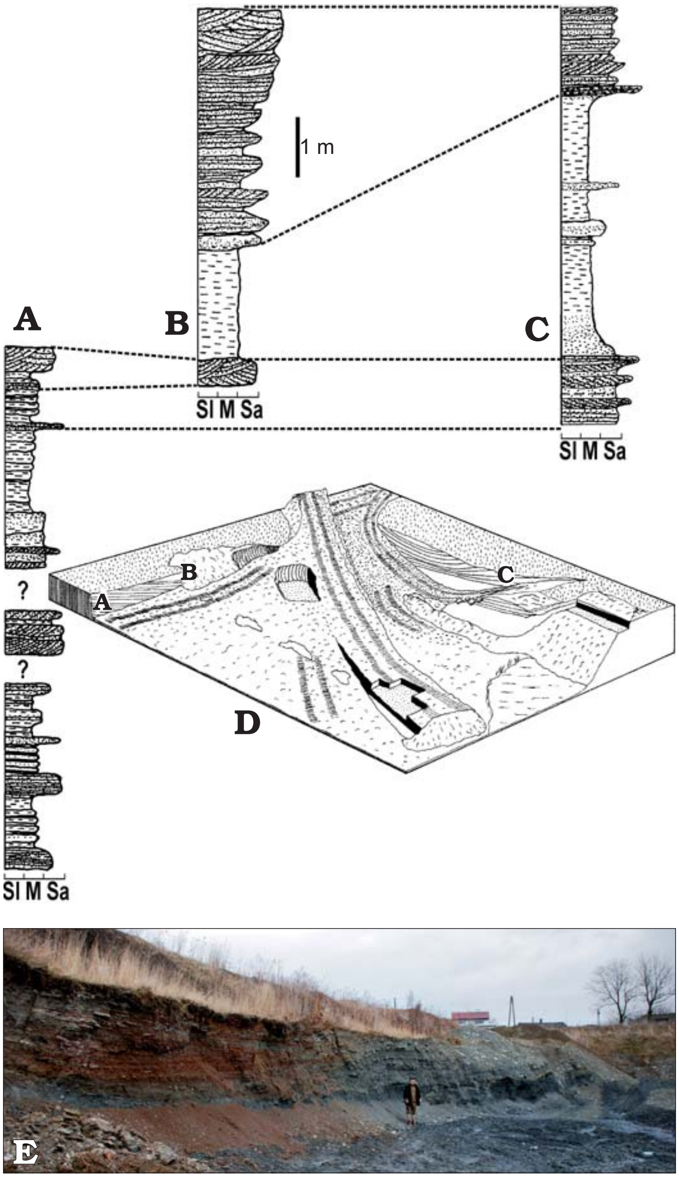

Fig. 1. Exposure of fossiliferous strata of probable Rhaetian or late Norian age in Lipie Śląskie clay-pit at Lisowice, southern Poland. **A–C**. Measured sections at locations shown on blockdiagram (**D**). **E**. View of section C from the SW. Abbreviations: Sl, siltstones; M, mudstones; Sa, sandstones.)

1980). Taken together, both macrofloral and palynological evidence indicates Rhaetian as the age of the Lisowice site.

Also suggestive of Rhaetian age are conchostracans of unusually small size for the Norian of the Germanic Basin (1.5–3.0 mm), similar to *Euestheria brodieana* (Jones, 1862) from the Rhaetian of England and United States (Kozur and Weems 2005; Heinz Kozur, personal communication 2007). A more thorough study of the fossil assemblage is under way and will be published separately.

Institutional abbreviations.—BGS, British Geological Survey, Keyworth, Nottinghamshire, UK; BMNH, Museum of Natural History, London, UK; ZPAL, Institute of Paleobiology of the Polish Academy of Sciences, Warsaw, Poland.

Description

Dicynodont.—Partially articulated skeleton and numerous bones of at least two individuals are dispersed in the claystone unit at the exposure.

