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Review

Review

Osteology and relationships of the Late Triassic giant dicynodont *Lisowicia*

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ABSTRACT

Unexpectedly abundant remains of herbivorous therapsids in the Late Triassic strata of southern Poland have significantly supplemented knowledge of their evolution. The skeletal morphology of the Late Norian (or Rhaetian) dicynodont *Lisowicia bojani* supports its close relationship to the Carnian *Woznikella*, both known from the Polish part of the Germanic Basin. Three evolutionary lineages of dicynodonts—Laurasian–Gondwanan *Rhadiodromus klimovi* → *Jachaleria candelariensis* lineage, Laurasian lineage *Shaanbeikannemeyeria xilougouensis* → *Lisowicia bojani*, and the Gondwanan lineage *Kannemeyeria simocephalus* → *Dinodontosaurus brevirostris*—are distinguished based on characters of cranial and postcranial elements. In the lineages characterized by the parietal oval in cross-section and the two distinct articulations on the sternum, there is a tendency to exclude the frontal from the orbital margin and to reduce the number of sacral vertebrae. In the lineage with the parietal narrow and triangular in cross-section, the frontal forms part of the orbit margin, there is a single joint on the sternum, and there is a tendency towards flattening the skull roof. In both lineages the shoulder girdle is convergently modified, the acromion process decreased, and joints on the sternum moved posteriorly.

Keywords: Lisowice; Lipie Śląskie; braincase; herbivory; pelvis

INTRODUCTION

The dicynodonts were short-tailed, quadrupedal therapsids, ranging from mouse to elephant size. These were probably the first terrestrial vertebrates that were able to exploit polysaccharides from tough plant cell walls and last for tens of millions of years (King 1981). They diversified into numerous lineages known from the Middle Permian (Lucas 2002) up to the end of Triassic (Dzik *et al.* 2008, Sulej and Niedźwiedzki 2019). During their evolution they multiplied their body size (Niedźwiedzki *et al.* 2011). As early as the Late Permian, *Rhachiocephalus magnus* (Owen) (Keyser 1975) (after Maisch 2003) was the largest terrestrial herbivore of its time. Mainly small-size dicynodonts are known from the Early Triassic, represented mainly by the Gondwanan *Lystrosaurus* species; however, mean body size of dicynodonts actually increases across the boundary. But, already in the Middle Triassic, large-size dicynodonts emerged in China (Sun 1963) and South America (Kammerer and Ordoñez 2021). A few species were also described from the Middle Triassic of Orenburg Province in Russia (Efremov 1938, Vjuschkov 1969, Kalandadze 1970, Sennikov 1996). The increasing size was probably a result of the appearance of large predatory archosaurs (Niedźwiedzki *et al.* 2011; contrary to: Sookias *et al.* 2012). But the real giants were discovered recently in the latest Triassic of Poland (Dzik *et al.* 2008, Sulej and Niedźwiedzki 2019). Their presence there was a surprise because dicynodonts were believed to have become extinct well before the Rhaetian (Benton 1994). Moreover, dicynodonts were unknown from Central Europe until their discovery in the Late Triassic localities, Lisowice and Woźniki (Sulej *et al.* 2011). The first Triassic dicynodonts from Germany have been described only recently by Schoch (2012).

Benton (2006) listed dicynodonts among the tetrapod groups that vanished during the alleged mass extinction at the Carnian/Norian boundary. *Jachaleria colorata* Bonaparte, 1970 from the Los Colorados Formation of Argentina and *J. candelariensis* Araújo and Gonzaga 1980 from the Caturrita Formation of Rio Grande do Sul, Brazil were considered to be the last dicynodonts of Carnian and Middle Norian age (Langer 2005a, b, Langer *et al.* 2007, 2018). According to King (1990), the Americas were 'the last bastion of dicynodonts'. She dated almost all the Late Triassic dicynodonts (*Ischigualastia jenseni* Cox, 1962,

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Stahleckeria potens, von Huene 1935, *Dinodontosaurus turpior* von Huene, 1935, and *Placerias hesternus* Lucas, 1904) as Norian.

However, Schultz *et al.* 2020 proposed a Middle Triassic age for *I. jenseni* and *S. potens*, but Kammerer and Ordoñez 2021 and Mancuso *et al.* 2021 confirmed their Carnian age. Recently, Langer *et al.* (2007, 2018), Martinez *et al.* (2011), and Martinelli *et al.* (2021) claimed that *J. candelariensis* is from the Norian, although the correlation of the Late Triassic terrestrial faunas remains ambiguous. No Rhaetian dicynodont was reported from the Americas. The dicynodont fragments from the Cretaceous of Australia (Thulborn and Turner 2003) are identified as Cenozoic mammal fossils (Knutsen and Oerleman 2020). The dicynodont *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from the latest Norian (or Rhaetian) of Poland contradicts the alleged mass extinction at the Carnian/Norian boundary (Dzik *et al.* 2008, Sulej and Niedźwiedzki 2019).

The *Lisowicia bojani* humeri, ZPAL V. 33/479 and ZPAL V. 33/MB/24, are about 60 cm in length and probably belonged to an animal of 2.5 m height, whereas the materials (part of the skull, scapula, and vertebra) of the second in size, *Barysoma lenzii* Cox, 1965 (conspecific with *Stahleckeria potens*), MCZ 1688, probably belonged to an animal of 1.8 m height [based on the proportions of the *Stahleckeria* skeleton (GPIT-PV-30792) in the University of Tübingen].

MATERIALS AND METHODS

Description of the locality

The geological section exposed at the brick-pit quarry in Lipie Śląskie-Lisowice was described and its geological age was discussed by Dzik *et al.* (2008), Pieńkowski *et al.* (2014), Szulc *et al.* (2015), and Sulej and Niedźwiedzki (2019). The locality is not especially fossiliferous, but the fossil assemblage is relatively diverse. The clay is rich in oncoids and calcareous concretions (Szulc *et al.* 2015, Tałanda *et al.* 2017). The plants are represented by tridimensionally preserved organs (including whole cones), pieces of coalified wood, and flattened seeds and sprouts (Dzik *et al.* 2008). The macrospore forms were described by Fuglewicz and Śnieżek (1980). A review of the flora from Lisowice was presented by Pacyna (2014). A flora almost identical to that from Lisowice was found at the nearby locality Marciszów by Wawrzyniak and Filipiak (2021).

Nuclei of articulated shells of the bivalve *Tihkia silesiaca* Skawina and Dzik, 2011 are common at Lisowice (Skawina and Dzik 2011). Rare conchostracans have been encountered. Ostracods are the most common microfossils. Trackways of reptiles and invertebrates are frequently preserved in the sandstone layers (Pieńkowski and Niedźwiedzki 2014). Teeth of dipnoans and scales of ganoid fishes are not rare (Skrzycki 2013). A non-marine coelacanth comes from there (Skrzycka *et al.* 2013). Shark spikes and teeth were also collected (Świło 2010). The bones of temnospondyl amphibians are sporadic. The bones of the archosaur (possibly a theropod dinosaur) *Smok wawelski* Niedźwiedzki *et al.*, 2012 were identified in two accumulations (Niedźwiedzki *et al.* 2012): one with the skull bones and the other with postcranial elements. Its probable coprolites were described by Zatoń *et al.* (2015) and Qvarnström *et al.* (2019). Teeth of the mammaliaforms *Hallautherium* sp. Clemens, 1980 are very rare (Świło *et al.* 2013) but bones of dicynodonts are relatively common. Their probable coprolites were described by Bajdek *et al.* (2014). The geochemical record of early diagenetic oxidation of the terrestrial organic matter in arid and semi-arid climate conditions was studied by Marynowski and Wyszomirski (2008). The stable isotopes from Lisowice indicate that this part of the Germanic Basin was supplied with the clastic material from the Bohemian Massif (Konieczna *et al.* 2014). Kowal-Linka *et al.* (2019) dated the youngest detrital zircons as 211 million years old.

Studied material

Bones of Triassic tetrapods were first collected in the brickyard at Lisowice in the 1990s by the quarry worker Marek Błyszcz, who interpreted them as pieces of fossil wood. The first bone that was later identified as coming from Lisowice and belonging to a dicynodont was transferred to me in 2006 by the fossil collector Piotr Menducki. The whereabouts of the locality was released by another fossil collector, Robert Borzęcki. The same year a femur shaft of a size suggestive of it belonging to a prosauropod was found by myself and Grzegorz Niedźwiedzki. A year later Jerzy Dzik found a complete humerus in a concretion, and, after he cleaned the bone, he recognized it as belonging to a dicynodont. On the last day of the one-month excavation in 2008, students found a large accumulation of bones of dicynodonts in the sandstone. In 2009, after unsuccessful attempts to construct an exhibition in place, we removed all the bones from the accumulation. More bones were found during subsequent excavations.

The dicynodont *Lisowicia bojani* is represented in the Lisowice material by almost all skeletal elements. The most important source of information enabling its skeletal reconstruction is the accumulation of bones found in 2008: ZPAL V. 33/720. It consists of 22 vertebrae, both ilia, ischia, and pubis, and many ribs (although most of them are incomplete). The elements of accumulation from 2008 were disarticulated, and they were mixed over an area of 3 × 3 m. The second series of specimens that represents one individual is the nearly articulated left femur with tibia and fibula, ZPAL V. 33/75, collected in 2007. In specimen ZPAL V. 33/MB/22, the three cervical vertebrae (fourth–sixth) are preserved, almost in articulation with the proximal part of the fifth and sixth ribs. The rest of the bones were found as isolated elements, and the same refers to the few bones of the skull.

The skull remains poorly known and is represented mainly by fragmentary elements. The postorbital and basioccipital are known from four and five specimens, respectively, but no bone of the snout is known (except for a piece that may possibly represent the premaxilla). The digits are very rare, only two last digits are known. Also, the caudal vertebrae are rare.

The material is housed in the Institute of Paleobiology PAN in Warsaw under the collection numbers ZPAL V. 33 and ZPAL V. 33/MB (for fossils donated by Marek Błyszcz).

I examined the material of *Placerias hesternus* at Berkeley, Tübingen, and Albuquerque. The *Dinodontosaurus turpior* material I studied at Porto Alegre (MCN, UFRGS) and Harvard University, *Stahleckeria potens* from Tübingen and the Harvard University, Museum of Comparative Zoology, *Ischigualastia jenseni* collection at Harvard MCZ, San Juan and Tucumán, *Rabidosaurus cristatus* Kalandadze, 1970, *Rhadiodromus* *klimovi* Efremov, 1940 in Moscow (PIN), *Wadiasaurus indicus* Chowdhury, 1970 in Calcutta (ISI), *Shaanbeikannemeyeria xilougouensis* Cheng, 1980, *Parakannemeyeria youngi* Sun, 1963, and *Sinokannemeyeria yingchiaoensis* Sun, 1963 in Beijing (IVPP), and *Kannemeyeria simocephalus* Weithofer, 1888 in Cape Town, Johannesburg, and London.

For comparative purposes I examined postcranial material of the kannemeyeriiforms *Dinodontosaurus tener* Von Huene 1935, 1936 (MCN 3584, MCP 130, MCP 4172, MCZ 1670, 1687, 3108, 3454, UFRGS PV0115T, PV0116T, and PV0161T); *Ischigualastia jenseni* (MCZ 3119, PVL 3807, and PVSJ 607); *Jachaleria candelariensis* (UFRGS PV0150T, PV0151T, and PV0287T); *Parakannemeyeria youngi* (IVPP 978, 979, and 972); *Placerias* '*gigas*' Camp and Welles, 1956 (UCMP 24782, 25069, 25093, 25361, 25373, 32393, 32394, and 32459); *Sinokannemeyeria yingchiaoensis* (IVPP V. 974); *Stahleckeria potens* (GPIT-RE-30792); and *Wadiasaurus indicus* (ISI R175/1). No permits were required for the described study, which complied with all relevant regulations. Of them *Pl.* '*gigas*' and *Pl. hesternus* were of special importance, providing information from different age horizons and enabling inference about the evolution of the most advanced dicynodonts.

A tibia with bite marks very similar to that from Lisowice was found in a nearby locality Zawiercie-Marciszów by Budziszewska-Karwowska *et al.* (2010). A part of the proximal head of the ulna identical with that of *Lisowicia bojani* was found reworked in Quaternary glacial sediments in Myszków (Sulej *et al.* 2019). Recently, a partial skeleton of a much smaller dicynodont was excavated at Woźniki (Szczygielski and Sulej 2023) in the stratum dated as Carnian (Sulej *et al.* 2011; but see also: Szulc *et al.* 2006, 2015, Racki and Lucas 2020).

Institutional abbreviations

GPIT—Institut für Geowissenschaften, Eberhard Karls Universität Tübingen, Tübingen, Germany; ISI—Indian Statistical Institute, Calcutta, India; IVPP—Institute of Vertebrate Palaeontology and Palaeoanthropology Academia Sinica, Beijing, China; MCN—Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; MCP—Museu de Ciências e Tecnologia, Pontifícia Universidade Católica, Porto Alegre, Brazil; MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; NMMNH—New Mexico Museum of Natural History and Science, Albuquerque USA; PIN—Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; PVL—Museo Miguel Lillo de Ciencias Naturales, San Miguel de Tucumán, Argentina; PVSJ—Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina; SAM—Iziko, the South African Museum, Cape Town, South Africa; UCMP—University of California Museum of Paleontology, Berkeley, CA, USA; UFRGS—Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; ZPAL—Institute of Paleobiology, Warsaw, Poland.

During the month-long excavation in 2007–2017, a caterpillar was used to remove the barren rock layers and to plough clays. The traditional hand methods with pickaxe or hammer were also used for removing fossils from the most promising layers. The specimens preserved in the mudstone demanded only cleaning in water. Those covered by limestone crust or enclosed in concretions were cleaned mechanically and brushed with dilute formic acid. After washing in water to remove calcium formate they were dried and impregnated with dilute cyanoacrylic glue. The procedure was repeated up to the desired result.

Large specimens were painted with white paint to better emphasize the shape of the bone on pictures. The most important elements were scanned in a tomography-type 'V/tome/x m' lamp 300 kV and by 3D scanner Einscan Pro 2X.

RESULTS

Bones' description and comparison

Cranium

The dicynodont material from Lisowice represents mainly postcranial elements; the cranial material is scarce. Only one piece represents a part of the ossified skull (skull roof ZPAL V. 33/MB/18). Most other specimens are isolated bones, among them the quadrate is the most numerous, probably because of taphonomic reasons.

Premaxilla: The poorly preserved specimen ZPAL V. 33/MB/16 may be a part of the right premaxilla. The bone is in the same piece of sediment with a stapes. The ventral edge of the bone is almost complete (only the anterior tip is broken). The ventral part of the lateral pitted surface is preserved. It is flat in the frontal part and strongly concave posteriorly near the naris. A similar concavity (although not so strong) I identified in *Placerias* '*gigas*' and in the Carnian *Woznikella triradiata* Szczygielski and Sulej, 2023 (Szczygielski and Sulej 2023). Posteriorly, a part of the suture with the maxilla is visible. The medial wall is very deep, as in the dicynodont from Woźniki. The widening of the premaxilla toward its dorsal part was illustrated in *Sinokannemeyeria yingchiaoensis* Sun, 1963 (Sun 1963: figs 8, 9) and in *Parakannemeyeria ningwuensis* Sun, 1963 (Sun 1963: fig. 45).

Maxilla: The posteroventral edge of the left maxilla (Fig. 1) is preserved in ZPAL V. 33/85. The space for the tusk is not present. The caniniform process of the maxilla is very thick and rounded; it is very similar to that in *Placerias* '*gigas*' (Camp and Welles 1956). The dorsal surface forms the suture for the lacrimal; the suture for the jugal is also visible laterally.

Frontal: The frontals are preserved in the partial skull roof ZPAL V. 33/MB/18 (Fig. 2) that consists of both frontals (anterior tips are broken), a fragment of the postorbital, the prefrontal, and lacrimal. The frontal is long and narrow at the edge of the anteriorly directed orbit, similar to that of *Placerias* '*gigas*' (Camp and Welles 1956), *Woznikella triradiata* (Szczygielski and Sulej 2023), and contrary to *Jachaleria candelariensis* (Vega-Dias and Schultz 2004), *Ischigualastia jenseni*, and *Stahleckeria potens*. Both preorbital and postorbital parts of the frontal are elongated. The relationship of the length of the bone (from the pineal foramen to the anterior tip) to the maximum width of the bone is, in *S. potens* 1.18, in *Ischigualastia jenseni* 1.18, *P.* '*gigas*' 2.27, in *J. candelariensis* 1.32, and in *Lisowicia bojani* around 2.0. This value shows that *L. bojani* and *Pl.* '*gigas*' had much more elongate frontals than other dicynodonts.

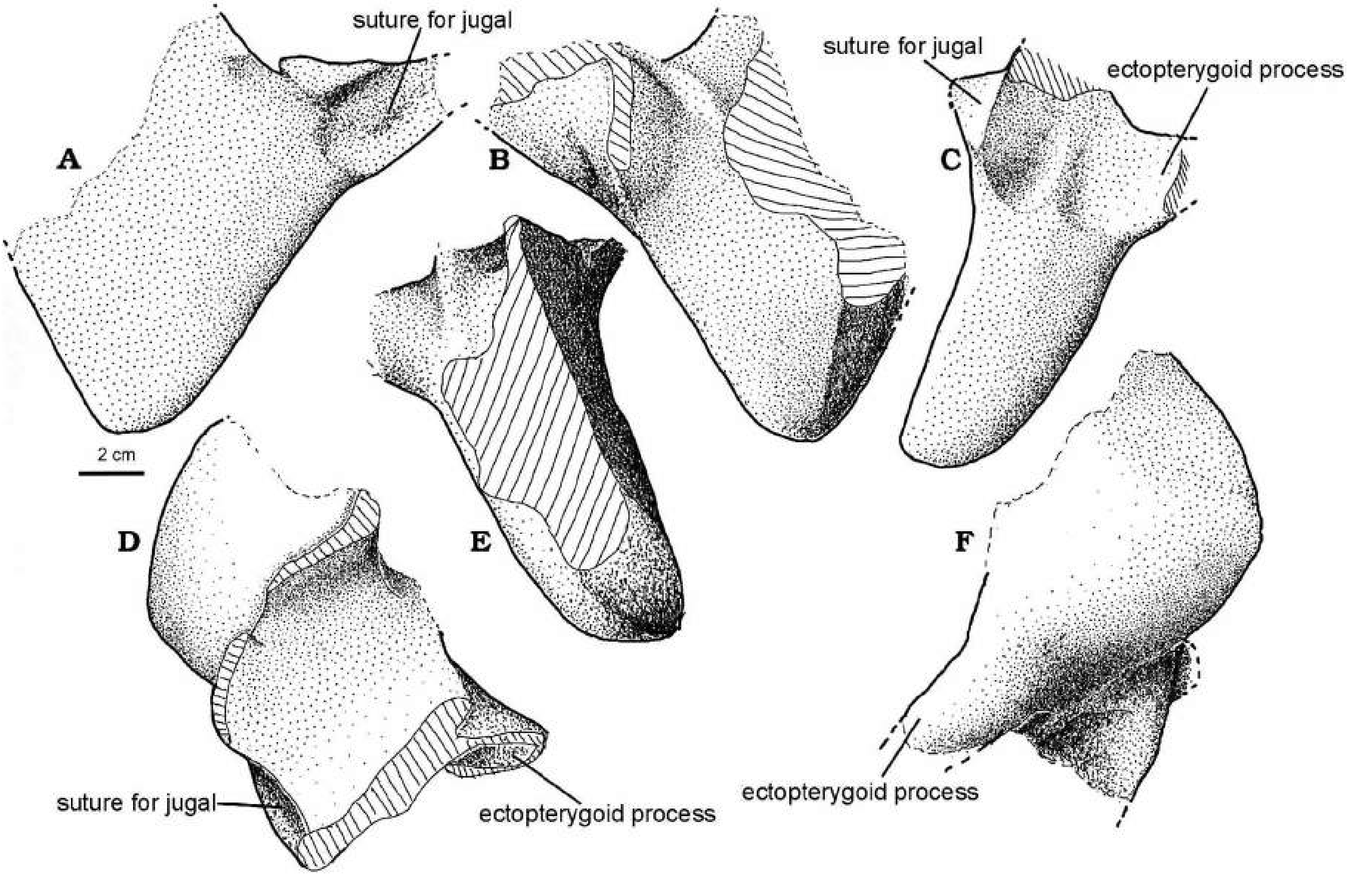

Fig. 1. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Reconstruction of left maxilla based on ZPAL V. 33/85, in lateral (A), medial (B), posterior (C), dorsal (D), anterior (E), and ventral (F) views.

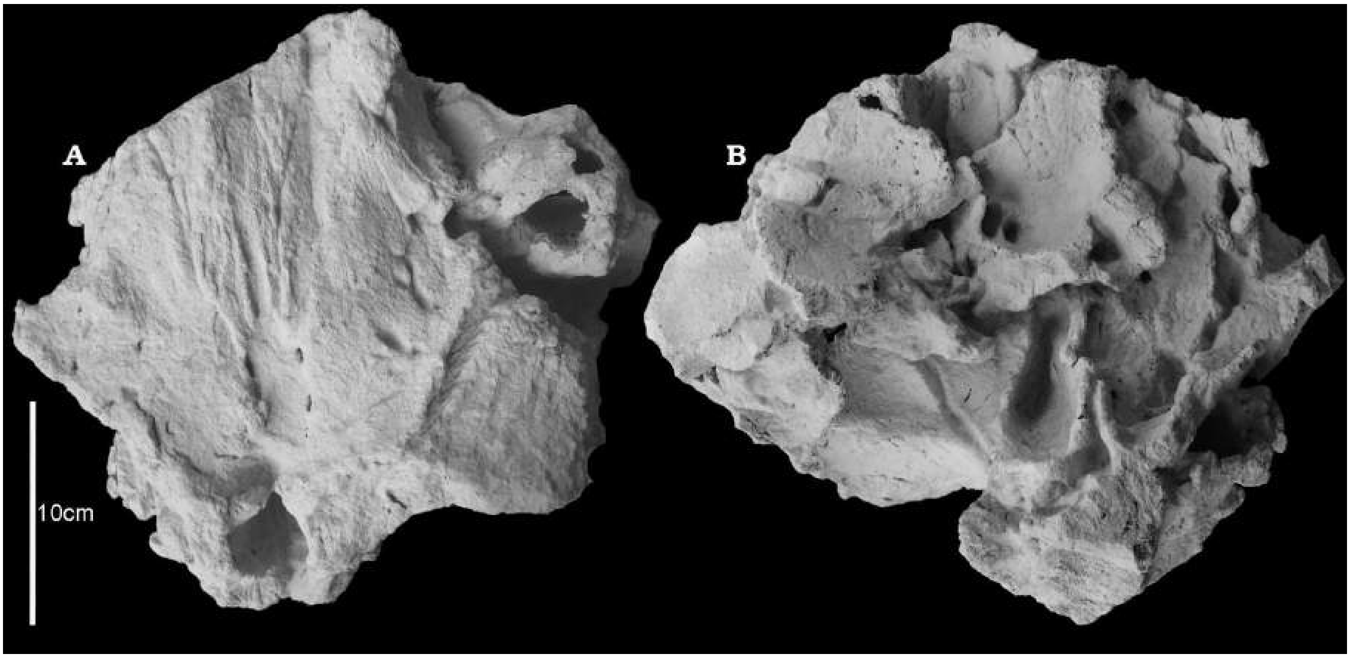

Fig. 2. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. The skull roof ZPAL V. 33/MB/18 in dorsal (A), and ventral (B), views.