The left maxilla (ZPAL V33/85), represented by the posteroventral edge lacking the tusk, displays a short ventral process similar to that of *Ischigualastia* (Cox 1965). Articular condyles of the right quadrate (ZPAL V33/84) suggest that the skull was approximately 47 cm wide (across the quadrates), if its proportions were similar to *Ischigualastia*.

Unlike other dicynodonts, the 49 cm long humerus (ZPAL V33/96; Fig. 2C) lacks the entepicondylar foramen on the distal head, and the distal end of the deltopectoral crest is bent anteriorly to become narrow and rounded ventrally. The posterior part of the humerus head is similar to proportions as that of *Ischigualastia*. The distance between the deltopectoral crest and supinator process is small and the shaft is only weakly twisted, like the condition in *Ischigualastia*. The complete supinator process is prominent and narrow. The merged capitulum and trochlea of the humerus are smaller than in *Ischigualastia*, *Placerias* (Camp and Welles 1956), and *Stahleckeria*.

The femur (ZPAL V33/75; Fig. 2D) is wider (in anterior view) and generally more massive than in other Triassic dicynodonts, apparently in connection with its unusually large size (56 cm length). The lateral edge of the distal head is even more convex in anterior view than in *Wadiasaurus* (Bandyopadhyay 1988), *Stahleckeria* or *Ischigualastia*, and it is straight in *Placerias* (Camp and Welles 1956) and *Jachaleria* (Vega-Dias and Szultz 2004). The spherical dorsomedially directed proximal head makes it similar to *Wadiasaurus, Stahleckeria*, and *Placerias*. In the Polish form and *Stahleckeria,* the femur head is directed more ventrally than reconstructed in *Placerias*. Its trochanter major is the longest of all these genera. The tibia (50 cm length) is massive, but does not differ significantly from *Stahleckeria* and *Placerias*. The fibulae (ZPAL V33/76 and ZPAL V33/77) are generally similar to *Stahleckeria*, although the proximal head is narrower and generally slender then in this genus. The straight mesial side of the distal head (in anterior view) is like *Placerias* (it is strongly concave in *Stahleckeria*).

Benton (2006) listed dicynodonts among the groups that vanished in the mass extinction at the Carnian–Norian boundary. *Jachaleria colorata* Bonaparte, 1970 from the Los Colorados Formation of Argentina and *Jachaleria candelariensis* Araújo and Gonzaga, 1980 from the Caturrita Formation of Rio Grande do Sul, Brazil are considered to be the last dicynodonts of middle Norian age (Langer 2005; Langer et al. 2007). The new finding shows that Late Triassic dicynodonts survived at least to the late Norian and possibly to the Rhaetian. Dicynodonts apparently occurred in southern Poland for the whole Late Triassic, as indicated by another occurrence under study at Woźniki, 30 km E of Lisowice, where a medium-sized species (ZPAL V. 34/1) is associated with a temnospondyl (ZPAL V. 34/28). The unexpectedly large size of the last Polish species confirms the general evolutionary trend of increasing body size in the Triassic (Ray 2006), a repetition of a similar succession in