The angle of the suture with the postorbital is similar in *Lisowicia bojani* and *Placerias* '*gigas*'. The margin of the orbit is two times shorter in *L. bojani* than in *P.* '*gigas*' (the skull of *L. bojani* is estimated as being almost two times larger). Unfortunately, although nine specimens of the frontal of *P.* '*gigas*' are known, they are of similar size, which prevents tracing its ontogeny.

Prefrontal: The only poorly preserved and crushed prefrontal is present in the skull roof ZPAL V. 33/MB/18 (Fig. 2). But the only recognizable aspect is that the bone is thin. Its shape remains unknown because its margins are broken.

Parietal: The parietal in ZPAL V. 33/741 is triangular in lateral view (Fig. 3), similar to that of *Placerias* '*gigas*' (Camp and Welles 1956). In dorsal view the bone is wide and has a long suture with the postorbital. The shape of the lower part of the parietal is very characteristic of *Lisowicia bojani*, *P.* '*gigas*', and *Rabidosaurus cristatus*. In all of them the bone has a pointed ventral part, with sutures (clearly visible in *P.* '*gigas*' and *R. cristatus*) probably for the supraoccipitals according to Camp and Welles (1956). The view of the braincase structure of *P.* '*gigas*' (Fig. 49) presented here is based on the revised reconstruction of the skull of *P. gigas* made by Cox (1965), a personal examination, and is different from that by Camp and Welles (1956). Accordingly, also the inclination of the supraoccipital is not so strong. The postparietal is much more extended vertically then envisioned by Camp and Welles (1956).

In *Placerias* '*gigas*' the posteroventral side of the parietal has sutures for the postparietal in the upper part and for supraoccipitals in the lower part, but in *Jachaleria candelariensis*, *Ischigualastia jenseni*, and *Stahleckeria potens*, the parietal has an elongate suture with the squamosal. It cannot be such in *Rabidosaurus cristatus*, *P.* '*gigas*', and *Lisowicia bojani* because the supraoccipital was inserted between these two bones. It forms a wall of bones between the parietal and squamosal, visible not only in the posterior side of the skull, as in most dicynodonts, but also on the anterior side. Admittedly, recognition of the sutures in large skulls is difficult. In the case of both *P.* '*gigas*' and *L. bojani* only single specimens of the bone are available.

Squamosal: The specimen ZPAL V. 33/712 is the central part of the squamosal of a rather small individual. ZPAL V. 33/746 represents a small fragment of the lateral ridge at the base of the zygomatic arch with its dorsal edge and a little of the ventral edge. Part of the lateral plate with an edge is also preserved. The specimen ZPAL V. 33/738 represents the dorsal part of the lateral wing of the right squamosal. The dorsal edge is well preserved and is slightly convex in posterior view, without any protuberances or callus, as in *Placerias* '*gigas*'. It is also similar to the condition in *Jachaleria candelariensis*.

In both specimens (ZPAL V. 33/712 and 738) the distinct prominence in the lateral area in the connection between the zygomatic arch and the lateral plate is visible. In the specimen ZPAL V. 33/721, the long ridge is visible ventral to this prominence, but it is probably a result of breaking and displacing of a part of the bone. The anterior process (zygomatic arch) is very similar to that of *Placerias* '*gigas*' (UCMP 32375). Also, the angle between the zygomatic arch and lateral plate is right (in posterodorsal view), similar to *P.* '*gigas*', but different than in *Jachaleria candelariensis*.

The specimen ZPAL V. 33/MB/17 is in one block of the rock with the central part of the squamosal, a part of the preoccipital, and the cervical vertebra. The vertical ridge is preserved on the posterior surface at the level where the squamosal is connected to the quadrate. Such a ridge has not been reported in other dicynodonts.

Postorbital: Four bones are known, three as single elements, ZPAL V. 33/1431, ZPAL V. 33/708 (Fig. 4), ZPAL V. 33/709, and ZPAL V. 33/MB/4, and one as a part of the skull roof, ZPAL V. 33/MB/18. Not one is complete. The posterior process to the parietal is unknown. It may be reconstructed (Fig. 4) based on the shape of the suture for the postorbital on the parietal, ZPAL V. 33/741. The postorbital is very massive, especially the part that contacts the frontal. In the specimen ZPAL V. 33/1431, the bone is 7 cm thick at the suture with the frontal, above the orbit. The base of the posterior process shows that it was rather wide in dorsal view. Its surface is very robust. The border of the thickening is distinct because it forms a deep groove on the lateral side of the bone.

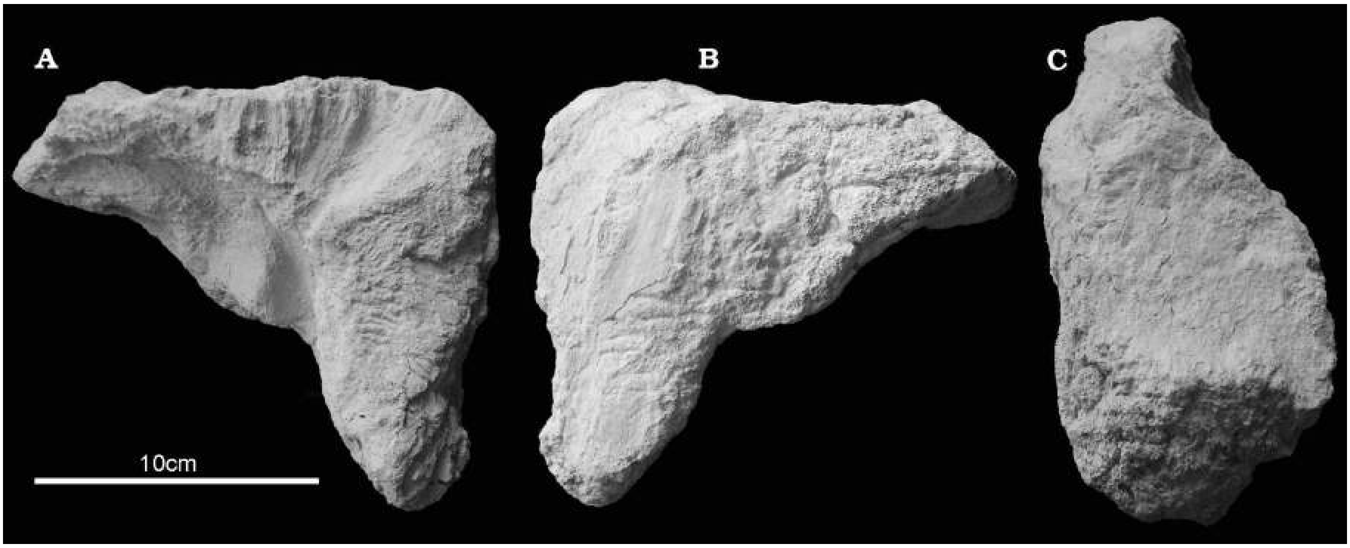

Fig. 3. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. The right parietal ZPAL V. 33/741 in lateral (A), medial (B), and dorsal (C), views.

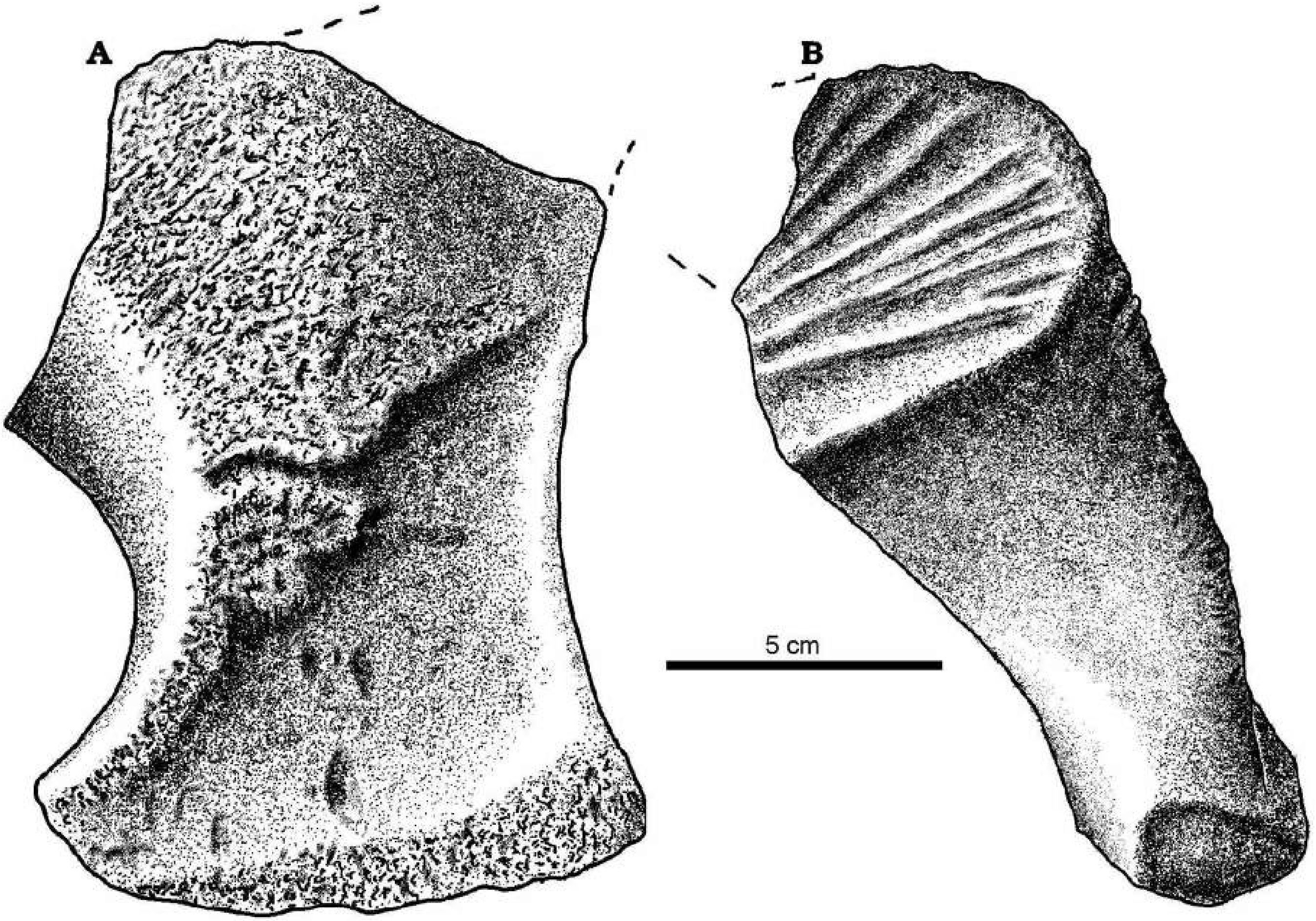

Fig. 4. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Reconstruction of left postorbital based on ZPAL V. 33/708, in lateral (A), and anterior (B) views.

The postorbital is similar to *Placerias* '*gigas*' in its robustness and the width at the level of the orbit. The only difference is that in anterior view *P.* '*gigas*' has the postorbital strongly curved, but *Lisowicia bojani* has its lateral side rather straight in anterior view. In both species the postorbital is oblique (in lateral view) posteriorly, whereas in *Ischigualastia jenseni* (based on MCZ 3119) and *Jachaleria candelariensis* it is oblique anteriorly.

Quadrate and quadratojugal: The right jaw condyles are present in two specimens, ZPAL V. 33/84 and ZPAL V. 33/735 (Fig. 5). The specimen ZPAL V. 33/739 represents the left quadrate with a visible contact area for the quadratojugal. In the specimen ZPAL V. 33/735, the quadrate is almost complete and in articulation with the posterior part of the mandible. The dorsal process is large and longer that the quadratojugal, in contrast to *Jachaleria candelariensis*, *Ischigualastia jenseni*, and *Stahleckeria potens* (in *Placerias* '*gigas*' this character is unknown). On the medial side of the process the face for the opistoticum (Cox 1959) is visible. The inferred face for the prooticum is covered by sediment. The quadrate (or quadrato-jugal) foramen is clearly visible in the same place as that illustrated by, for example, Efremov (1940), Cox (1959), and Tatarinov (1965), but contrary to Damiani *et al.* (2007), who were misled by a part of the quadrate–quadratojugal suture identified as the real quadrate foramen.

The anterior massive process of the quadrate for contact with the pterygoid is clearly visible in the specimen ZPAL V. 33/84. Also, the articulation area with the stapes is well preserved. It is concave in posterior view and convex in ventral view. According to Camp and Welles (1956), the extrastapedial groove in *Placerias* '*gigas*' is located dorsal to the surface for the stapes, but it is not visible or, probably, was misinterpreted by them. The pterygoid pit described by Camp (1956) for *P.* '*gigas*' is also not visible in *Lisowicia bojani*. According to Cox (1965), at the base of the quadratojugal there should be a notch for the tympanicum, but this region is preserved only in ZPAL V. 33/735 with a quality of preservation that enables recognition of this structure.

Lisowicia bojani has a unique shape of the articulation surface of the quadrate. The medial ridge has only one surface (Fig. 5). In cross-section it is visible as slightly curved (ZPAL V. 33/84) or straight (ZPAL V. 33/735). In *Kannemeyeria simocephalus* (NHM R3739) the surfaces of the medial ridge are perpendicular in cross-section (or in posterior view), and the lateral ridge is slightly curved. In *Jachaleria candelariensis* both ridges are similarly slightly curved (Vega-Dias and Schultz 2004: fig. 4), but the medial one is larger (Vega-Dias and Schultz 2004: fig. 2), whereas in *K. simocephalus* the lateral is larger. *Stahleckeria potens* and *Placerias* '*gigas*' have this articulation surface, as in *K. simocephalus*. Damiani *et al.* (2007) incorrectly show the quadrate foramen in place of the quadrate–quadratojugal suture. It

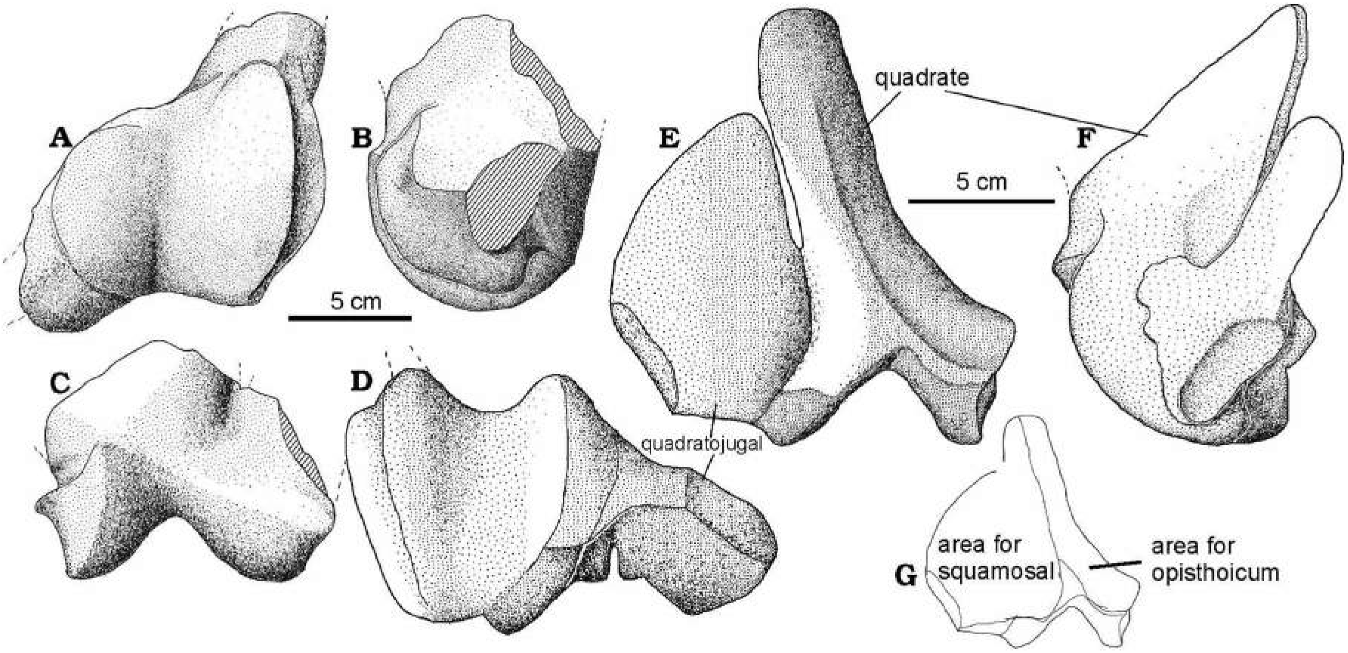

Fig. 5. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Reconstruction of quadrate and quadratojugal based on right ZPAL V. 33/84 (A–C) and left ZPAL V. 33/735 (D–G), respectively, in ventral (A, D), lateral (B, F), posterodorsal (C), and posterior (E), views. G, scheme with labelled area for other bones.

is not clearly visible in *L. bojani*, but the small pit may be interpreted as a remnant of this foramen.

Lacrimal: ZPAL V. 33/717 is an almost complete left lacrimal. The bone is very similar to the lacrimal of *Stahleckeria potens*, as illustrated by Camp and Welles (1956: fig. 46). It is robust in the posterior part (the face for jugal is very thick). Also, the lateral side is robust, but its anterior part is broken. The dorsal side is smooth and wide; the foramen for the lacrimal canal is not preserved. The dorsal and lateral sides become thin in the anterior part and set at a right angle to each other.

Pterygoid: ZPAL V. 33/730 is a rather problematic fragment of the pterygoid with only the ventral margin and lateral side preserved. The medial side is preserved only in the posterior part. The ventral edge is strongly concave in lateral view. The posterior part has the shape of a narrow ridge. It is very thick, and the medial part is massive.

Braincase

Pieces of various individual braincases are represented by ZPAL V. 33/MB/3, ZPAL V. 33/531, ZPAL V. 33/711 (with occipital condyle), and ZPAL V. 33/710 (basioccipital). Most of the bones building the braincase are well ossified and massive (Figs 6, 7). The basioccipital is strongly co-ossified with the exoccipital, and the suture between them is not visible. The suture between the basisphenoid–parasphenoid and the basioccipital–basisphenoid is a little posterior to the anterior edge of the tuberosity, as in *Placerias* '*gigas*'. In *Stahleckeria potens* its position is more anterior (Camp and Welles 1956: figs 51, 52). The anterior edge of the basisphenoid under the opening of the VII nerve is very different than that illustrated for *P.* '*gigas*', *S. potens*, and *Kannemeyeria simocephalus* by Camp and Welles (1956). In the specimen ZPAL V. 33/531, the hypophyseal fossa is clearly visible (Fig. 6). In its upper part are foramina for the VI nerve, described as for the VII nerve by Camp and Welles (1956: figs 20, 50, 51). In the ventral part of the hypophyseal fossa two foramina are visible, and they are the entrances of canals ending on the ventral side of the basisphenoid. They are not visible in *P.* '*gigas*'(Camp and Welles 1956: fig 19). Vega-Dias and Schultz (2004) described them as the carotid foramina. The surface of the bottom of the canal for the spinal cord is straight in lateral view (in cross-section), whereas in *S. potens* and *P.* '*gigas*' it curved down frontally at the place where the opening for the X, XI nerves occurs (Camp and Welles 1956: figs 52, 51). Such a curve is also clearly visible in the specimen P-25781 identified by Lucas and Hunt (1993) as *Ischigualastia jenseni*? but by Kammerer *et al.* (2013) as Stahleckeriidae indet..

The ridge between openings for the vestibule in the bottom of braincase is very delicate, especially in the *Placerias* '*gigas*' specimen UCMP 2417 it is very distinct, and the openings are very close to each other. The morphology of braincases of *P.* '*gigas*' in the Berkeley University collection is enormously variable. Camp and Welles (1956: fig 19) showed the ventral side of the basisphenoid with almost all of the area covered by pterygoid and vomer, whereas in *Lisowicia bojani* almost all of the ventral area of the basisphenoid is flat.

The occipital condyle is almost complete in ZPAL V. 33/711, but its posterior surface is broken. The ventral part of the condyle curves anteriorly as in *Placerias* '*gigas*' and *Ischigualastia jenseni*. The ventral part of the condyle was very large and played an important role during skewing the head down.

The most detailed analysis of the braincases of dicynodonts was made be Surkov and Benton (2004). Unfortunately, only one character that differentiated Triassic dicynodonts (nr 8. high dorsum sella) can be identified in *Lisowicia bojani*, and its state is similar to *Placerias* '*gigas*'.

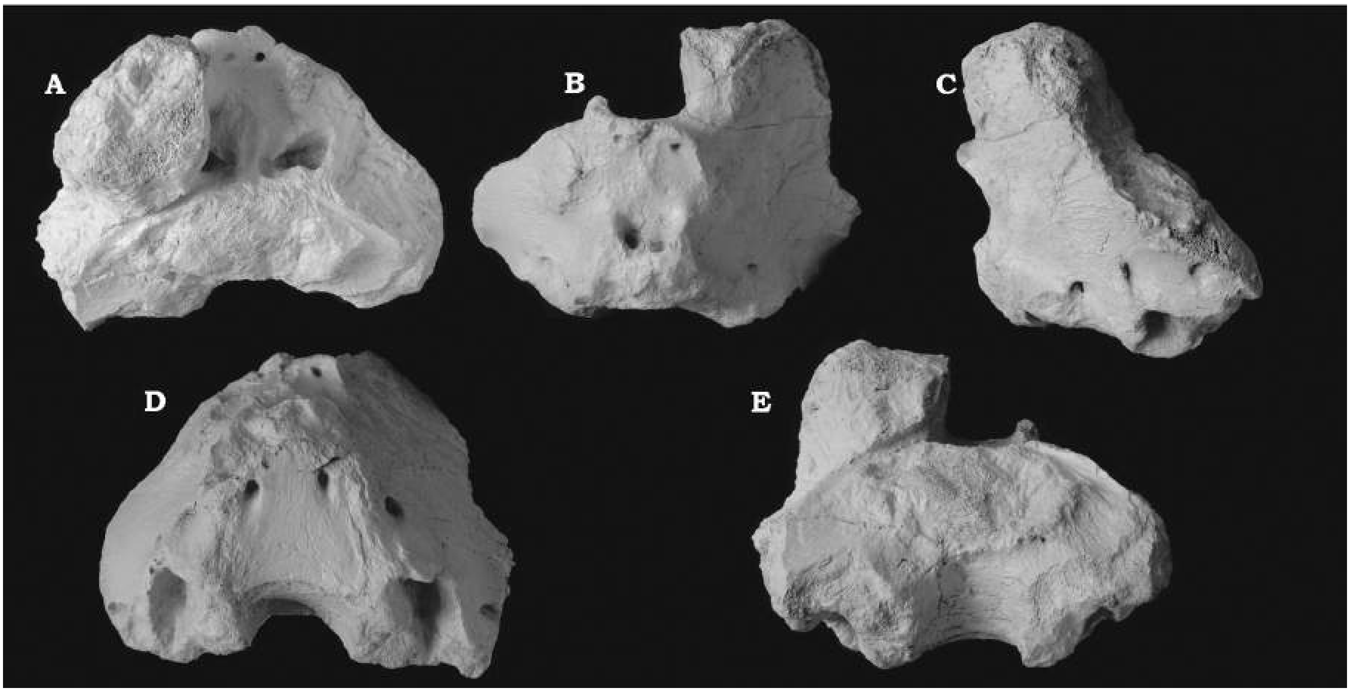

Fig. 6. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Braincase ZPAL V. 33/531 in dorsal (A), anterior (B), lateral (C), and ventral (D), posterior (E) views.

Sphenoid: The specimen ZPAL V. 33/755 is the septosphenoid according to Camp and Welles (1956), but the ethmoid according to Castanhina *et al.* (2013). The bone is almost complete, only the ventral and anterior tips and ventral part of the right side are damaged. The element is triangular in lateral view, with the base of the triangle sutured to the frontal. These sutures are very distinct, with radial ridges in the posterior rectangular part and large prominence in the central part. Between sutures for the left and right frontal is a deep groove identified by Camp and Welles (1956) as the olfactory tract canal. At the posterior end of that groove there are two (left and right) distinct processes, probably the same, which Camp and Welles (1956) described as the frontosphenoid. The posteroventral side consists of the lateral thick ridge and a central wide trough. The edge was probably originally sharp but is damaged. No known dicynodont had a similar septosphenoid. Based on the proportions of size in *Stahleckeria potens*, the whole skull was 1.1 m long.

Stapes: Two specimens of the left stapes were found. In ZPAL V. 33/743, only the dorsal process is complete, and the extrastapedial process (Cox 1959) is broken. Also, the ZPAL V. 33/MB/16 stapes has only dorsal and anterior sides clearly visible (Fig. 8); the dorsal process is broken. Its morphology is very similar to that of *Placerias* '*gigas*'.

Opisthotic: Probably the right opisthotic is partly preserved in ZPAL V. 33/657. A suture for the squamosal on its anterior side has radiated ridges. The suture with the supraoccipitale is badly preserved. The anterior surface is smooth and concave in dorsal view, almost identical in the shape of its anterior side as in the *Stahleckeria potens* skull fragment described by Romer and Price (1944).

Mandible

The mandible is known only from its posterior part.

Surangular: It is preserved in two specimens ZPAL V. 33/735 (right) and ZPAL V. 33/736 (left). This is an almost flat element; its articulation is clearly visible. The most striking aspect is the large angle between dorsal and ventral edges that is clearly visible on the lateral side (Fig. 8). The dorsal edge forms a distinct structure clearly visible in lateral view in front of the articular as in *Angonisaurus cruickshanki* Cox and Li, 1983 and *Woznikella triradiata* specimen ZPAL V.34/4 (Szczygielski and Sulej 2023). It resembles the hamate process of temnospondyls. In medial view the deep surangular is visible above the prearticular, and there is a narrow fenestra between these bones. The latter forms a straight border of a rectangular fenestra for the Meckelian cartilage. In the specimen ZPAL V. 33/736, the mandibular fenestra (Maisch 2003) is partly preserved.

Angular: The angular is represented by four specimens: the almost complete ZPAL V. 33/723 (left), anterior part in ZPAL V. 33/735 (right), posterior part in ZPAL V. 33/737 (left), and anterior and medial parts in ZPAL V. 33/745 (left). The small specimen ZPAL V. 33/723 is 4.6 cm in height in its middle narrow part, whereas the largest ZPAL V. 33/745 is around 9 cm in height (the dorsal edge is broken). The bone is very similar to that of *Ischigualastia jenseni* and *Stahleckeria potens* in its strongly concave central ventral edge, unlike *Placerias* '*gigas*'. In the specimen ZPAL V. 33/737, a distinct angular fossa (Camp and Welles 1956) is present. In ZPAL V. 33/735, the suture with the dentary is visible (Fig. 9), and a shelf occurs ventral to the suture with the dentary, as in *I. jenseni* and *S. potens*. The reflected lamina was very small in early dicynodonts, but the stage represented by *Lisowicia* is most similar to the dinocephalian therapsids (Kuhn

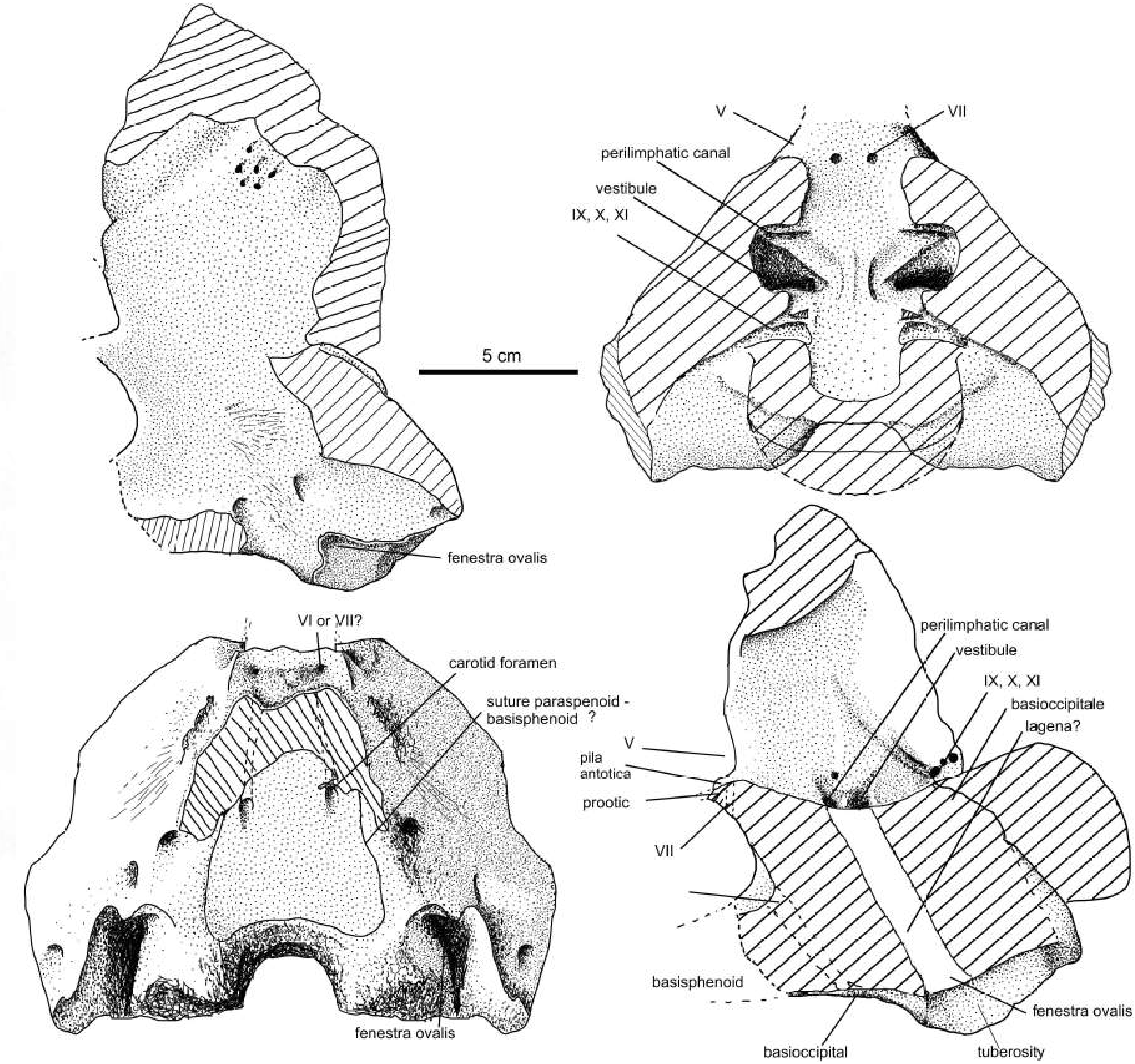

Fig. 7. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Reconstruction of braincase based on ZPAL V. 33/531 and ZPAL V. 33/711, in lateral (A), dorsal (B), ventral (C), and medial (D) views.

1971 after Boonstra 1963), which have a small fenestra above the angular, like *Lisowicia bojani*.

Prearticular: Two specimens, ZPAL V. 33/735 and ZPAL V. 33/736, are represented. The bone is very wide. In most dicynodonts it has dorsal and ventral edges parallel, but in *Lisowicia bojani* the prearticular edges extend dorsally and ventrally toward the front of the bone (Fig. 9). It has a concave central edge and rectangular fenestra visible in both specimens in lateral view. This is probably the fenestra for Meckelian cartilage (Cox 1959). Between the dorsal edge and the surangular the adductorial fossa (Maisch 2003) is visible.

The retroarticular process is very short and set strongly anteriorly with respect to the articulation. A shorter retroarticular is known only in *Woznikella triradiata*, but it does not extend to the front of the mandible (Szczygielski and Sulej 2023).

Articular: Two specimens, ZPAL V. 33/735 and ZPAL V. 33/736, are represented. The articular is situated much above the surangular, as in *Sinokannemeyeria*. Perhaps a similar disposition is also seen in *Dinodontosaurus brevirostris*. Crompton and Hotton (1967) described the condyle recess in the anterior dorsal part of the articular. It is visible in the mandibles of *Kannemeyeria simocephalus* (Camp 1956: fig. 43a), but it does not occur in *Lisowicia bojani*. The unique shape of the articulation surface of the quadrate does not reflect on the articulation surface on the articular.

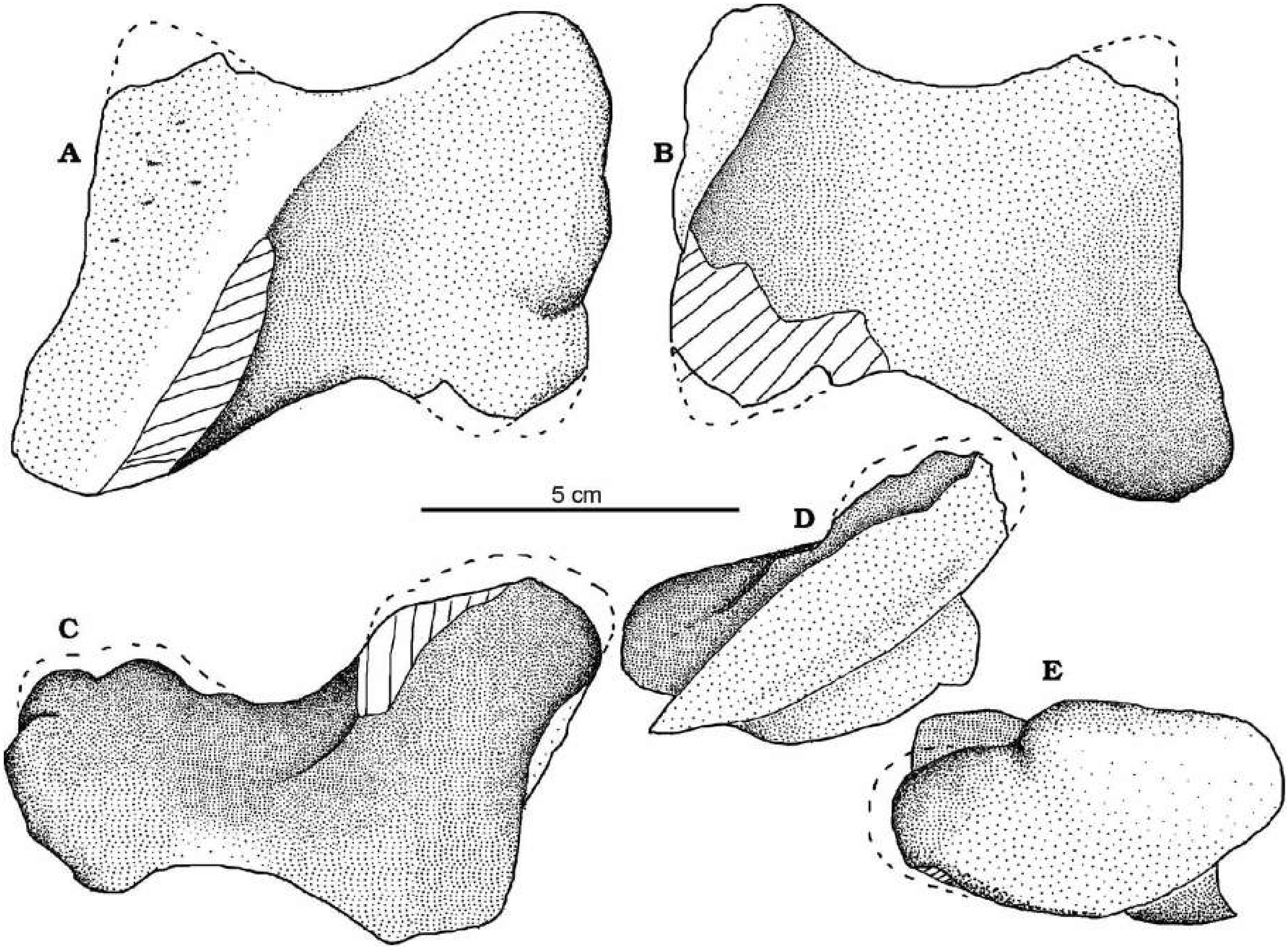

Fig. 8. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Reconstruction of left stapes based on ZPAL V. 33/743, in dorsal (A), ventral (B), anterior (C), lateral (D), and medial (E) views.

Axial skeleton

The description of the vertebrae is based mainly on the elements that originated from a bone accumulation from one individual, ZPAL V. 33/720. The vertebrae are well preserved and almost complete. In most of them, tips of the spinous processes are broken or bitten. A few broken parts can be fitted together. The number of vertebrae is the same as in the articulated specimen of *Sinokannemeyeria yingchiaoensis* (IVPP/V. 974; Sun 1963). Some general patterns in morphology along the vertebral spine are recognized. The prezygapophyses are oblique and short in the cervical vertebrae and flat in dorsal ones. In the last known dorsal (16) they are oblique and very long. The spinous processes are thicker and longer up to the 16th vertebra.

Most characteristic is the low height of the neural arches of the cervical vertebrae, especially in comparison to the dorsal ones. Such large differences were not noticed in other dicynodonts and probably relate to the large size of the animal. Similar differences are present among the present-day elephants and rhinoceroses. Another difference between the cervical and dorsal vertebrae is in the size of their centra. The cervical centra are of a large diameter, whereas they are much smaller in the dorsal vertebrae, but, for instance, in the theropod *Tarbosaurus bataar* Maleev, 1955 the gradient is reversed. In fact, very short centra of cervical vertebrae are typical of large dicynodonts (personal observation).

Proatlas: The intercentrum of the proatlas is poorly preserved in the specimen ZPAL V. 33/767 and is very similar to that of *Placerias* '*gigas*'. It is very low and has a crescent shape in anterior view. The three neural arches of the atlas are known from the accumulation ZPAL V. 33/720, specimen ZPAL V. 33/742, and ZPAL V. 33/750. The contact area for the occipital condyle and the axis are distinctive and merge into one surface (Fig. 10). Both the dorsal and ventral processes are flat and thick. They have a generalized construction; their lateral side is almost flat, and they are slightly directed posteriorly. This basic form is different with respect to the shape of the neural arch of the atlas of *Woznikella triradiata*, in which the process shape is very complex.

Atlas–axis complex: The atlas–axis complex from individual ZPAL V. 33/720 (accumulation) is well preserved (Figs 11, 12), only the tip of the spinous process is broken. In the specimen ZPAL V. 33/751, the centrum of the atlas–axis complex is broken. In general shape it is like that in other dicynodonts.

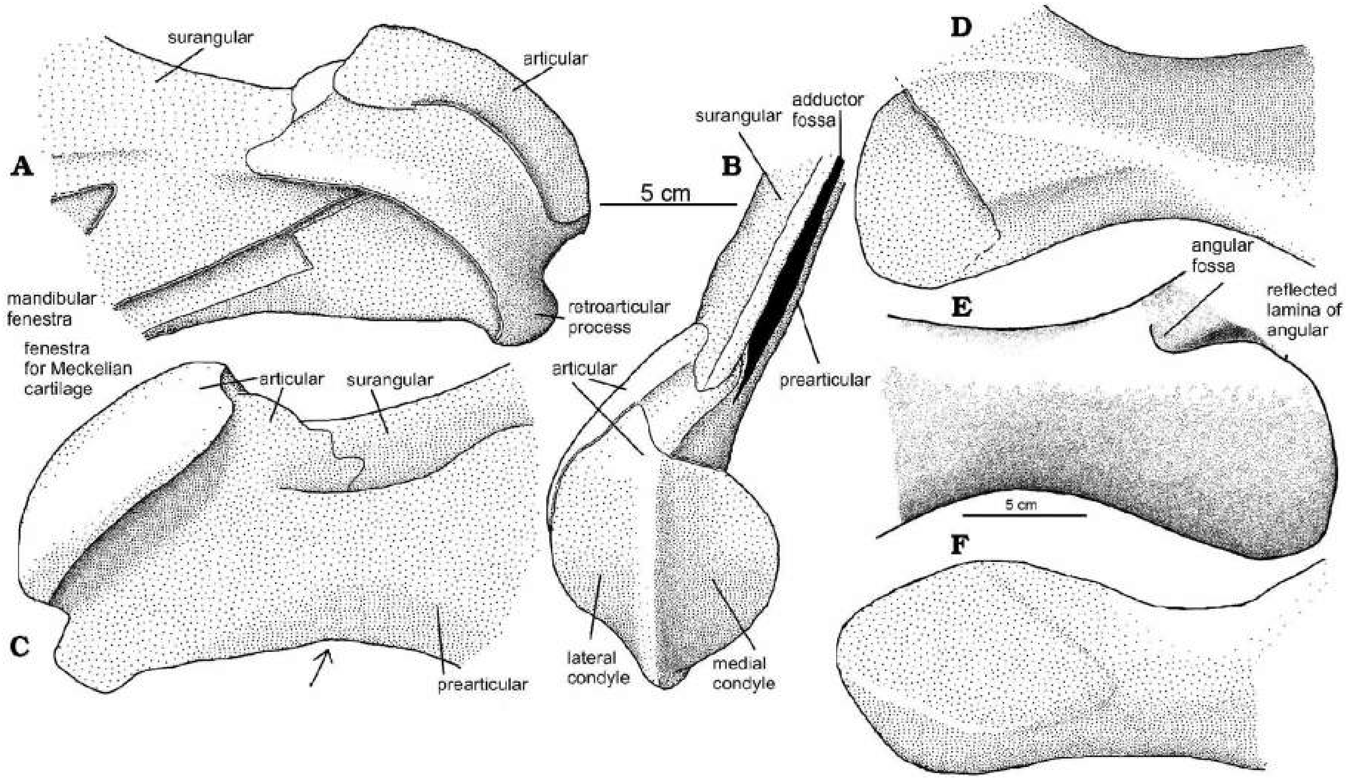

Fig. 9. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019, from Lisowice-Lipie Śląskie. Reconstruction of mandible bones based on ZPAL V. 33/736 (A–C), ZPAL V. 33/737 (angular D, E), and ZPAL V. 33/735 (F), respectively, in lateral (A, E, F), dorsal (B), and medial (C, D) views.

The anterior articulation surface consists of three areas of similar size. The middle one is for contact with the atlas, and dorsolateral to it are areas for the neural arch of the atlas. Small processes are developed laterally. The posterior articulation surface has a triangular lower part.