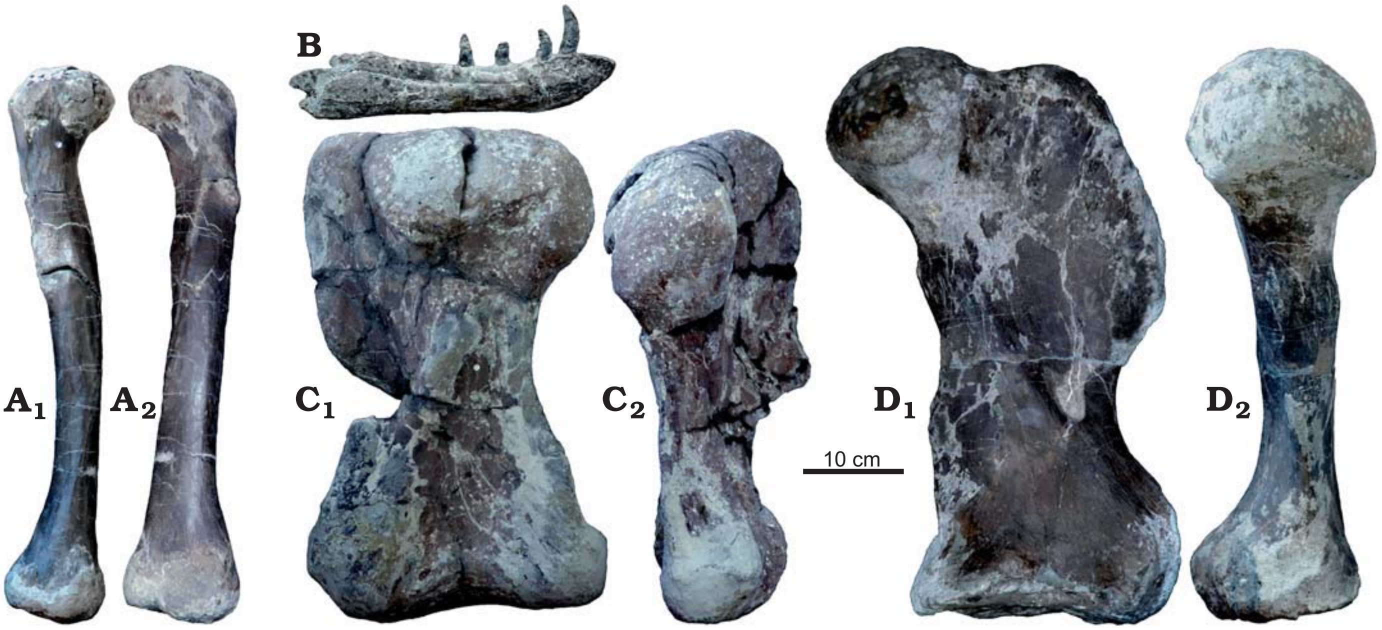

Fig. 2. Selected bones of large tetrapods from the Late Triassic of Lisowice, southern Poland. **A**, **B**. Theropod dinosaur. **A**. Left femur ZPAL V33/45 in lateral (A_1) and anterior (A_2) views. **B**. Right dentary ZPAL V33/25 in lateral view. **C**, **D**. *Ischigualastia*-like dicynodont. **C**. Left humerus ZPAL V33/96 in posterior (C_1) and medial (C_2) views. **D**. Left femur ZPAL V33/75 in anterior (D_1) and medial (D_2) views.

the Permian (terminated with *Rhachiocephalus*). Near the end of the Triassic, dicynodonts achieved large rhino proportions and became the dominant terrestrial herbivores in certain faunas, as suggested by numerical dominance of dicynodont bones and lack of any other large herbivore at Lisowice. Survival of the dicynodonts to near the end of the Triassic adds also credibility to the report of their occurrence in the Cretaceous of Australia (Thulborn and Turner 2003).

Large theropod dinosaur.—Bones of a large predatory archosaur were found as four accumulations in a 2-meter thick horizon at the Lisowice clay-pit, one representing the skull bones and others with postcranial elements. They fit each other in size and morphology and seem to represent the disarticulated skeletons of two individuals.

The skull differs from “rauisuchians” in that the frontals (ZPAL V33/21) form the anterior part of the supra-temporal fossa. In the braincase (ZPAL V33/15), a sheet-like crista tuberalis is visible, characteristic for theropods (Galton and Knoll 2006). It is ventrally short, as in the coelophysoids (Raath 1984) whereas in most theropods (e.g., *Piatnitzkysaurus*, *Sinraptor*, and *Dilophosaurus*), the crista tuberalis is very deep (see Rauhut 2004). A lateroventrally directed bony sheet of the crista ventrolateralis is developed in the posterior part of basisphenoid. The condition is not as vertical as in more derived neotheropods (e.g., *Dilophosaurus* and *Allosaurus*). Laterally, above the basisphenoid sinus, a pneumatic recess, known also in *Coelophysis rhodesiensis* (Raath 1984) is visible. *C. rhodesiensis*, *Ceratosaurus*, and *Allosaurus* have a very narrow depression, but in the neotheropods the depression is wide, although not as much as in the Polish form. The base of the paroccipital process is higher than the dorsal rim of the occipital condyle, a plesiomorphic condition compared to coelophysoids and *Dilophosaurus* (Raath 1984; Welles 1984).