Third or fourth vertebrae: Their centra are very short, and their anterior sides are almost round, whereas the posterior ones have a sharp ventral edge (Fig. 13). The parapophysis is small, and its position is very low. The openings for arteries are visible on the lateral side. The transverse process is vertical and low. Its end is not preserved. Parts of the neural arch are preserved also as the specimens ZPAL V. 33/656 and ZPAL V. 33/655. The spinous process is very short and narrow, although at the level of zygapophysis it becomes very wide, more than in the dorsal vertebrae. In lateral view the prezygapophyses and postzygapophyses are very close to each other. The prezygapophyses form a slope in their frontal part (where the centrum is in vertical position). It suggests that the neck was curved slightly dorsally, as in the juvenile *Dinodontosaurus brevirostris* reconstructed by Morato (2006: fig. 32).

Fourth or fifth vertebrae: The centrum is a little longer than in the third vertebra. It has its anterior and posterior sides in the shape of a horizontally flattened oval (Fig. 14). The parapophysis is large and in a slightly higher position than in the previous vertebra. The opening for arteries is visible on the lateral side. The whole transverse process is known, and it is large and vertical in lateral view with a straight anterior side. On its posterior side a distinctive ventral pit occurs. The zygapophyses are almost at the same level. The spinous process is broken.

The ventral side of the centrum is of variable shape, in the V. 33/MB/22 and V. 33/720 specimens it is a normal concave surface, but in the middle of specimen V. 33/MB/17 a distinct vertical keel occurs.

Fifth and sixth vertebrae: In the specimen ZPAL V. 33/MB/22, the cervical vertebrae (fourth to sixth) are preserved almost in articulation with the proximal part of the fifth and sixth ribs. The vertebrae are compacted dorsoventrally (based on comparison with the not compressed fourth cervical vertebrae in V. 33/720). In the fifth vertebra the parapophysis is very large, and in the next vertebra it merges with the transverse process, which has a very massive dorsal part. It is enormously wide in lateral view, which is probably an adaptation to the large size of the animal. A horizontal ridge occurs on the dorsal edge on the anterior side of the transverse process in the sixth vertebra. In the next vertebra it is larger and vanishes in the 10th vertebrae. The spinous processes are unknown. Only the posterior part for the fifth vertebra with the postzygapophysis is preserved.

Seventh vertebra: The centrum anterior and posterior sides are in the shape of a vertical oval with a flat dorsal edge (Figs 15, 16). The parapophysis merges with the transverse process so strongly that its border is not visible. The parapophysis is narrower than in the sixth vertebra. The transverse process has distinct anterior and posterior ledges on its dorsal edge, which in anterior view is almost horizontal. The vertical ridge running from the centrum dorsolaterally is visible on the posterior side of the transverse

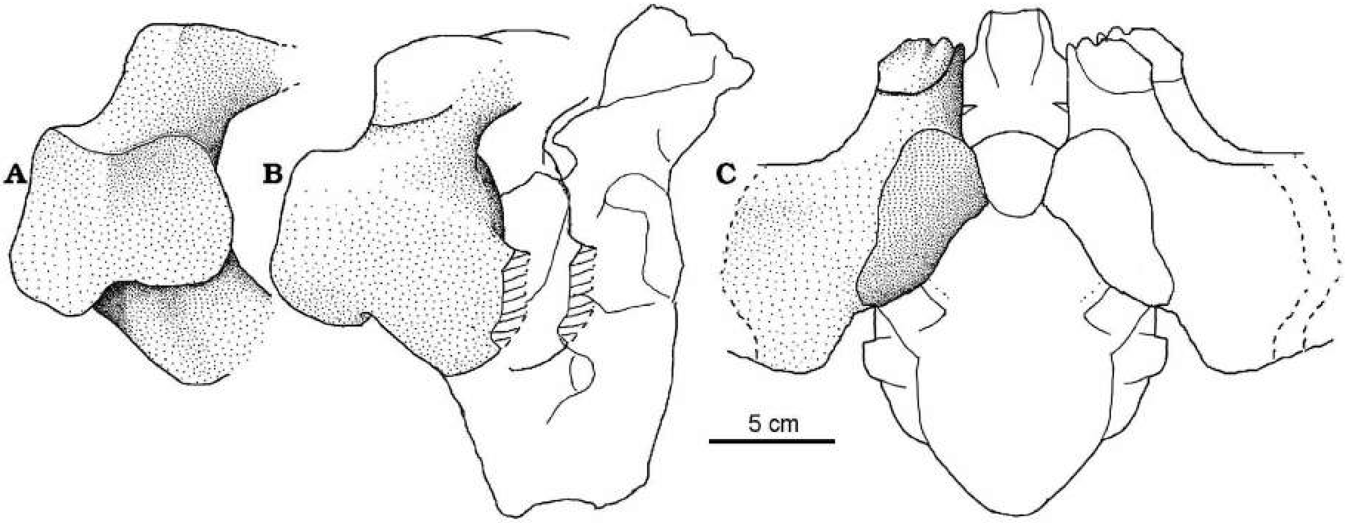

Fig. 10. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Reconstruction of left atlas neural arch based on ZPAL V. 33/720 and on ZPAL V. 33/742, in medial (A), lateral (B), and anterior (C) views. Axis as line drawing in background.

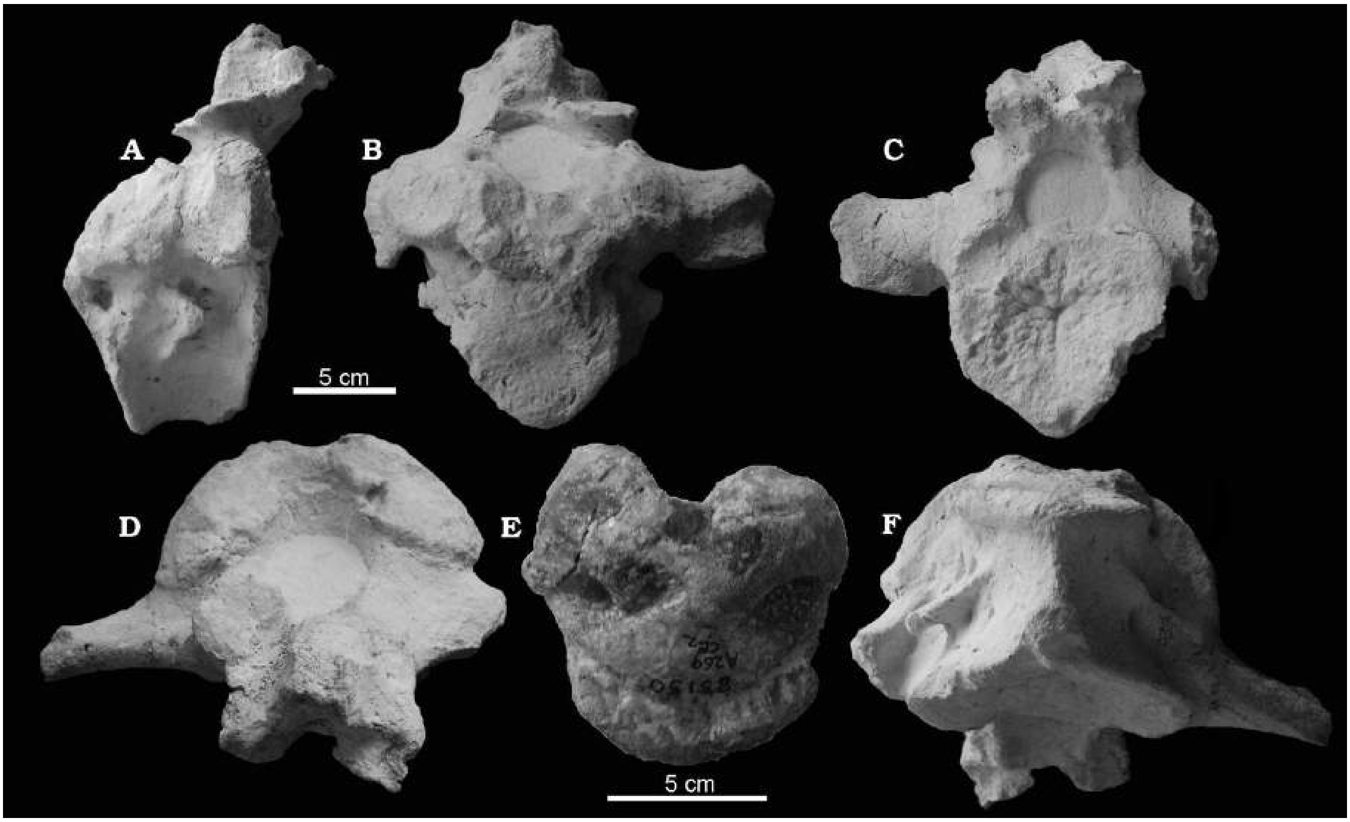

Fig. 11. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Axis ZPAL V. 33/720, in lateral (A), anterior (B), posterior (C), dorsal (D), and ventral (F) views. E, atlas of *Placerias* '*gigas*' from MCZ in anterior view.

process. In the next vertebra it becomes more distinct and more vertical. The spinous process is very narrow in anterior view and wide in lateral view.

Dorsal vertebrae: Dorsal vertebrae (from the middle part of the dorsal section) are well preserved (although the spinous processes are incomplete). The dorsal part of the transverse process is longer (in anterior view) than in *Stahleckeria potens*, and the plane of contact with the rib is more oblique (in anterior view) than in that species. The dorsal vertebrae of *Lisowicia bojani* have united articulation surfaces for the ribs (diapophysis and parapophysis) in contrast to *Placerias* '*gigas*' and *Woznikella triradiata* (Szczygielski and Sulej 2023) in which they are always separated.

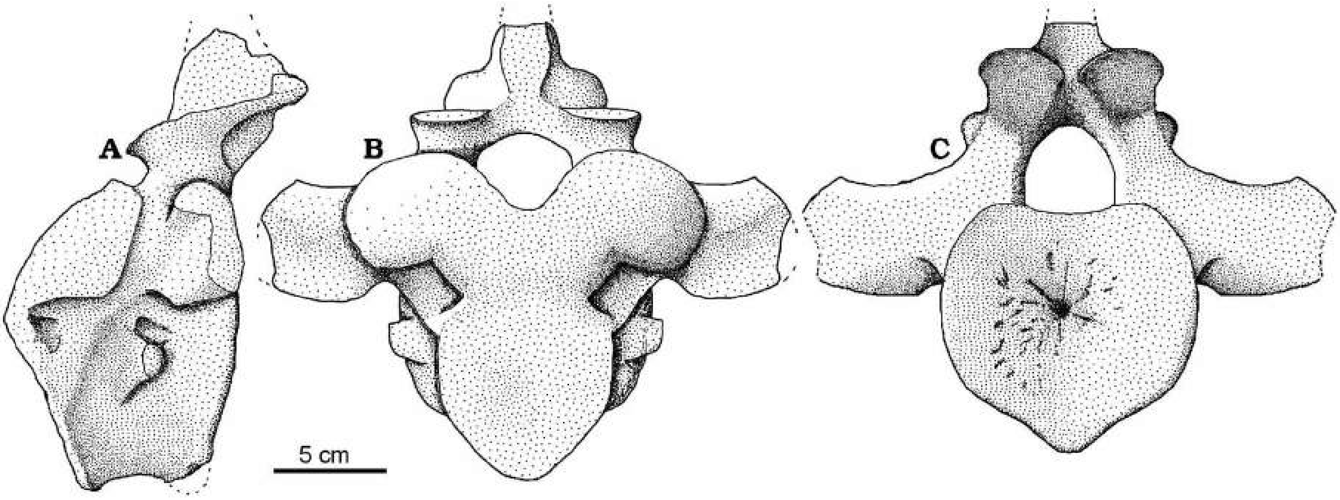

Fig. 12. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Reconstruction of axis based on ZPAL V. 33/720, in lateral (A), anterior (B), and posterior (C) views.

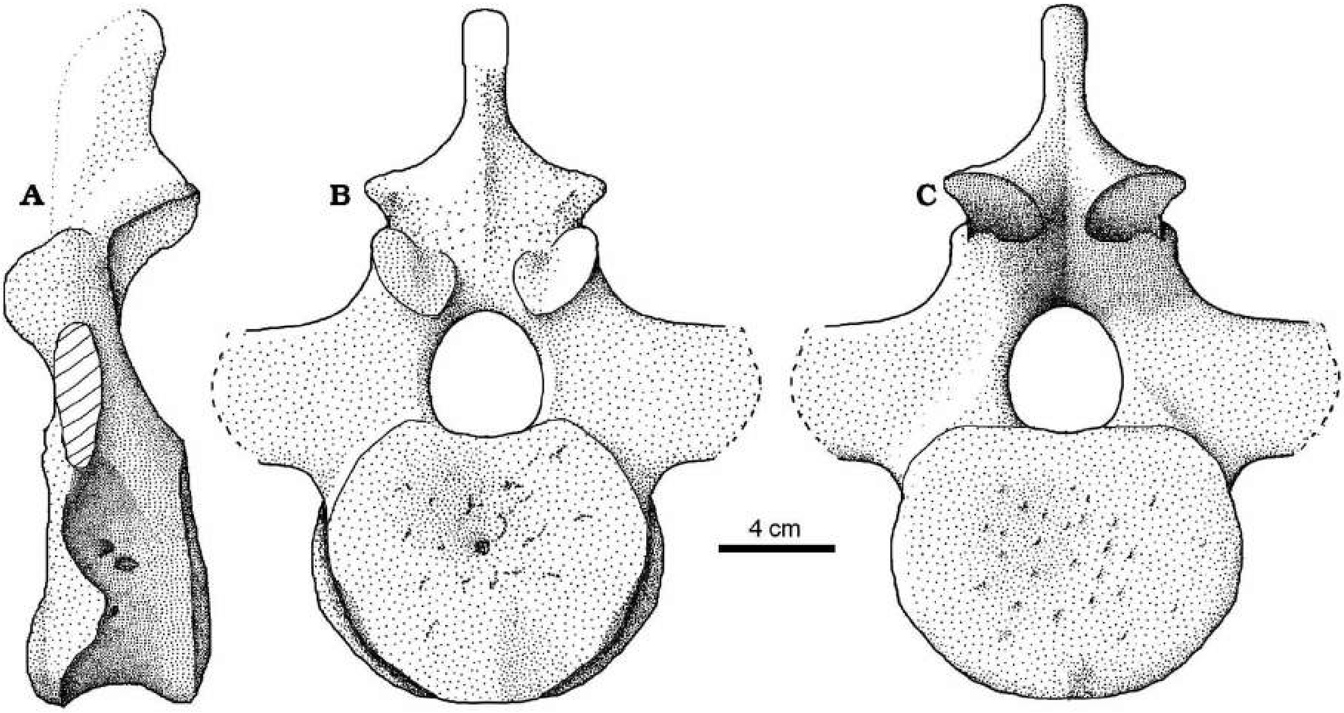

Fig. 13. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Reconstruction of cervical vertebra (third or fourth) based on ZPAL V. 33/720, in lateral (A), anterior (B), and posterior (C), views.

Vertebrae 13 and 14: The centrum is elongated vertically in posterior view (Figs 17, 18). A groove in the shape of a reversed horseshoe is visible on its anterior side (it occurs in vertebrae from the seventh to the 15th and probably further). On the posterior side is a single central pit. The parapophysis has a very high position (just under the prezygapophysis). It slopes posteriorly and narrows dorsally. Its anterior side is folded down anteriorly so its surface is visible in anterior view. The diapophysis is horizontally flattened (in lateral view) and directed posteriorly. In front of the postzygapophysis is the vertical blade in the midline of the vertebra, which in lateral view forms a step. The spinous process has a wider dorsal part (in anterior view). The most unique feature of the vertebrae from this region is the ridge on the spinous process, which runs from the transverse process far dorsally on the spinous process.

Vertebrae 15-17: The centrum is similar to that of vertebrae 12 and 13. The merged parapophysis and diapophysis are more slightly sloped than in vertebrae 13 and 14. The parapophysis is visible in anterior view, but the diapophysis is directed laterally (Figs 17, 19). The spinous process is very thick in anterior view but narrow in lateral view. At its top a massive 'mace'-like expansion is developed. It is strongly sloped posteriorly. A similar slope

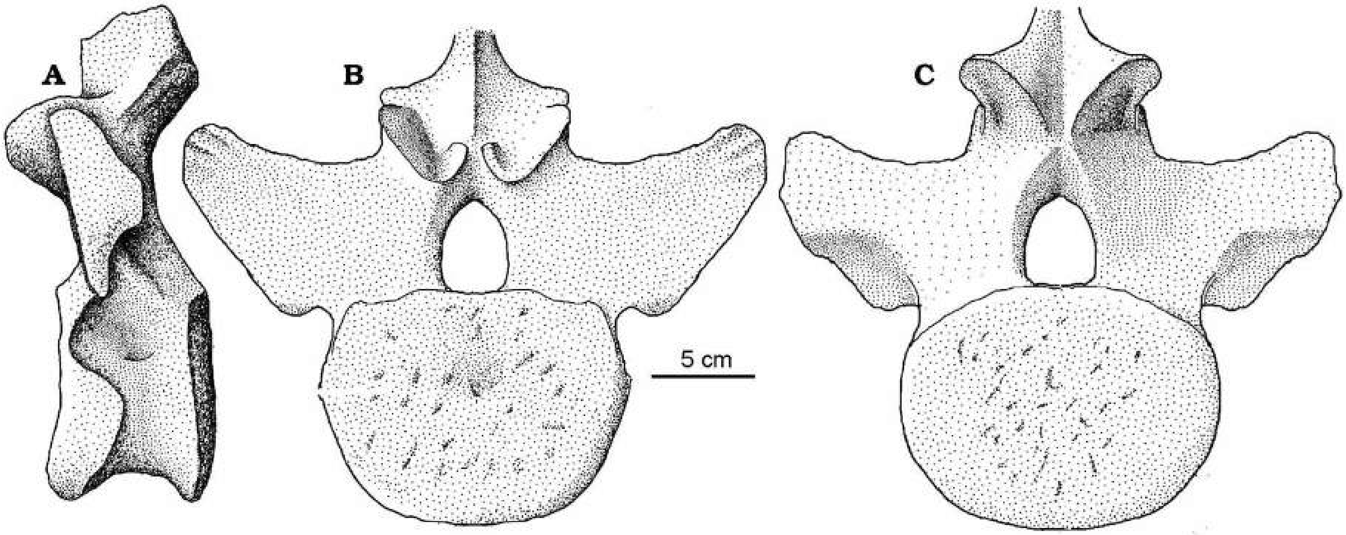

Fig. 14. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Reconstruction of cervical vertebra (fourth or fifth) based on ZPAL V. 33/720, in lateral (A), anterior (B), and posterior (C), views.

is present in *Sinokannemeyeria* and in the present-day elephant. The living hippo and rhinoceros do not possess such a character.

The vertebrae 18-25 are not present in the available fossil material.

Sacral vertebrae: The sacral vertebrae (Figs 20, 21) are represented in two individuals (ZPAL V. 33/720 and ZPAL V. 33/83); in both, the four vertebrae and ribs are in an articulated position and in both the spinous processes are broken. The better-preserved specimen ZPAL V. 33/720 comes from the large accumulation of *Lisowicia* bones. The three sacral vertebrae are articulated together with their ribs and with one vertebra in front of them. This presacral vertebra has an articulation for the rib, which is much higher than in the sacral vertebrae. Probably it is the last lumbar vertebra. The total number of four sacral ribs is inferred from traces for them on the ilium from the same accumulation. The fourth sacral vertebra is not present. Its transverse process corresponds to a small fourth trace on the ilium.

The centrum of the last lumbar vertebra and the first sacral are high and wide, and they are rectangular in anterior view. The next centra are lower, so the last one is almost half of the height of the first one. They are also narrower. A distinct ridge occurs on the ventral side of the third centrum. It probably had a triangular posterior surface, but it is broken. The joint for the articulation of the ribs has a complex shape. The ventral part of the 26th vertebra is curved anteriorly. The first sacral vertebra has a large vertical surface for the rib articulation, which is wider ventrally and extends to the ventral border of the centrum. The second vertebra has this surface even longer and wider ventrally, with a very narrow dorsal part. In the third sacral vertebra the surface for the rib is curved posteriorly in its ventral part. The fourth sacral vertebra has a wide and low transverse process that is fused with the sacral rib. The alternative is that *Lisowicia* had only three sacral ribs, and the fourth rib is truly the first caudal.

In *Stahleckeria potens* and *Rhadiodromus klimovi* eight sacral vertebrae are fused, have a ventral keel, and their spinous processes are very low and located above the connection with the centra.

Caudal vertebrae 30 and 31: It is not clear if the 30th vertebra was a part of the sacrum or not. Here it is referred to as the first caudal vertebra (Fig. 22) because it is too low to belong to the sacrum. Two caudal vertebrae were found in the large bone accumulation. They have elongated centra with a triangular cross-section. It is difficult to decide which of them was closer to the skull; probably the one with the larger vertebral foramen. The surface of articulation in this vertebra is V-shaped. The transverse process is large and flat in one vertebra and thick in the other. The elongated foramina occur on the centrum at the base of the transverse process. The prezygapophyses are very elongated. The small size of the caudal vertebrae compared to the first sacral suggests that the tail was very short, as in present-day elephants. Similar caudal vertebrae are not known in other dicynodonts.

Ribs

The ribs are poorly preserved. Most of them are broken (Fig. 23). Only the middle parts of the shaft are often collected. But, a few of the almost complete ribs are represented and they show variability in their shapes [similar to '*Dicynodon trigonocephalus*' Broom, 1940; Kammerer *et al.* (2011) and Kammerer (2019)]. Generally, two kinds of ribs can be distinguished. The cervical and pectoral ribs are flat and very wide in anterior view, whereas the lumbar ribs are almost round in cross-section. The sacral ribs are short and high in anterior view.

Cervical ribs: The anterior cervical ribs are not known. In the specimen V. 33/MB/22 the cervical vertebrae four to six are preserved almost in articulation with the proximal parts of the fifth and sixth ribs. The ribs are very wide in anterior view (Fig. 24), and their two heads can be distinguished. They probably were in the region of the pectoral cage covered with the scapula. This means that the neck was very short.

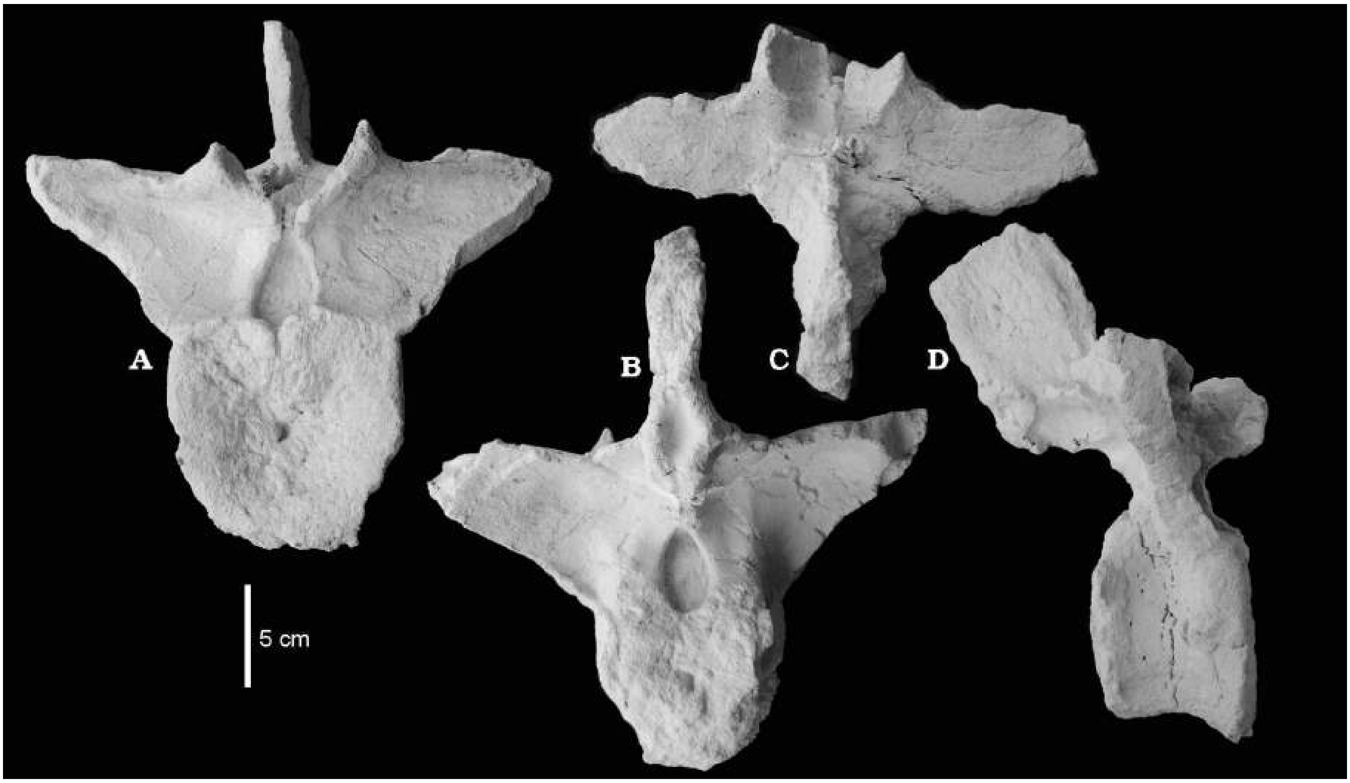

Fig. 15. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Cervical vertebra (seventh?) ZPAL V. 33/720, in anterior (A), posterior (B), dorsal (C), and lateral (D) views.

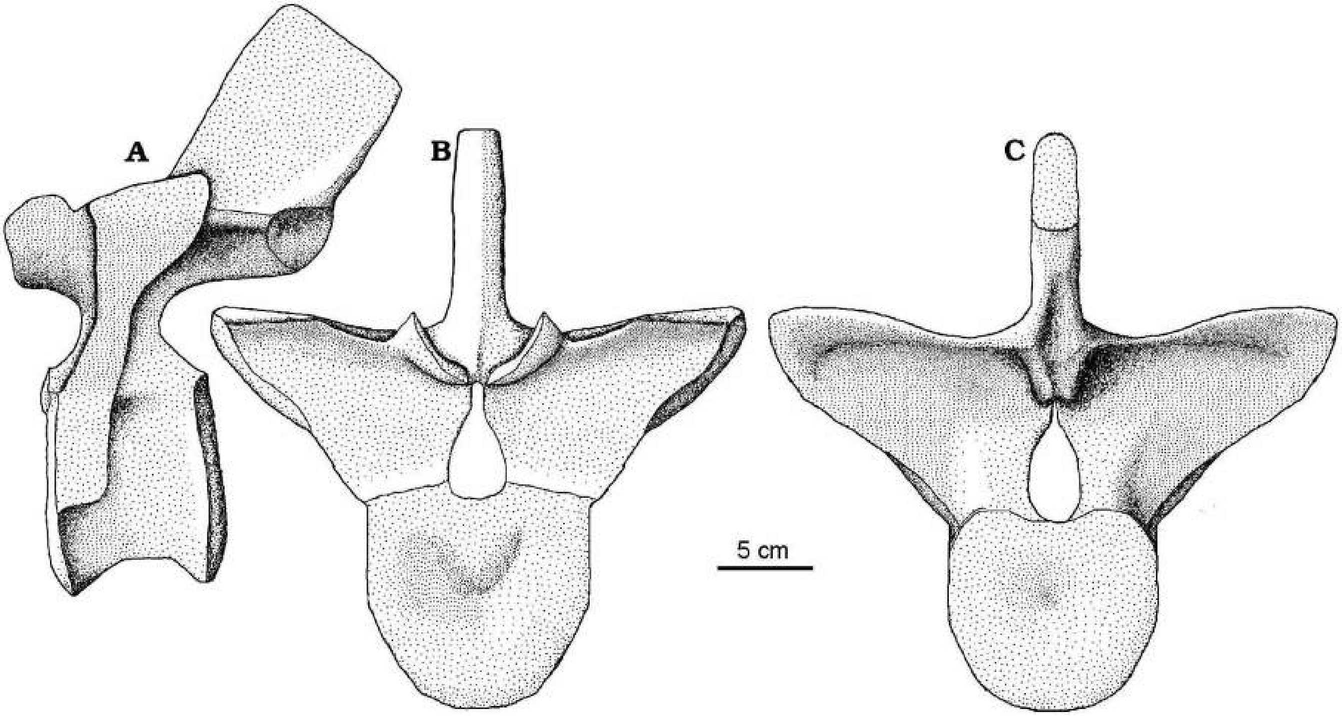

Fig. 16. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Reconstruction of cervical vertebra (seventh?) based on ZPAL V. 33/720, in lateral (A), anterior (B), and posterior (C), views.

The head in the fifth or sixth rib (V. 33/720) is 18 cm wide (in anterior view), and, in the middle part of the rib, is 9 cm wide (also in three ribs from accumulation V. 33/MB/22). Ribs of this kind have a distinct long ridge on the anterior side in the proximal part; it begins near the tuberculum. The posterior side is concave. The distal part of the rib is almost straight (in anterior

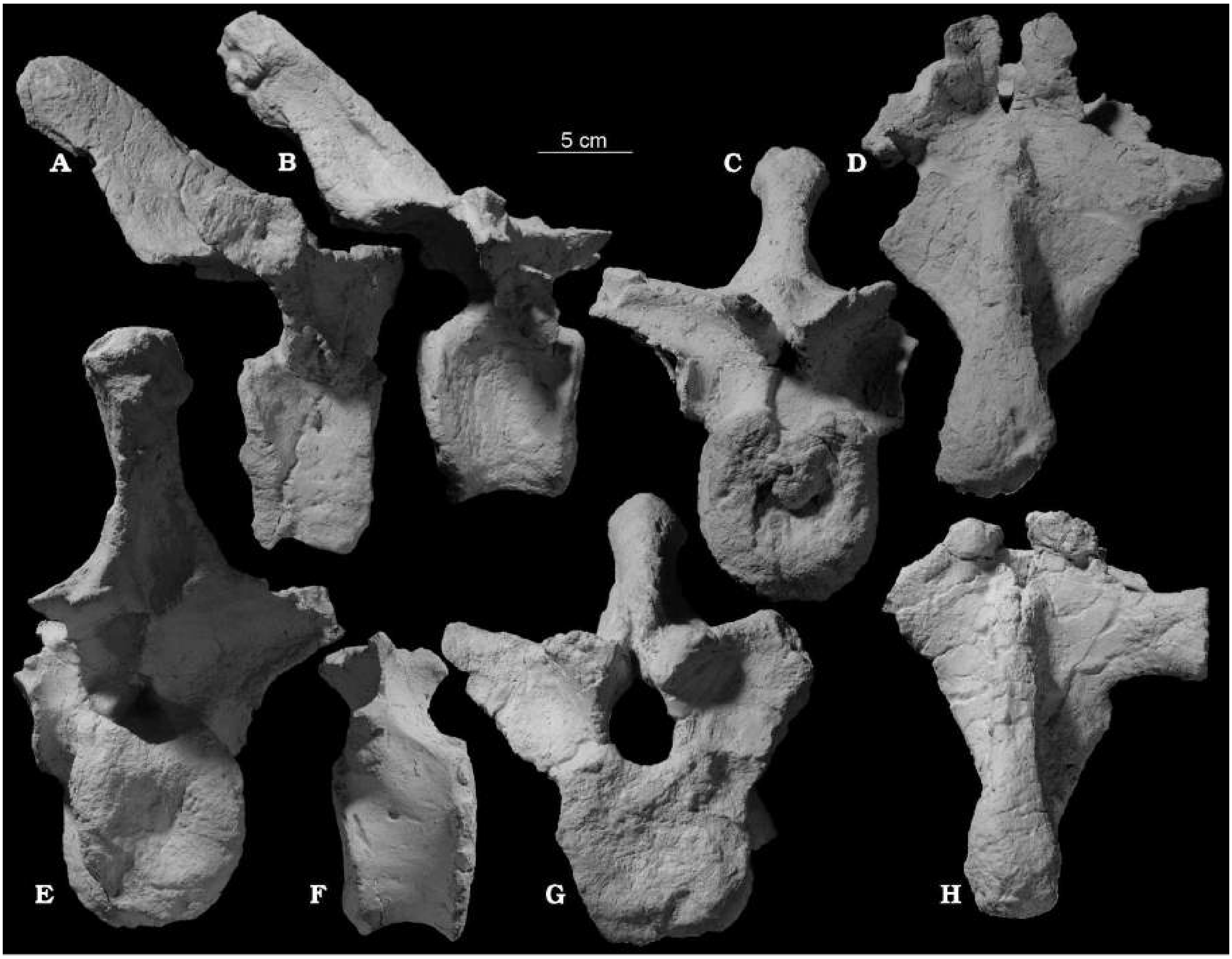

Fig. 17. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Dorsal vertebrae ZPAL V. 33/720, in lateral (A, B, F), anterior (C, G), dorsal (D, H), and posterior (E) views. Vertebrae on picture B, C, D, E is the first and F is the last in this sequence; detailed position in the spine is unknown.

view) and very narrow (in lateral view). These ribs were probably set almost vertically in anterior view, as in present-day deer, cows, and rhinoceros. In specimens located more posteriorly, the inner edge is strongly concave to make place for the bowels. The edges of the shaft in cross-section are round in the medial part and pointed along the outer edge.

The cervical ribs in dicynodonts were so wide that in the museum collections of *Placerias* they have been labelled as clavicles, although Camp and Welles (1956: 289) wrote that 'clavicles were not definitely identified in the material'. Similar wide ribs were attributed to *Sinokannemeyeria* by Sun (1963).

Pectoral rib: The ribs are represented by the almost complete, 88-cm long specimen V. 33/715 and many other fragments. The cross-section of the shaft is round in the medial part and pointed at the outer edge. The rib is curved (in anterior view) at its whole length and is wide (8 cm) in the middle. This means that the *Lisowicia* pectoral ribs were more massive then in *Stahleckeria potens*, in which they were narrow.

Sternum: Three specimens are present: ZPAL V. 33/754, 33/759, and 33/760. The sternum of *Lisowicia bojani* has already been described by Sulej and Niedźwiedzki (2019). They pointed out its extreme height and the articulation condyles on its posterolateral corner. The ventral–dorsal position the sternum is reconstructed based on the partly articulated material of *Sinokannemeyeria yingchiaoensis* (Sun 1963: pl. 5). According to this specimen the ventral side of the sternum is flat. The medial ridge and lateral articulating surfaces occur on the dorsal side. However, Sun (1963) and Cox (1965), based on articulated skeletons of *S. yingchiaoensis* and *Dinodontosaurus turpior*, presented a sternum with its dorsal medial ridge directed frontally, contrary to Huene (1935) and Camp and Welles (1956). This anteroventral position of the sternum is also different from that in the Permian dicynodonts known from articulated specimens, e.g. *Cistecephalus* BP/1/2915 (Cluver 1978: fig. 6) or gorgonopsian *Aelurognathus tigriceps* Broom and Haughton, 1913 [redrawn from Broom (1930: fig. 108) by Sigogneau-Russell (1989); see also Sidor and Mann (2024)]. Additionally, in *A. tigriceps* the anterolateral corner of the sternum is in articulation with the posterior

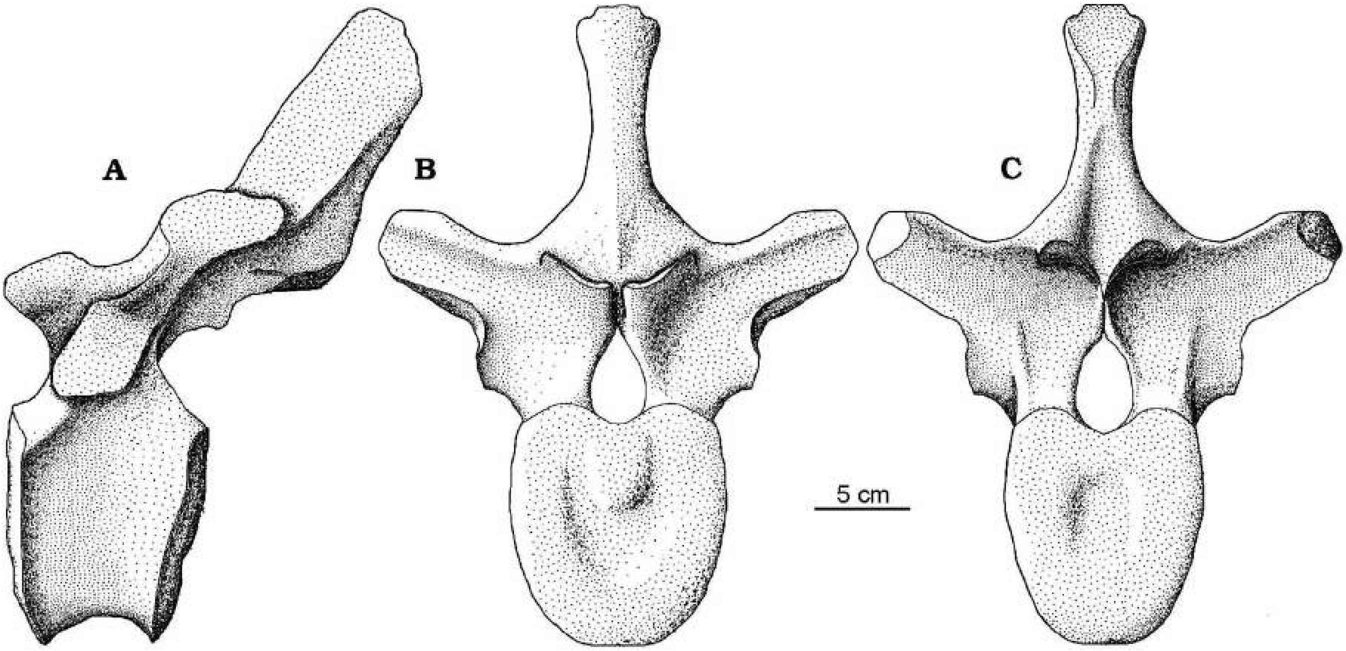

Fig. 18. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Reconstruction of dorsal vertebra (13?) based on ZPAL V. 33/720, in lateral (A), anterior (B), and posterior (C), views.

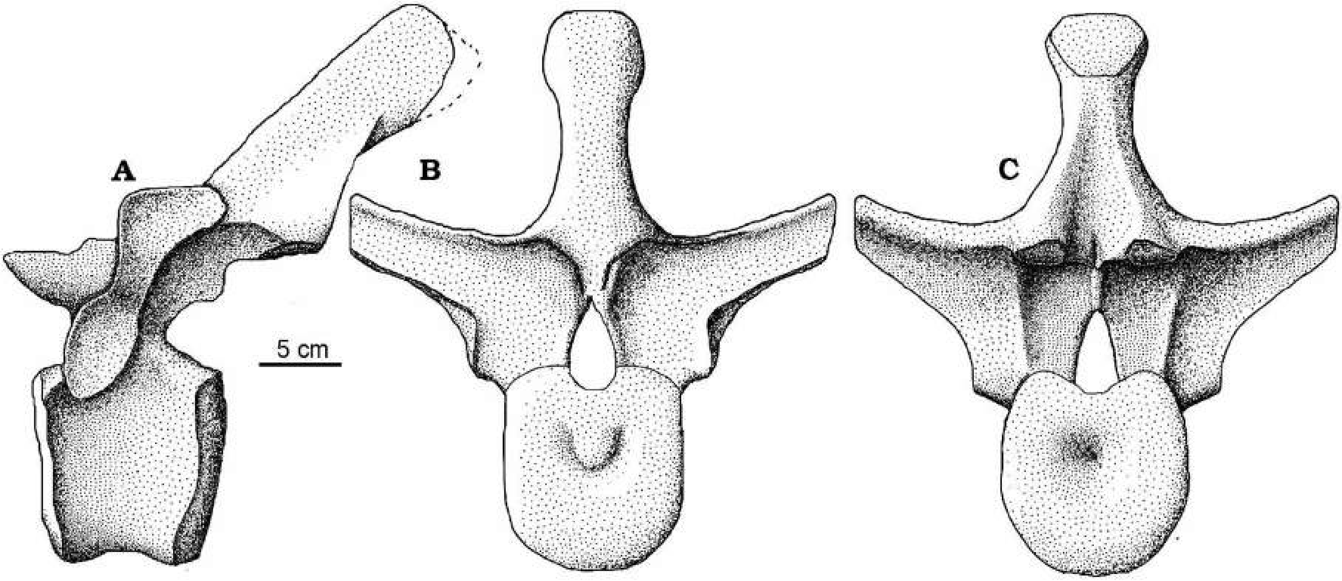

Fig. 19. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Reconstruction of dorsal vertebra (15?) based on ZPAL V. 33/720, in lateral (A), anterior (B), and posterior (C), views.

process of the coracoid, similar to present-day ostrich and the embryo of the opossum *Trichosurus* Kerr, 1792 (Watson 1917).

In *Lisowicia bojani* the articulating surface on the dorsal side of the sternum consists of two parts, merged in a single articulated area and visible only in lateral view. As described by Sulej and Niedźwiedzki (2019), the upper condyle probably articulated with the first dorsal rib as in *Trichosurus* (Watson 1917), and the ventral condyle articulated with the posterior ventral process of the coracoid. The dorsal side of the sternum is asymmetrical in all three specimens, with the lower medial part of the left with an anterior ridge. The additional concavity in the left ridge was probably the place for the heart, which is its normal position in present-day dogs and cats. This is also suggested by the location of dorsal ridges on the sternum in most Late Triassic dicynodonts. Their expansions were apparently limited by a ventral organ, presumably the heart.

Lumbar ribs: Many fragments of the lumbar ribs are known, the longest being the specimen ZPAL V. 33/721, and there are specimens with a preserved head, e.g. ZPAL V. 33/713 and ZPAL V. 33/722. The heads are short and oval (Fig. 24). Near the head a low ridge is visible on the anterior side. The middle part of the

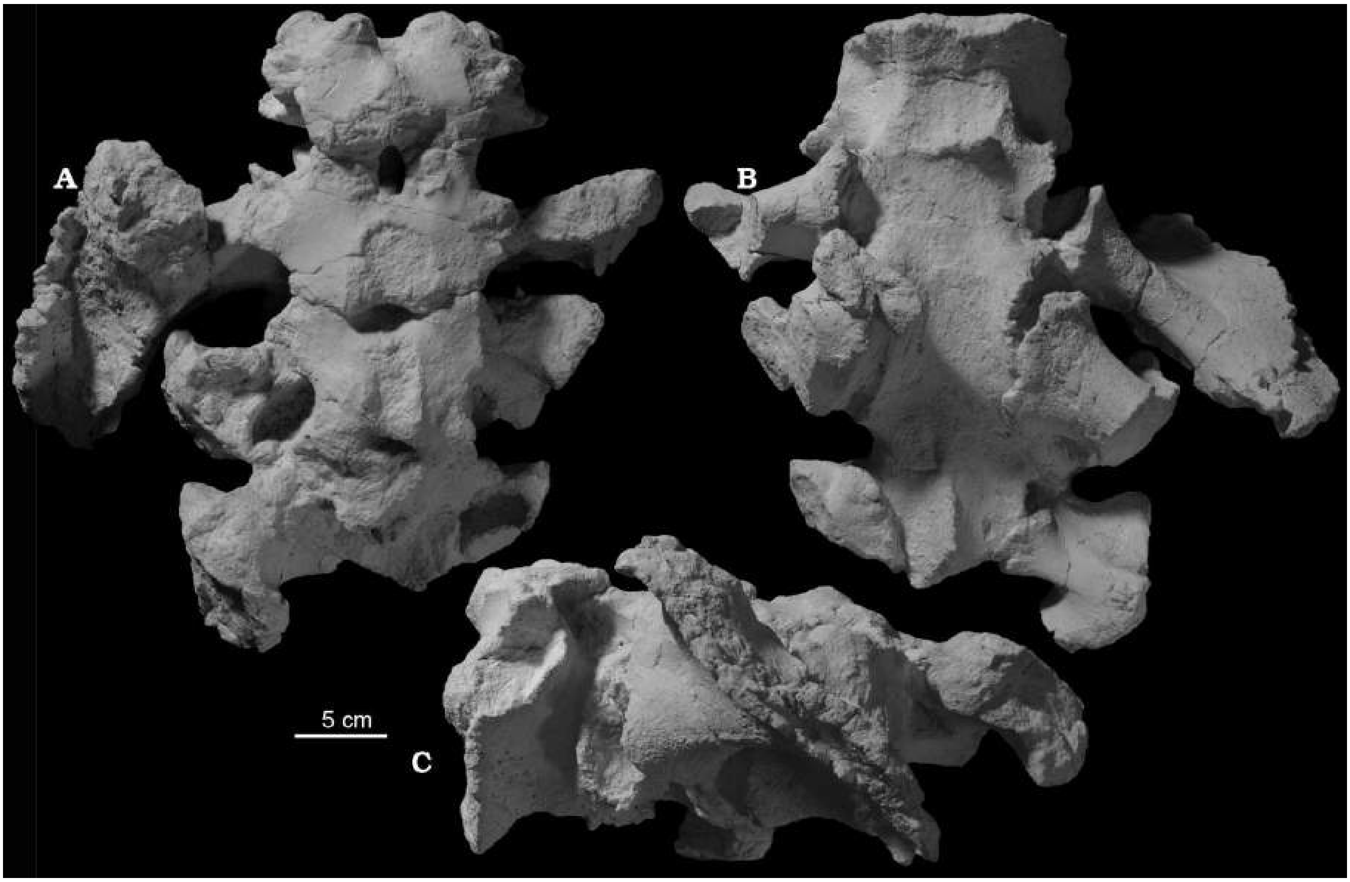

Fig. 20. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Sacrum ZPAL V. 33/720, in dorsal (A), ventral (B), and lateral (C) views.

ribs is rectangular or round in cross-section, and they are very curved and narrow.