The teeth (ZPAL V33/50 and ZPAL V33/51) show transverse enamel wrinkles that sweep ventraly and away from the serrations on the distal margins of the labial and lingual surfaces.

Like most theropod dinosaurs, the Lisowice form bears a lateral ridge ventral to the tooth margin, which extends throughout the length of the dentary (Fig. 2B), which makes it similar also to the “megalosaurid” dentary (cast BMNH R2912, from holotype natural sandstone mold BGS 6532) from the Rhaetian of England (Galton 1998, 2005).

The location of the humeral greater tubercle relative to the internal tuberosity is proximal, as in most theropods (Rauhut 2003). The humeral shaft (ZPAL V33/46) is longitudinally twisted in the Lisowice dinosaur, unlike basal theropods, which have nearly parallel proximal and distal articular surfaces. They became increasingly rotated in more derived forms (e.g., tetanurans, ceratosaurs).

The femur (ZPAL V33/45; Fig. 2A) is massive and elongated. In posterior view, tibiofibularis crest is relatively narrow mediolaterally and its long axis is longitudinal, unlike the condition in neoceratosaurs.

In the partially preserved pubis (ZPAL V33/220), the distal blade is oriented almost vertically, and the obturator foramen is open ventrally. In many tetanuran theropods, there is a tendency towards reduction of the bony plate that encloses the foramen, and it is not fully enclosed in bone in *Allosaurus*, *Coelurus*, sinraptorids, *Siamotyrannus*, and carcharodontosaurids (Rauhut 2003). Because both the cranial material and the pelvis show some dinosaur features we suggest that all these bones represent a theropod species.