Sacral ribs: Lisowicia has four sacral ribs, but only three are known (Figs 20, 21). They are clearly visible in the specimens ZPAL V. 33/720 and ZPAL V. 33/83. The first sacral rib is the longest and highest one. It forms a very wide and high joint for articulation with the ilium. In its reconstruction (Fig. 21) the shape of the joint for the ilium was based on the trace of the rib on the ilium from the same individual, ZPAL V. 33/720. Its dorsal part is convex, whereas the ventral one is rather concave. A similar morphology is observed in the remaining sacral ribs. The third rib is also very high, but the fourth one is rather low with a rectangular surface for the ilium.

Stahleckeria potens has eight sacral vertebrae, but *Lisowicia bojani* has only four sacral ribs and all of them are connected to the ilium. Most of the sacral ribs in dicynodonts are very small spinous processes. This may be interpreted as related to a short tail that did not move up and down, but the very large transverse processes of the caudal vertebrae suggest strong lateral movement.

Pectoral girdle

The bones of the pectoral girdle are well represented in the material. All represent individuals of a similar size. As in *Placerias* '*gigas*', *Jachaleria candelariensis*, and *Ischigualastia jenseni*, the clavicle was not found. This may mean that *Lisowicia bojani* did not have this bone, which is functionally possible based on the absence of this bone in living proboscideans.

Scapula: The scapula of *Lisowicia bojani* was described by Sulej and Niedźwiedzki (2019). Here more data on the scapula of *L. bojani* and its reconstruction are given. Four left scapulae, ZPAL V. 33/74, V. 33/82, V. 33/451, and V. 33/468 (the scapulocoracoid), and four right ones, V. 33/80, V. 33/425, V. 33/726, and V. 33/761, are available (Figs 25, 26).

The small triangular acromion process in *Lisowicia bojani* is similar to that of *Jachaleria candelariensis* (Araújo and Gonzaga 1980: fig. 6). The very robust attachment to the musculus triceps scapularis and general proportions of the scapular blade are like that in *Ischigualastia jenseni*. The strongly concave anterior border of the scapula may relate to the increased attachment for the m. supracoracoideus and m. coracobrachialis, which are crucial in the vertical position of the humerus (Sulej and Niedźwiedzki 2019). No other dicynodont had this attachment so large.

Sulej and Niedźwiedzki (2019) stated that in *Lisowicia bojani* the glenoid of the scapulocoracoid is directed posteroventrally (ZPAL V. 33/468) in a way similar to that in *Placerias* '*gigas*' or *Ischigualastia jenseni*. They emphasized that this direction is opposite to that of the Late Permian and Early to Middle Triassic dicynodonts. In the less derived forms, the glenoids were directed posterolaterally. The surface of articulation with the humerus is visible in lateral view, contrary to *P.* '*gigas*', *I. jenseni*, and *Wadiasaurus indicus*, which show that it was directed more

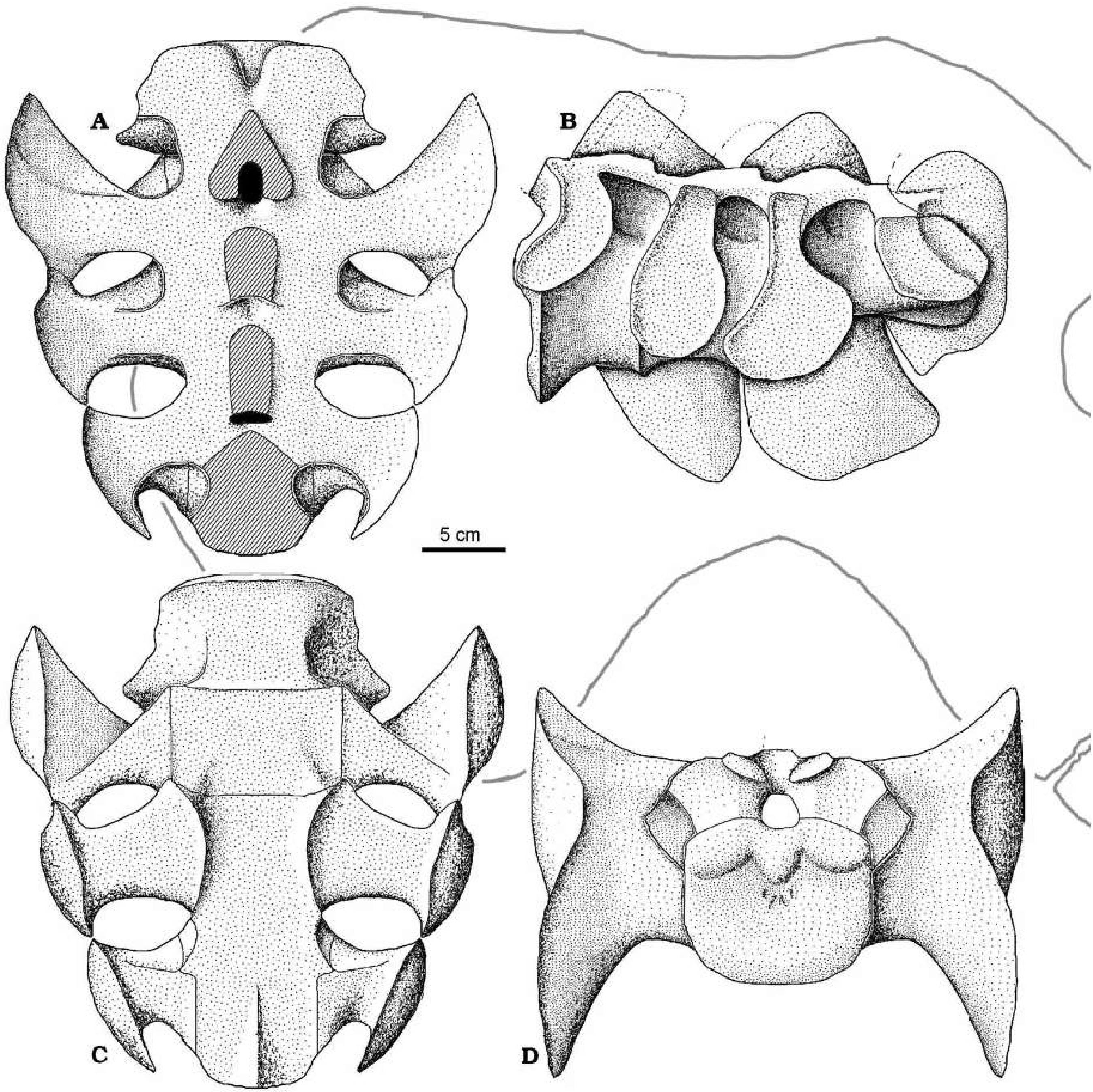

Fig. 21. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Reconstruction of sacrum based on ZPAL V. 33/720, in dorsal (A), lateral (B), ventral (C), and anterior (D) views. In background, outline of ilium in articulation with sacrum in lateral view (B).

posteriorward. The plane of that surface on the scapular part is almost perpendicular with respect to the posterior edge of the scapular blade in these genera, whereas in *L. bojani* it is oblique. The scapular and coracoid contribution to the glenoid is similar in most Late Triassic dicynodonts, but in *L. bojani* the part formed by the coracoid is much smaller.

Procoracoid and coracoid: These elements have already been described by Sulej and Niedźwiedzki (2019). Three disarticulated procoracoids were found: two left specimens that have their ventral parts broken ZPAL V. 33/702 and ZPAL V. 33/703, and the almost complete and well-preserved right specimen ZPAL V. 33/728. The posteroventral process of the coracoid is in good condition in the specimen ZPAL V. 33/468. Its posterior tip has the surface suggestive of articulation with the sternum (Figs 27 and 28), as in *Trichosurus*.

Humerus: The humerus ZPAL V. 33/96 is the holotype of *Lisowicia bojani*. Five almost complete specimens (Figs 29, 30) were collected (ZPAL V. 33/96, V. 33/466, V. 33/532, ZPAL V. 33/MB/23, and V. 33/MB/24) and some fragments, among them the very large proximal head V. 33/479. The holotype left

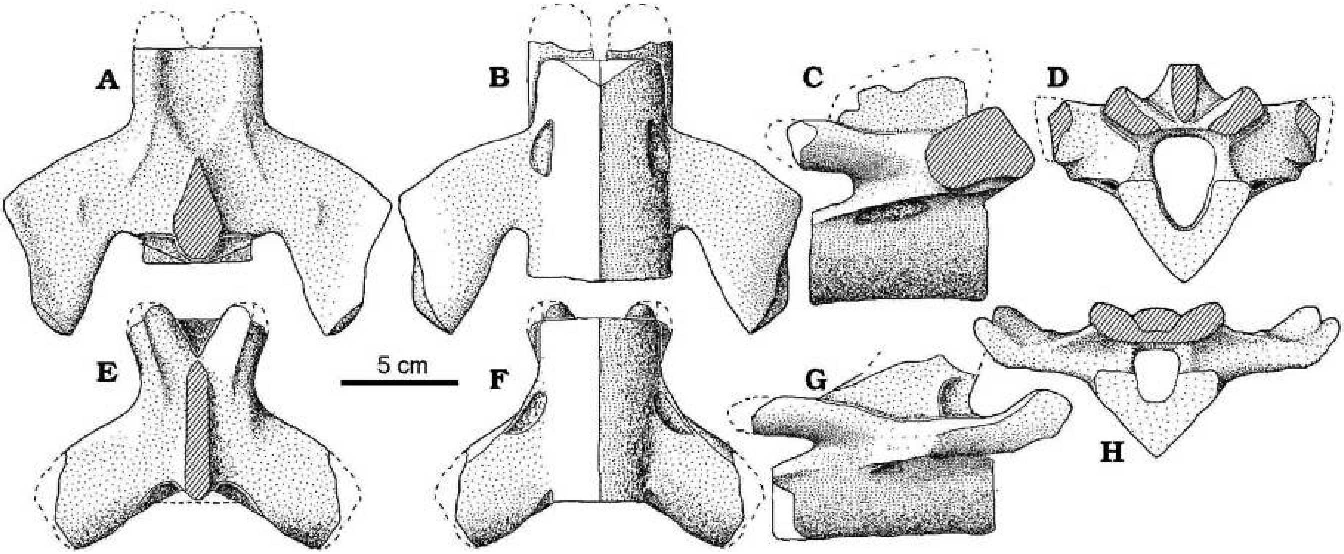

Fig. 22. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Reconstruction of caudal vertebrae based on ZPAL V. 33/720, first? caudal (A–D) and second? caudal (E–H), respectively, in dorsal (A, E), ventral (B, F), lateral (C, G), and anterior (D, E) views.

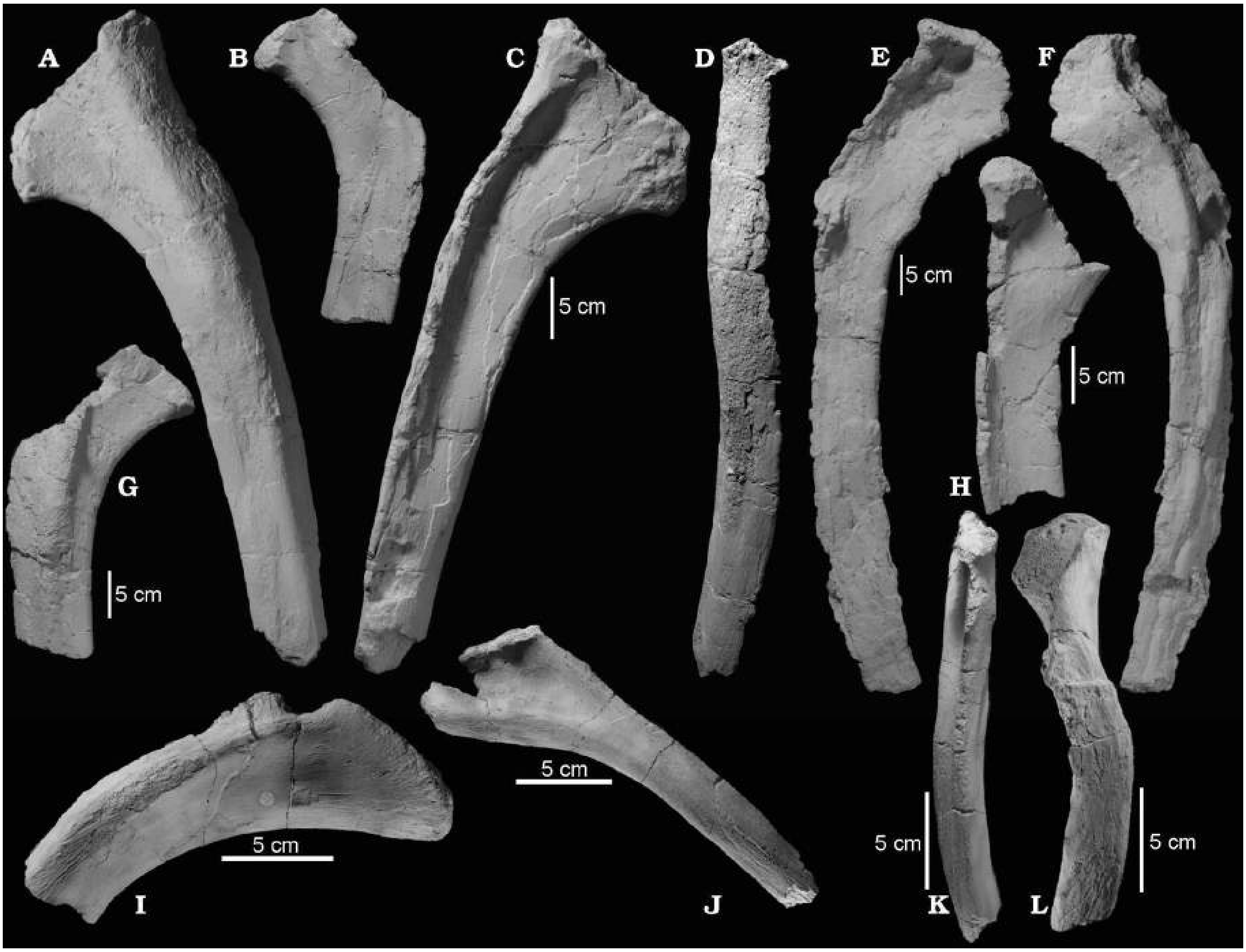

Fig. 23. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Ribs: cervical ZPAL V. 33/720 (A, C, D), ZPAL V. 33/720 (B, G), dorsal? ZPAL V. 33/715 (E, F), ZPAL V. 33/720 (H), lumbar ZPAL V. 33/713 (I, L), ZPAL V. 33/722 (J, K), respectively, in anterior (A, F, G, I), posterior (B, C, E, H, J), lateral (D), and dorsal (K, L) views.

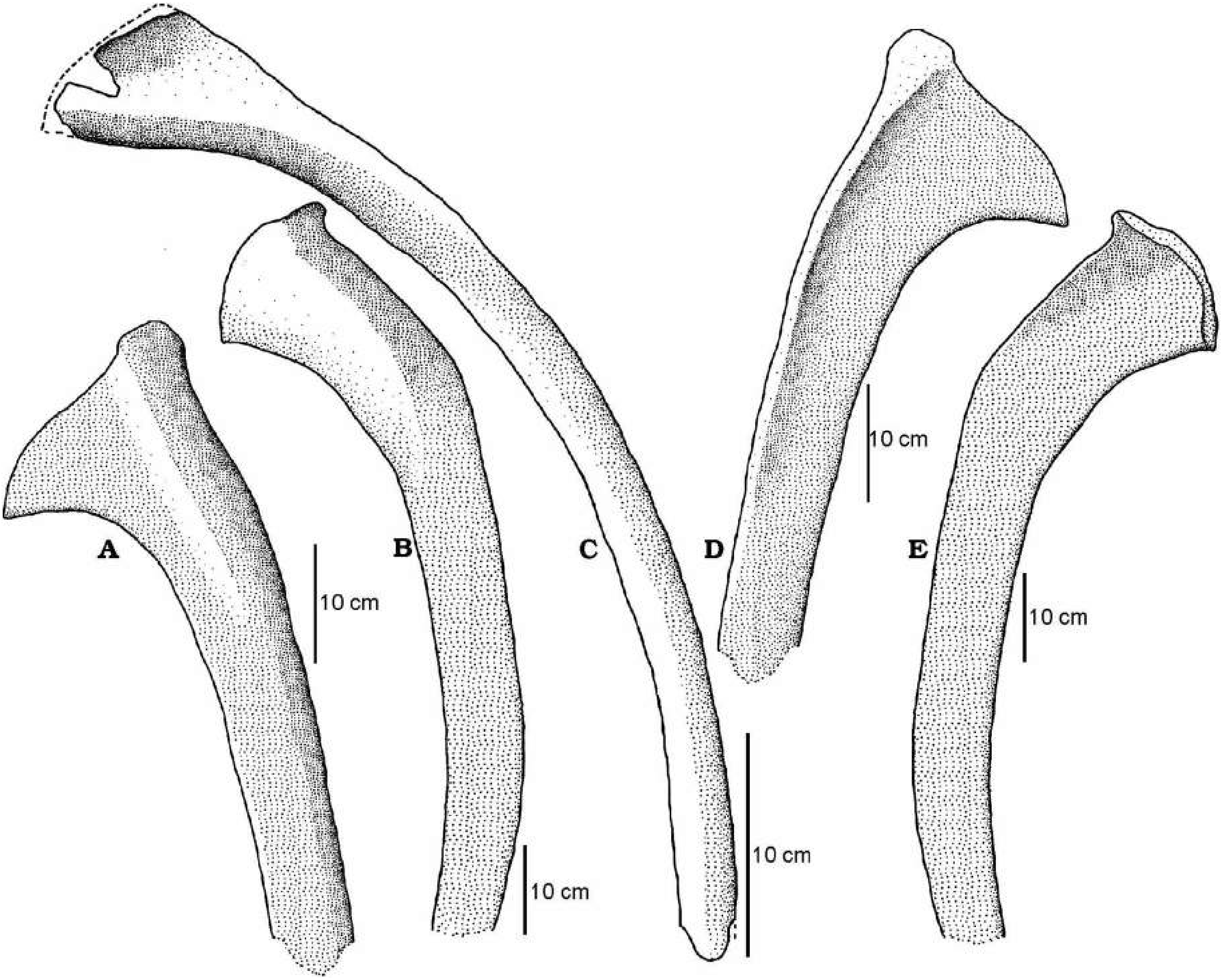

Fig. 24. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Reconstruction of ribs based on cervical ZPAL V. 33/720 (A, D), dorsal (pectoral?) ZPAL V. 33/715 (B, E) and lumbar ZPAL V. 33/721 and ZPAL V. 33/722 (C), respectively, in anterior (A-C), and posterior (D, E), views.

humerus is of 48 cm length, like the right humerus ZPAL V. 33/466. The largest humeri are V. 33/479 and V. 33/MB/24. The specimen ZPAL V. 33/MB/24 is the shaft of the left humerus with both heads missing. Based on the width of this shaft (the medial area on the ventral side is 15 cm) and the proportion from the specimen ZPAL V. 33/532, the whole bone was 61.5 cm long. The animal with that humerus had an estimated 2.6 m height, the size of a living elephant. The largest complete humerus has the deltoid crest less turned towards the distal head then smaller specimens, which suggests a growth allometry in *Lisowicia*.

Most of the important characters were listed by Sulej and Niedźwiedzki (2019), e.g. the lack of an entepicondyle foramen, both heads almost in the same plane, distinctive and narrow supinator process, very large posterior joint for the scapula, the glenoid joints for the radius and ulna small, the glenoid for ulna slightly convex, the distal end of the deltopectoral crest bending frontally, and the small distance between the deltopectoral crest and supinator process.

The Carnian *Woznikella triradiata* shows a supinator process similar to *Lisowicia bojani*, which is unique among dicynodonts (Szczygielski and Sulej 2023). In both species it is straight, elongated, and slightly oblique in anterior view. The only dicynodonts with a similar supinator process are *Zambiasaurus submersus* Cox, 1969, *Pentasaurus goggai* Kammerer (2018: fig. 14), and probably *Placerias* '*gigas*' (Camp and Welles 1956: fig. 30; e.g. UCMP 25361).

The medial process of the proximal head is clearly visible in anterior view in *L. bojani*. It is large and strongly developed ventrally. Unique is its anterior position and the very wide distal part. In this character it is like *W. triradiata* (Szczygielski and Sulej 2023). In *Placerias* '*gigas*' it is much shorter, and in *Stahleckeria potens* much narrower, whereas in *Ischigualastia jenseni* it is not visible in anterior view.

Ulna: Four ulnae specimens are available, left ZPAL V. 33/470 (Figs 31, 32), left and the largest one but compressed ZPAL V. 33/662, and small gnawed right V. 33/661. The fragment ZPAL

Fig. 25. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Scapulocoracoid ZPAL V. 33/468 (A, D, E, F), V. 33/761 (C, D), in lateral (A, D), medial (B), posterior (C, F), and anterior (E) views.

V. 33/MB15 is of the shaft. The ulna ZPAL V. 33/470 was described by Sulej and Niedźwiedzki (2019). In all specimens the olecranon process is not co-ossified with the main element. The shaft has a concave lateral surface and a flat medial surface. It is concave only at the articulation surface with humerus (Fig. 30). At the distal head it is convex. The proximal head has an articulation for the humerus that is deeply concave in lateral view. It has the shape of a reversed asymmetrical heart. The joint for the radius on the lateral side is almost vertical. The whole medial and upper sides are for contact with the humerus. The distal head is triangular with rounded tips.

The olecranon has a flat medial side. On its lateral side a distinct edge is located between the lateral concave part and dorsal part. The cartilaginous articulation of the main body and the olecranon process in such large bones suggest that the muscles attached to this process did not play any important role; the situation as in *Placerias* '*gigas*' and probably in *Woznikella triradiata*. In *Ischigualastia jenseni*, *Jachaleria candelariensis*, and *Sinokannemeyeria yingchiaoensis*, the olecranon process is fused with the main body.

Radius: Three radii are available, the most complete ZPAL V. 33/665 and two larger, V. 33/663 and V. 33/664, with one or both heads not preserved. The radius ZPAL V. 33/665 (Figs 33, 34) was described by Sulej and Niedźwiedzki (2019) and here it will be supplemented by a more detailed description and reconstruction. The shafts of both the largest radii show that the distal head is very large. The specimen V. 33/700 has the head relatively smaller (Fig. 32), which may be interpreted as a growth allometry or that this specimen is not the radius. All these bones have their shafts triangular in cross-section. The specimen ZPAL V. 33/700 compared with the heads of the radius of *Sinokannemeyeria yingchiaoensis* (Sun 1963: fig 19) seems to represent the left bone, although the shape of the distal half of the shaft is different. This character is probably variable. It is well visible in articulated skeletons of *S. yingchiaoensis* and *Parakannemeyeria youngi* (Sun 1963: fig. 33).

The radius of *Lisowicia bojani* in general proportions (in the widest view of the bone) is similar to *Sinokannemeyeria yingchiaoensis* and *Placerias* '*gigas*', and it is narrower than in *Ischigualastia jenseni* and *Jachaleria candelariensis*. In *Stahleckeria potens* it is different, but it seems to be a taphonomic bias. In fact, the radius in most dicynodonts is very uniform, and the distinction between left and right is difficult to see, even in the articulated specimen of *Dinodontosaurus tener* MCZ 1670. The radius heads of *L. bojani* are more round rather than oval (Sulej and Niedźwiedzki 2019), like most Late Triassic dicynodonts. They are also very convex as a whole head or partly (like the proximal

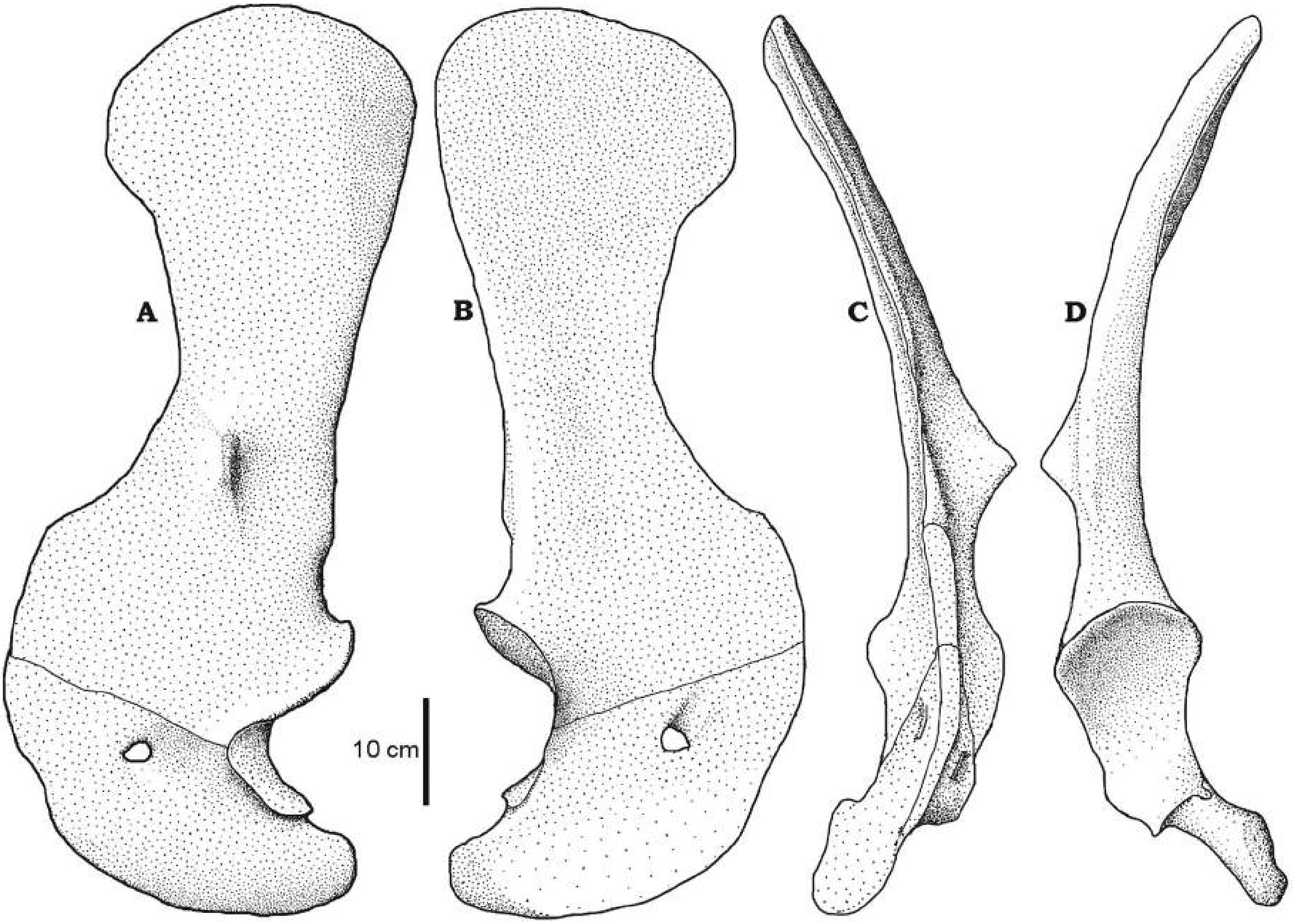

Fig. 26. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Reconstruction of scapulocoracoid based on ZPAL V. 33/468 and 761, in lateral (A), medial (B), posterior (C), and anterior (D) views.

head). In *L. bojani*, a large concavity for the ulna is visible in lateral view on the shaft of the proximal head. In *Parakannemeyeria youngi* (left radius V.972), a similar structure is visible but on the opposite side of the bone. A distinct structure in the shape of a small ridge is present on the proximal head in its posterior part. This may be the area where the radius contacts the posterior process of the ulna's head.

The distal head is very massive and very convex, like the proximal head. The head surface is not visible in anterior view because it is directed posteriorly. An attachment of muscle in the shape of a ridge is visible on its medial side (Sulej and Niedźwiedzki 2019).

Ulnare or patella: The specimens ZPAL V. 33/716 and V. 33/758 are flat bones (left and right), both sides with rugosities (Figs 35, 36). One side is slightly convex, the other flat. With great difficulty they may be interpreted as ulnare [based on the reconstruction of Camp and Welles (1956: fig. 38)]. The alternative is the patella like that in *Kingoria* (Cruickshank 1967, King 1985). Camp and Welles (1956) based their identification of bones in disarticulated material on Romer and Price's (1944: fig. 10) specimen of *Kannemeyeria* and on the articulated manus of *Stahleckeria potens*. This cannot be applied to the *Lisowicia* material. All the bones from the wrists and ankles belonging to *Parakannemeyeria youngi* (V. 979) are massive except for the ulnare, which is concave on both sides, unlike *Lisowicia*.

Radiale: Three specimens of radiale are available (Fig. 37). The specimen ZPAL V. 33/453 is a right complete bone; the others, ZPAL V. 33/747 and V. 33/454, are left and incomplete. The bone is rather rectangular than quadrate, like the radiale of *Placerias* '*gigas*' (Camp and Welles 1956: fig. 39). However, the bone is different enough to consider the possibility that it is the tibiale.

Digits: Only two specimens of the last digits were found, ZPAL V. 33/744 and V. 33/749. Both are flat (Fig. 38), with a waist in front of the joint for articulation with the preceding digit. The width is, respectively, 5.4 and 8.1 cm, and the length is 6.8 and 10.6 cm at the maximum height of 3.0 and 3.7 cm. The extreme rugosity of these elements relative to those of other dicynodont unguals is notable. The morphology suggests that they were adapted for digging. The unguals of *Placerias* '*gigas*' are rectangular, whereas in *Lisowicia bojani* they are more triangular and their distal parts are narrower than the medial ones. The articular surfaces on the phalanges of the *Parakannemeyeria youngi* hand indicate that the fingers were positioned diagonally to the ground, not flat.

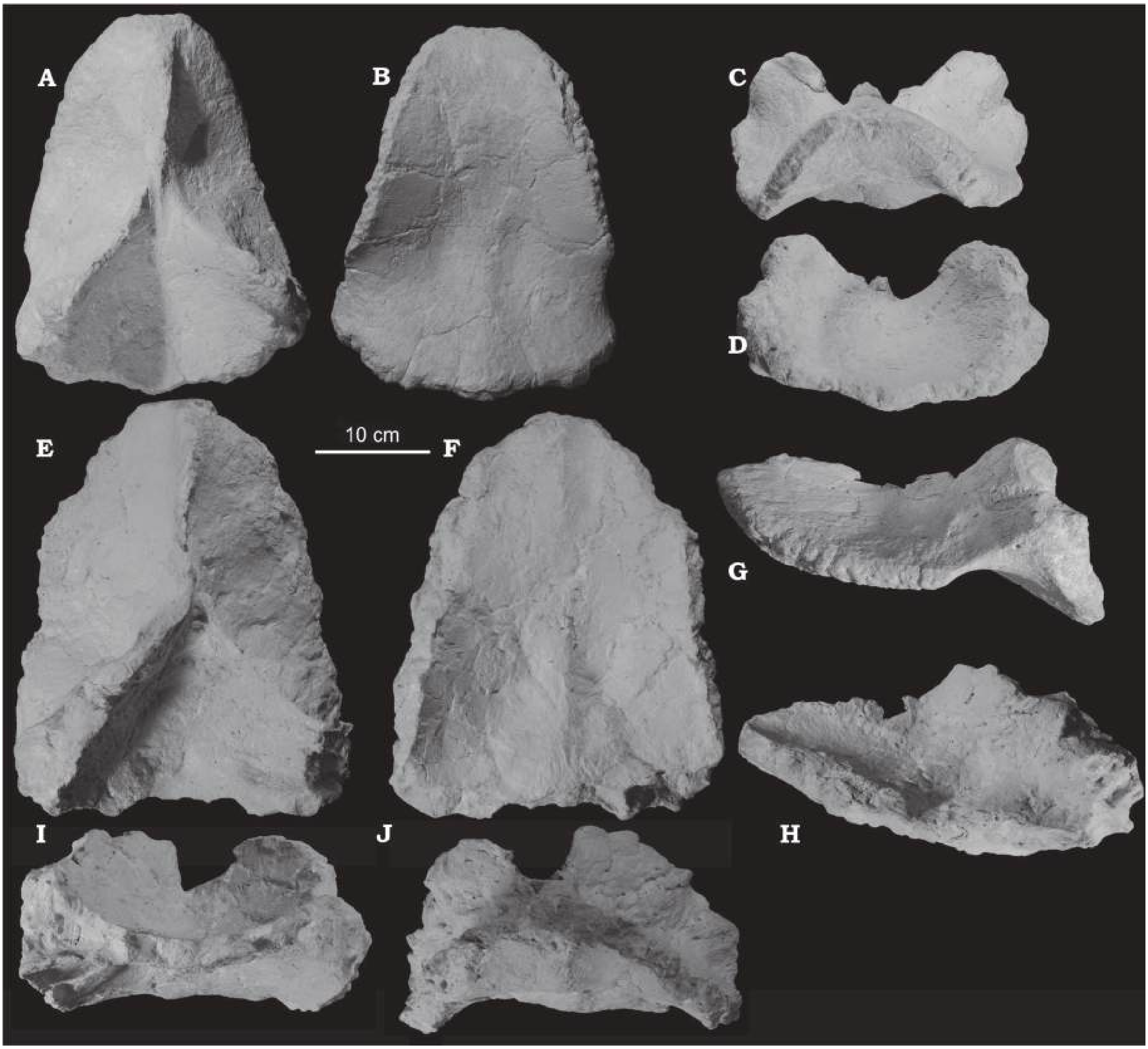

Fig. 27. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Sternum ZPAL V. 33/760 (A-D, H), ZPAL V. 33/759 (E-G, I, J), respectively in dorsal (A, E), ventral (B, F), anterior (C, J), posterior (D, I) and lateral (G, H) views.

Pelvic girdle

Ilium: Three specimens are available: an anterior part of the iliac blade ZPAL V. 33/699, a part with the edge of the acetabulum V. 33/464, and the best-preserved left and right ilia from the accumulation ZPAL V. 33/720. The anterior half of iliac blade is strongly curved laterally just anterior to the joint with the first sacral rib (Fig. 39). The joints for all sacral ribs are at the level just above the acetabulum. In this character *Lisowicia bojani* is similar to *Ischigualastia jenseni*; other Late Triassic dicynodonts have sacral ribs articulated far frontally from the acetabulum. *Lisowicia bojani* has four sacral ribs, whereas *Stahleckeria potens* has eight, and *Placerias* has six? [according to Camp and Welles (1956)]; *Jachaleria candelariensis* has five sacral ribs joined to the whole area of the iliac blade.

The length of the first sacral ribs, larger than the fourth, shows that the part of the ilium with the acetabulum was curved laterally so the acetabulum was set also laterally. It is very important because some authors (e.g. Huene 1935) forgot this and showed the ilium in anterolateral position claiming that it is a lateral view.

The part of the ilium directed laterally is extremely large in *Lisowicia bojani*, similar to *Eubrachiosaurus* Williston, 1904. In *Stahleckeria potens* it is smaller and directed less laterally, whereas in *Jachaleria candelariensis* it is very small. It remains unknown in *Placerias* '*gigas*'.

Pubis: Three bones are available. The anteroventral part of the left pubis ZPAL V. 33/207 and V. 33/753 are preserved, and both have broken posterior parts with an articulation for the ischium. Only one right bone ZPAL V. 33/720 (accumulation) is well

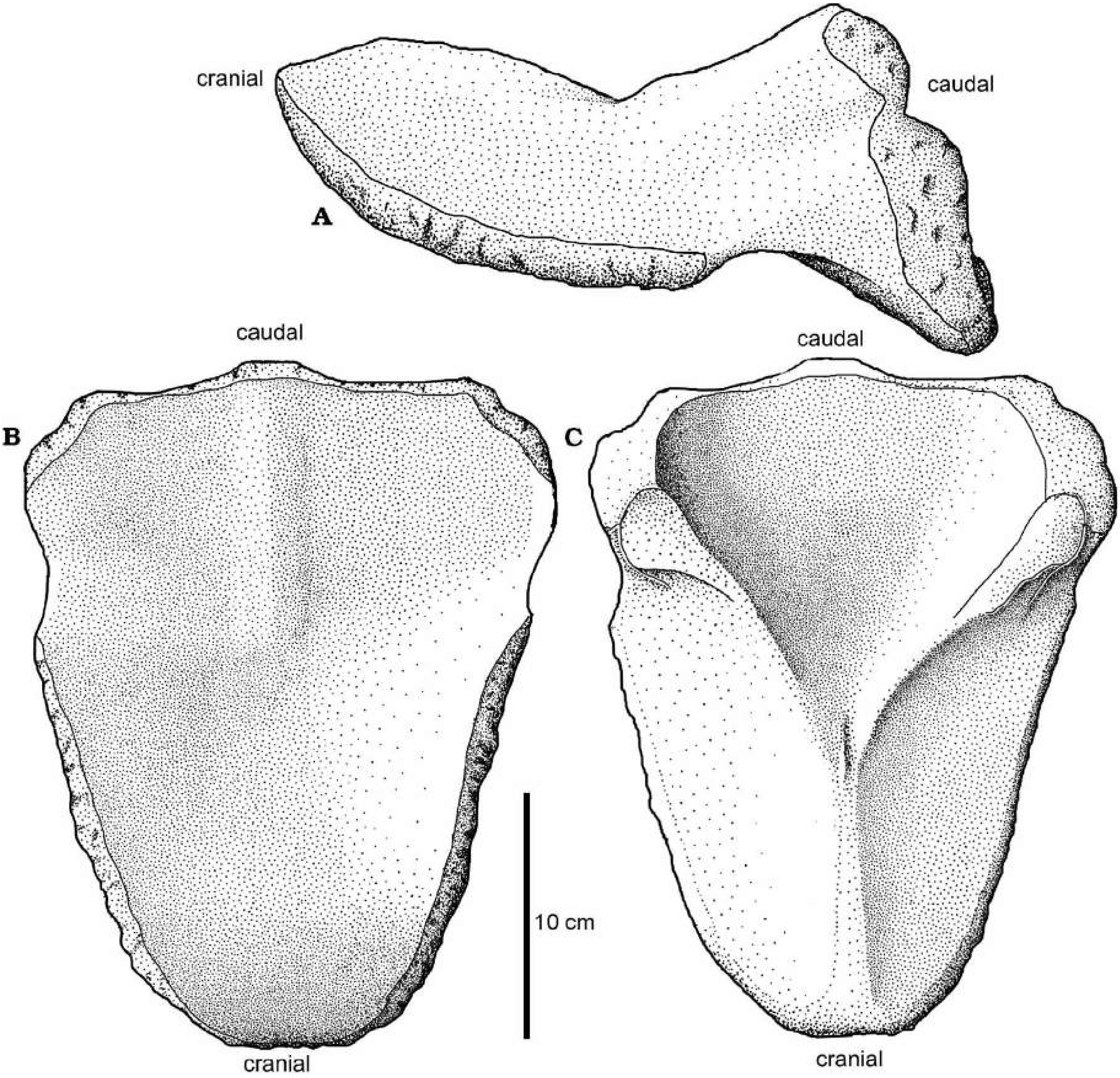

Fig. 28. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Reconstruction of sternum based on ZPAL V. 33/760, in lateral (A), ventral (B), and dorsal (C), views. In case of (B) and (C) the cranial side is below.

preserved. Elongated ridges are visible on the main body in its medial part on the lateral side. The glenoid part is very shallow. The anterior edge in lateral view is concave but not as strongly as in *Placerias* '*gigas*'. The ventral edge is crushed but it seems that it is straight, whereas in *P.* '*gigas*' it is strongly convex.

Ischium: A pair of ischia from the accumulation of bones ZPAL V. 33/720 is available. The left specimen is almost complete, only the postero-central tip is broken. The glenoid edge is very distinctive and massive; this makes the glenoid part very deep. Its lateral edge is strongly curved, contrary to *Placerias* '*gigas*' in which it is almost straight. The ridge on the ventral blade is prominent in the left specimen and visible in lateral view, but in the right, it is more posteriorly located, almost like in *P.* '*gigas*', which means that position of this ridge is variable.

The ischium of *Lisowicia bojani* is similar to those of *Stahleckeria potens* and *Dinodontosaurus brevirostris*. The attachment for the m. puboischiotibialis forms a ventrally directed convexity, like *S. potens*, although lower. The attachment for the m. ischiotrochantericus is very small, like in *Parakannemeyeria youngi* and *Kannemeyeria simocephalus*, in contrast to being large in *Wadiasaurus indicus* and *Placerias* '*gigas*'.