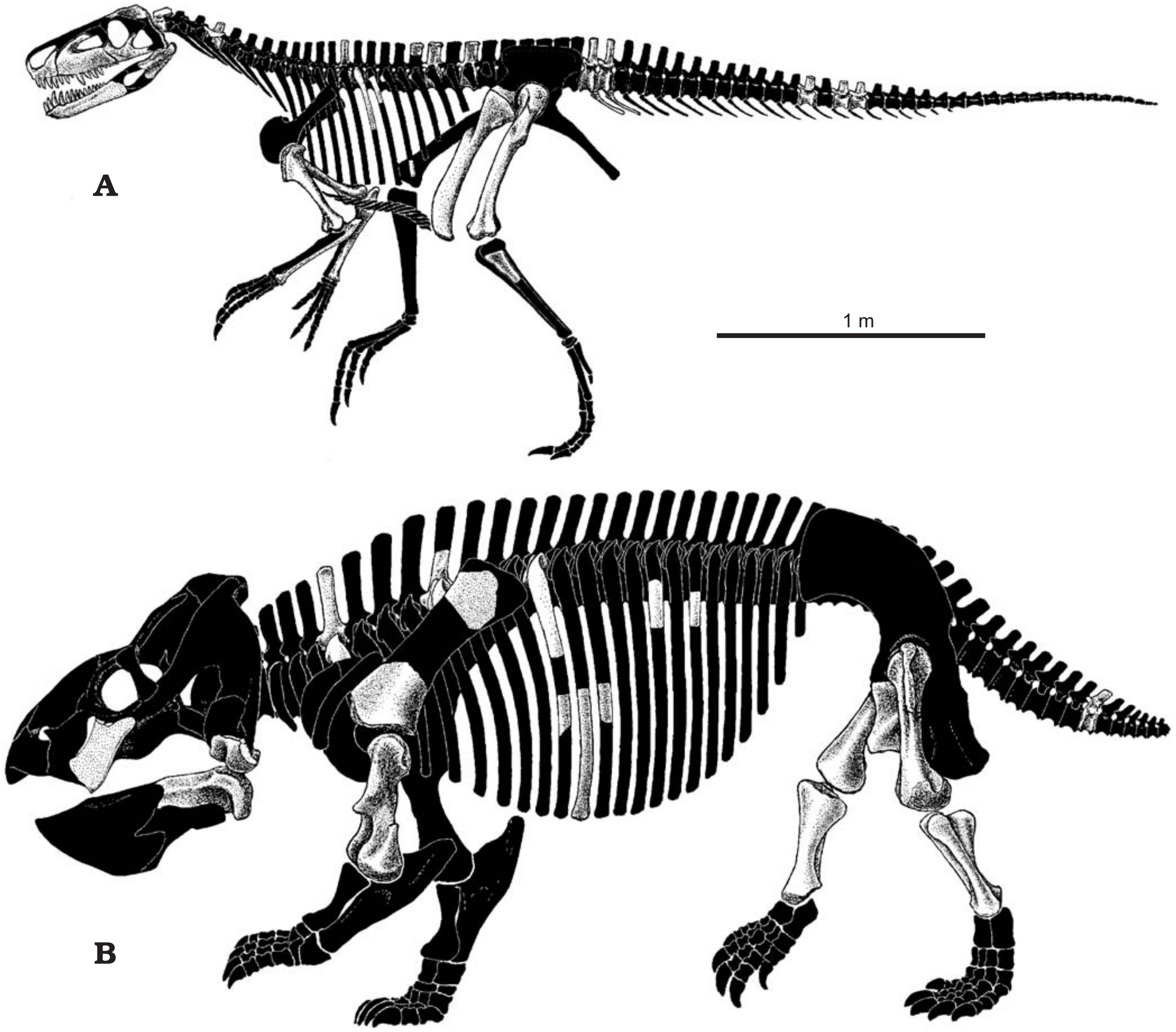

Fig. 3. Preliminary skeletal reconstructions of the basal theropod (A) and the *Ischigualastia*-like dicynodont (B) from the Late Triassic of Lisowice. Bones represented in the collection are stippled.

The new find shows that large theropods inhabited Laurasia as early as the Late Triassic. Their skull was initially massive and deep, with shortening haven taken place later, in the Jurassic. The fossil record of large theropod dinosaurs was previously restricted to the Early and Middle Jurassic sediments of North America, Europe and Asia (Rauhut 2003; Allain et al. 2007). Large, about 40–45 cm long, tridactyl footprints (ZPAL V.33/219) were also found at Lisowice. Morphology of those footprints are very similar to ichnites from the Early and Middle Jurassic (Lockley and Hunt, 1995; Lockley and Meyer 2000).

Small archosaurs.—Smaller cervical vertebrae with elongated centra (ZPAL V33/41; ZPAL MB/1) are also known from Lisowice, similar in morphology to Late Triassic coelophysoid dinosaurs. In a sandstone intercalation near the top of the section footprints left by a theropod of body size comparable with that inferred from those vertebrae and digit proportions suggestive of a coelophysoid has been found. The coelophysoid neotheropods (e.g., *Coelophysis, Liliensternus,* and *Lophostropheus*) were typical elements of the Norian and Rhaetian dinosaur communities in Europe (Rauhut and Hungerbühler 1998; Ezcurra and Cuny 2007).

Isolated wing bones of a pterosaur (extremely elongated and with a wide medullar cavity), and further small archosaur bones represent other important elements of the assemblage.

Temnospondyls.—A large cyclotosaur is represented in the Lisowice assemblage by the exoccipital (ZPAL V33/5), fragments of the maxilla (ZPAL V33/6 and ZPAL V33/7), squamosal with an edge of the closed otic notch (ZPAL V33/4), fragments of the skull roof, and the mandible (ZPAL V33/13). The postcranial materials include a part of the clavicle (ZPAL

V33/11), and a complete femur (ZPAL V33/1). Judging from the mandible, this was one of the largest cyclotosaurs, with a skull length of 75 cm, larger than its relative from the late Carnian Krasiejów fauna in the area (Sulej and Majer 2005). This material and undescribed fragments from the Rhaetian of Germany (Schoch and Wild 1999) are the last capitosaurids in the Germanic Basin.

Plagiosaurids are represented by the exoccipital (ZPAL V33/193), dermal scutes (ZPAL V33/192) and a characteristic vertebral centrum (ZPAL V33/194) with large parapophyses at both ends.

Discussion

The composition of the Lisowice fossil assemblage is a curious mixture of advanced elements (gymnosperm flora, dinosaurs, and pterosaurs) with forms not expected to occur in latest Triassic strata (giant dicynodonts and capitosaurs). Partial articulation of the dicynodont (Fig. $2A_2$) skeleton and excellent preservation of all fossils excludes redeposition of the assemblage. Regardless of whether the strata are late Norian or early Rhaetian in age, the dicynodont from Lisowice is the last unquestionable dicynodont in the world with reliable stratigraphic origin and the only one known from the Late Triassic of Europe.

Dicynodonts were living in the region also much earlier in the Late Triassic, at the same time as the aetosaur-rauisuchian dominated assemblage of Krasiejów (Dzik and Sulej 2007), as proven by their occurrence at Woźniki, approximately 60 km eastward and inland from Lisowice. It appears that in central Europe, quite different vertebrate communities inhabited different continental ecosystems in the Late Triassic. Basal sauropodomorphs and coelophysoids in Württemberg (Rauhut and Hungerbühler 1998; Moser 2003) were coeval with dicynodonts and large and small theropods in Poland, as well as with aetosaurs, the possible ornithischian relative dinosauromorph *Silesaurus*, and rauisuchians (Dzik and Sulej 2007). They lived at the same time in different environments, as indicated by associated floral assemblages.

It is hard to decide with the available evidence whether the Lisowice giant dicynodont was living close to water reservoirs at the site where its remains are preserved, or was transported from a dry nearby region. The alluvial sedimentary environment of Lisowice does not preclude transport of the dicynodont and theropod carcasses from dry inland environments with xerophytic *Hirmeriella*-dominated flora, the source of large charcoal stumps associated with bones.

The new unexpected discoveries of dicynodonts in the Late Triassic of Poland nicely shows how misleading any local, or even regional, faunal succession may be, if used to generalize about the pattern of extinction (see also Irmis et al. 2007b).

Acknowledgements.—Robert Borzęcki (Warsaw, Poland), Piotr Menducki (Ostrowiec Świętokrzyski, Poland), and Marek Błyszcz (Lisowice, Poland) made us aware of vertebrate bones occurring at Lisowice-Lipie Śląskie. The excavations by Institute of Paleobiology PAN were supported by a research grant from the Polish Ministry of Science and Informatisation No. 1665/P01/2007/32 and National Geographic Polska.

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Jerzy Dzik [dzik@twarda.pan.pl], Instytut Paleobiologii PAN, Twarda 51/55, PL-00-818 Warszawa, Poland and Instytut Zoologii Uniwersytetu Warszawskiego, ul. Banacha 2, PL-02-097 Warszawa, Poland;
Tomasz Sulej [sulej@twarda.pan.pl], Instytut Paleobiologii PAN, ul. Twarda 51/55, PL-00-818 Warszawa, Poland;
Grzegorz Niedźwiedzki [gniedzwiedzki@biol.uw.edu.pl], Instytut Zoologii Uniwersytetu Warszawskiego, ul. Banacha 2, PL-02-079 Warszawa, Poland.