Femur: Four complete femora are available, the small ZPAL V. 33/75, ZPAL V. 33/756, ZPAL V. 33/757 (length 56 cm), and the largest ZPAL V. 33/763 (Figs 40 and 41). The width of the

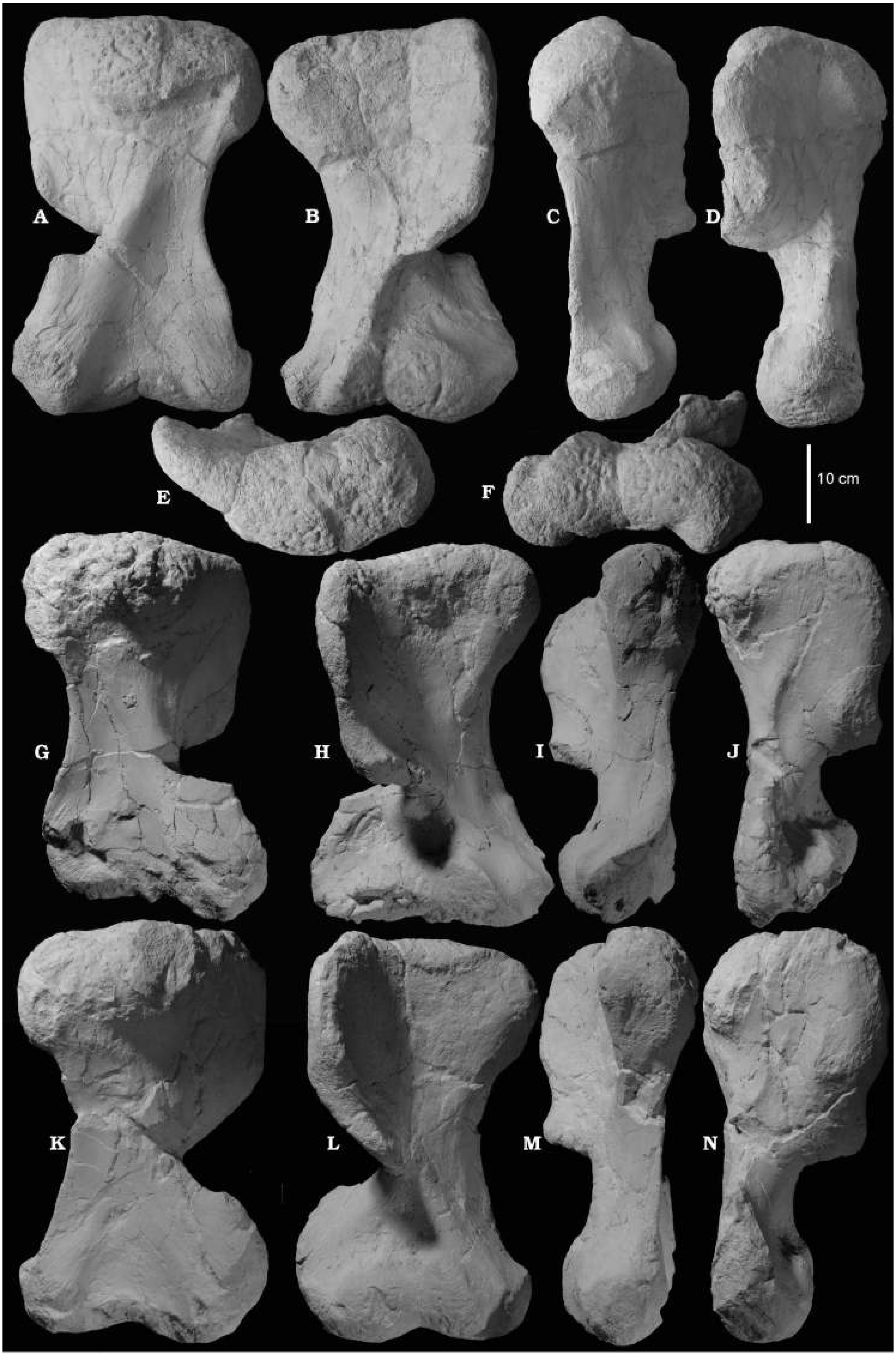

Fig. 29. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Humerus ZPAL V. 33/96 (A–F), V. 33/466 (G–J), V. 33/532 (K–N) in posterior (A, G, K), anterior (B, H, L), medial (C, I, M), lateral (D, J, N), proximal (E), and distal (F) views.

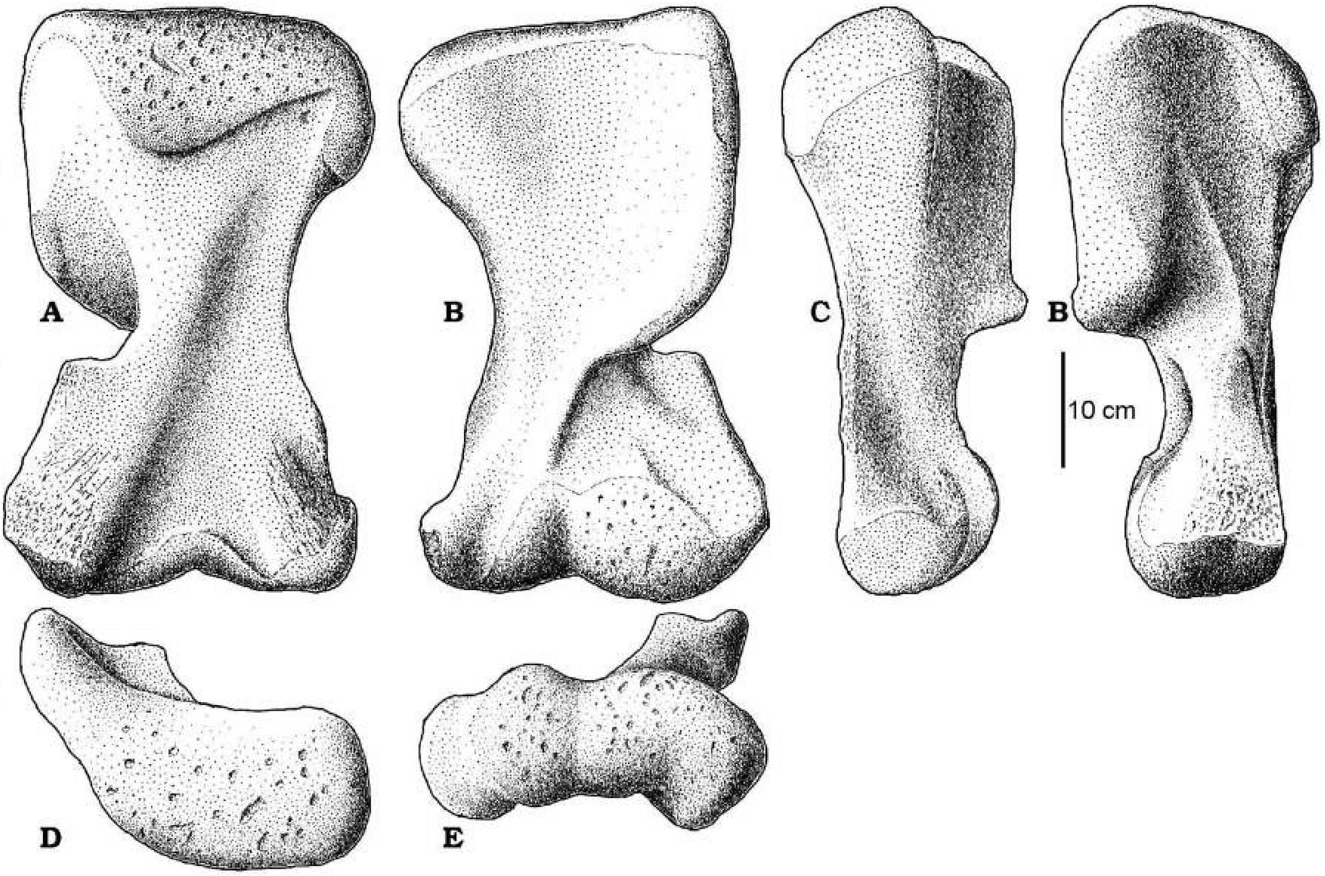

Fig. 30. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Reconstruction of humerus based on ZPAL V. 33/96, in anterior (A), posterior (B), medial (C), lateral (D), proximal (E), and distal (F) views.

preserved part of the proximal head (the most proximal part) in the specimen ZPAL V. 33/75 is 16–17 cm, its original complete diameter was probably ~26 cm, the width of the distal head is 27 cm, and its thickness 15.1 cm. The specimen ZPAL V. 33/763 has a length of 72.3 cm, and the thickness of the shaft is 7.6 cm. Based on proportions of that specimen, the length of the ZPAL V. 33/652 (only left shaft but very thick—9.2 cm and 20.9 cm wide) was about 80 cm.

The femur of *Lisowicia bojani* is similar to those of *Wadiasaurus indicus*, *Stahleckeria potens* (e.g. Kammerer *et al.* 2017), and *Placerias* '*gigas*', especially in its spherical proximal head (Fig. 40), which is dorso-medially directed. In *L. bojani* and *S. potens* it is directed even more ventrally than in it was reconstructed in *P.* '*gigas*'. All these species have a very long trochanter major (the longest in *L. bojani*). The femur is wider (in anterior view) and generally more massive in *L. bojani* than in other large Triassic dicynodonts, apparently in connection with the largest size. The lateral edge of the distal head is convex (in anterior view) like in *W. indicus*, *S. potens*, and *Ischigualastia jenseni* (even stronger than in these genera), contrary to straight in *P.* '*gigas*' and *Jachaleria candelariensis*.

Tibia: All of the five specimens are complete (ZPAL V. 33/75, V. 33/467, V. 33/764, V. 33/765, and V. 33/478 (Figs 42, 43). The right one represents only the distal head V. 33/477. The specimen V. 33/75 has length 45.5 cm, the dimensions of the proximal head are 23.0 cm × 19.0 cm, and of the distal head 18.0 × 11.5cm. V. 33/478 (left) length 42.0 cm, the width of the proximal head 23.0 cm × 18.0 cm, and the distal head 17.0 × 14.0 cm (probably the same individual as V. 33/75). The specimen V. 33/467 has length 51.0 cm, the dimensions of the proximal head 24.0 cm × 18.0 cm, and the distal head 20.0 cm × 16.5 cm. The specimen V. 33/477 is only a distal head 15.0 cm × 10.0 cm.

The tibia of *L. bojani* is a very massive bone (Fig. 40), almost identical to that bone in *Stahleckeria potens* and *Placerias* '*gigas*'. *Jachaleria candelariensis* has a unique, very large cnemial crest (in proximal view it is larger than the main body of the tibia). In *L. bojani* the oblique ridge on the lateral side of distal head became larger during ontogeny.

Fibula: Left and right fibulae are available. The largest specimen ZPAL V. 33/76 (left) is 44.5 cm long (Figs 44, 45). They are generally similar to *Stahleckeria potens*, although the proximal head is narrower and generally more slender then in *S. potens* (this may be an artefact because the only preserved left fibula has a strongly deformed proximal head). Contrary to *L. bojani* and *S. potens*, the fibular heads of *Placerias* '*gigas*' are more massive, and that results in a strongly concave medial side. Fibulae of *L. bojani* are like those of *P.* '*gigas*' in the medial side of the distal head being straight (in anterior view), and not so strongly concave as in *S. potens*. The proximal head is of various shapes. It has a large

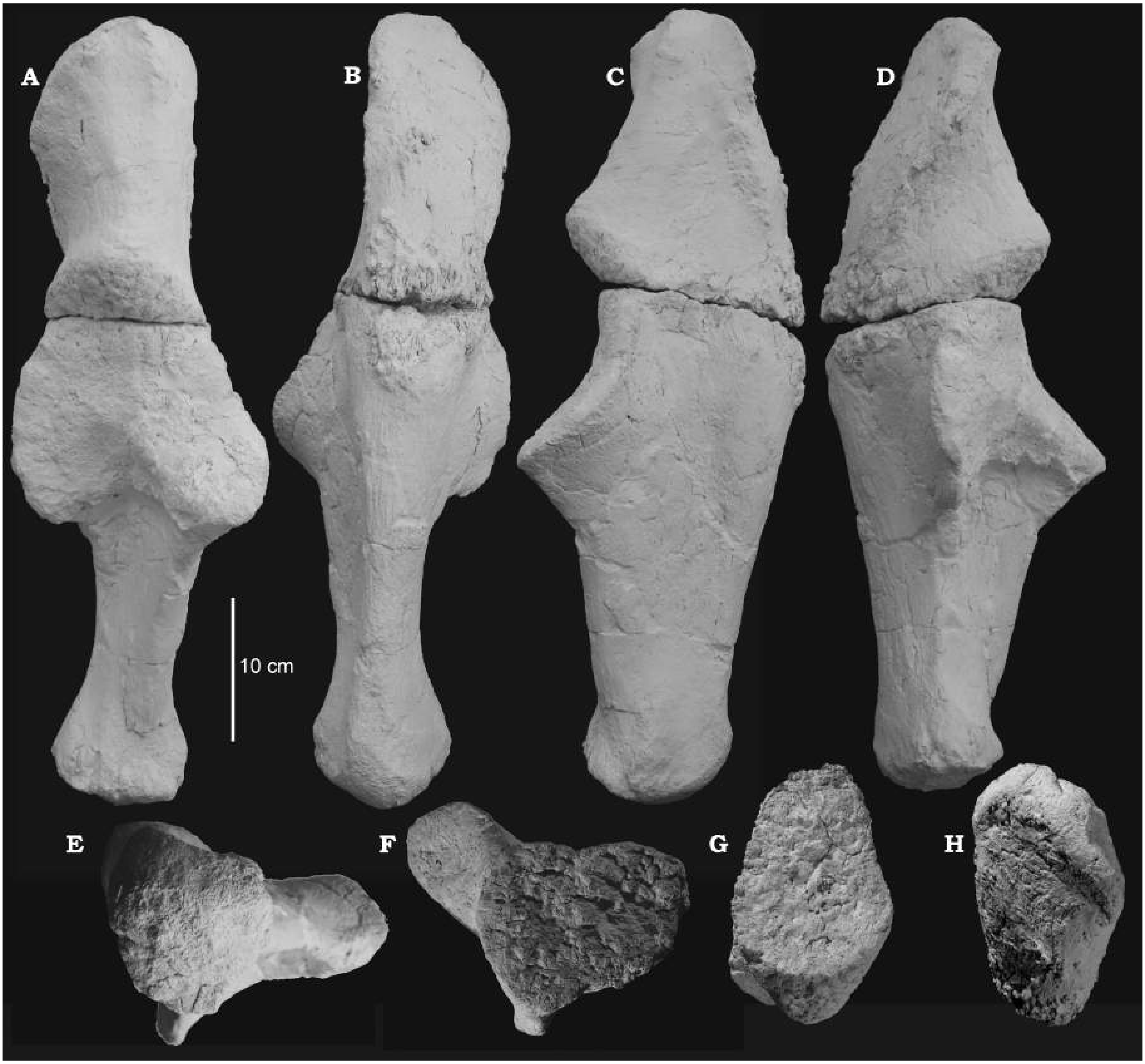

Fig. 31. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Ulna ZPA.33/470 in posterior (B), anterior (A), medial (C), lateral (D), distal (E), and proximal (F) views. Olecranon process in proximal (G) and distal (H) views.

fossa for the tibia in specimen V. 33/465 (right) and V. 33/75 (left) or the fossa is absent in V. 33/76 and V. 33/475. The anterior process is also variously developed. The anterior process is very distinct in V. 33/75, with a long articulation surface on its proximal part, but may have the shape of a knob out of articulation surface in V. 33/475 and V. 33/76.

The shaft bears a distinct ridge on its anterior side in the distal half (Fig. 43). This ridge has a wrinkled surface. On the posterior side a similar ridge is present in ZPAL V. 33/465 and V. 33/76, but in V. 33/75 and V. 33/475 it is poorly visible. The distal head has its articulation surface directed more frontally than the proximal head. The articulation surface is round in V. 33/465, triangular in V. 33/475, or oval in V. 33/76 and V. 33/75.

Comments on the skeleton of *Placerias* '*gigas*'

Camp and Welles (1956) found *Placerias hesternus* different from *P.* '*gigas*'. These dicynodonts have different humera (especially in shape of entepicondylus and supinator process) and they come from localities approximately 150 km apart. Most authors consider them as part of the Blue Mesa Formation based on lithostratigraphy and presence of metoposaurids and phytosaurs (Lucas 1993, Martz *et al.* 2017). Ages from outcrop of the Blue Mesa Member range from ~223 to ~218 Mya (Gehrels *et al* 2020). It is still very probable that strata from these localities are of different ages. The *P.* '*gigas*'-type horizon is the basal Bluewater Creek Formation at the Placerias quarry near St. Johns, Arizona, dated as Late Carnian (Lucas *et al.* 2012). The *P. hesternus*-type horizon is the Blue Mesa Member of the Petrified

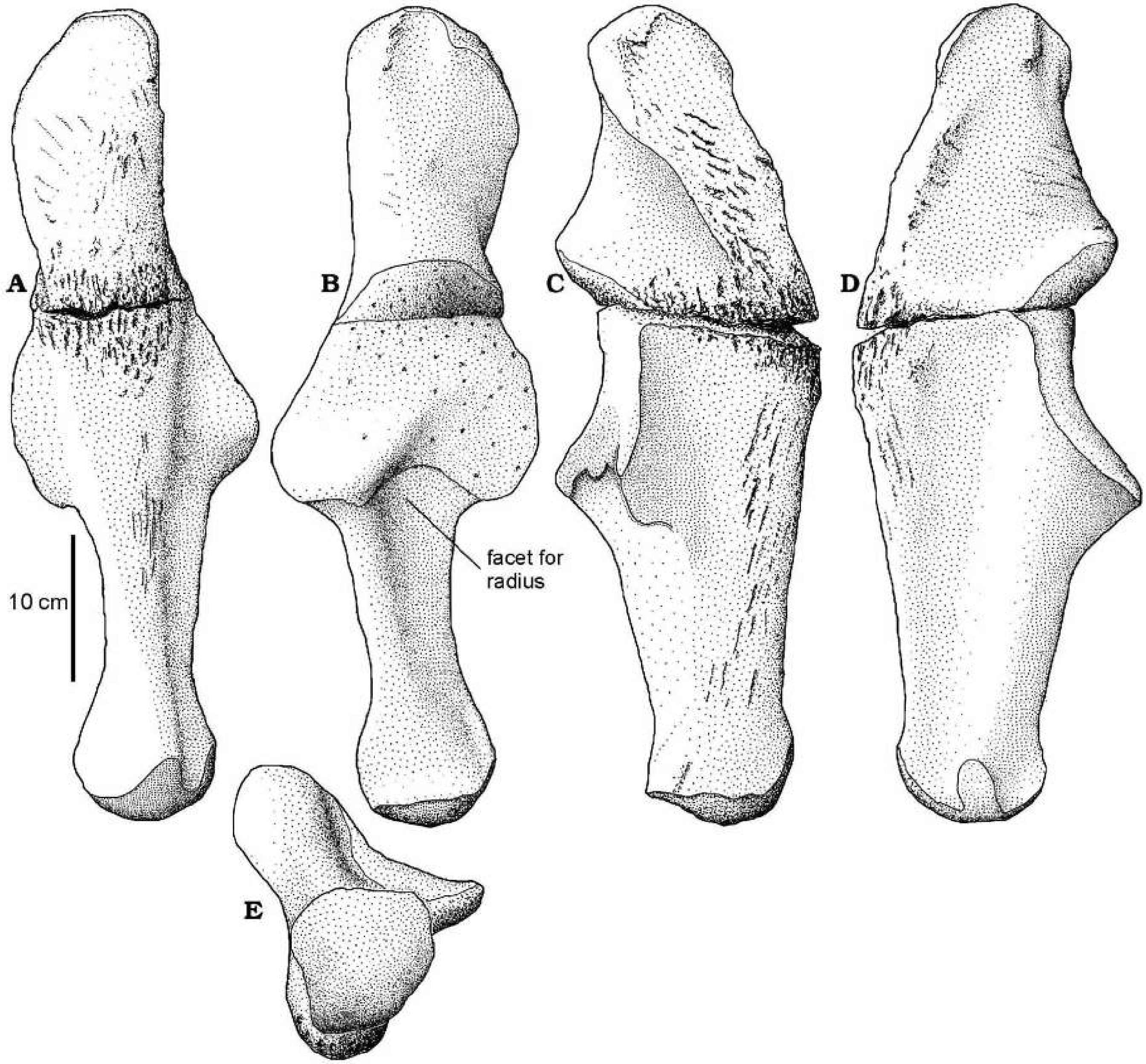

Fig. 32. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Reconstruction of ulna based on ZPAL V. 33/470, in posterior (A), anterior (B), lateral (C), medial (D), and distal (E) views.

Forest Formation (Lucas 1904, Lucas and Heckert 1996) from just north-east of Cameron, Arizona, dated as Adamanian as well (Heckert 2004). The histology of *P.* '*gigas*' was studied by Green *et al.* (2010).

The only dicynodont with taxonomically important similarity to *Lisowicia bojani* is *Placerias* '*gigas*'. Both have very long frontals that significantly contribute to the orbital margin, very wide parietals (triangular in medial section), sharp ventral edges of the maxillae, and wide postorbitals. Already Kammerer *et al.* (2013) and Sulej and Niedźwiedzki (2019) have included *L. bojani* in the Placeriinae. The problem with *P.* '*gigas*' is that its skull is known only from fragments or single bones from different individuals, although the material is very rich. For instance, the postorbitals were arranged into different ontogenetic stages (Camp and Welles 1956). Unfortunately, there are no other skulls of the Late Triassic dicynodonts that are similar to *Placerias* and *Lisowicia*. The lack of any complete skull makes fitting their isolated skull elements difficult. The only species that possessed the frontal that forms much of the orbital margin and has a very wide parietal (and triangular in medial section) is *Rabidosaurus cristatus* from the Anisian of Russia (Kalandadze 1970), although its frontal is much shorter than that of *Placerias* and *Lisowicia*. Some aspects of the reconstruction of the skull architecture of *P.* '*gigas*' and *L. bojani* skull were based on this species. Reconstruction of other elements refers to *Woznikella triradiata* (Szczygielski and Sulej 2023), in which the right frontal, nasal, and premaxilla from a single individual are preserved and are very similar to *P.* '*gigas*' and *L. bojani* (although probably juvenile).

Fig. 33. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Radii ZPA.33/665 and ZPA.33/700 in anterior (A, G), (posterior C, H), medial (D, I), lateral (F, J), distal (B), and proximal (E), views.

The original description by Camp and Welles (1956) was based on materials from the Placerias Downs' Quarry in Arizona. According to Ramezani *et al.* (2014) the strata exposed there are of Norian age. Other North American dicynodonts of Norian age (Ramezani *et al.* 2014) are *P. hesternus* from the Blue Mesa Member Pekin/Cumnock Formation in North Carolina (Long and Murry 1995, Langer 2005b) and *Eubrachiosaurus browni* from the Popo Agie Formation of Wyoming (Williston 1904, Kammerer *et al.* 2013). Most authors synonymize *P.* '*gigas*' with *P. hesternus*, but they are probably of different geological age and may represent distinct stages in evolution.

The new dicynodont *Argodicynodon boreni* Mueller *et al.*, 2023 from the Dockum Group of Texas, is almost half the size of *Placerias* '*gigas*'. The cladistic analysis showed affinities to *Placerias* and *Moghreberia nmachouensis* Dutuit, 1980, but its small size and the incompleteness of the skull and postcranium makes comparison to other Laurasian dicynodonts very difficult; it is possible that it is a juvenile, and that many of the features that supposedly distinguish it from *Placerias* are ontogenetic.

Cranium

The first reconstruction of the *Placerias* '*gigas*' skull was published by Camp and Welles (1956). An improved reconstruction with corrected position of the quadrate was presented by Cox (1965). More recent comparative study of the material and other Late Triassic dicynodonts exposed some other ambiguities

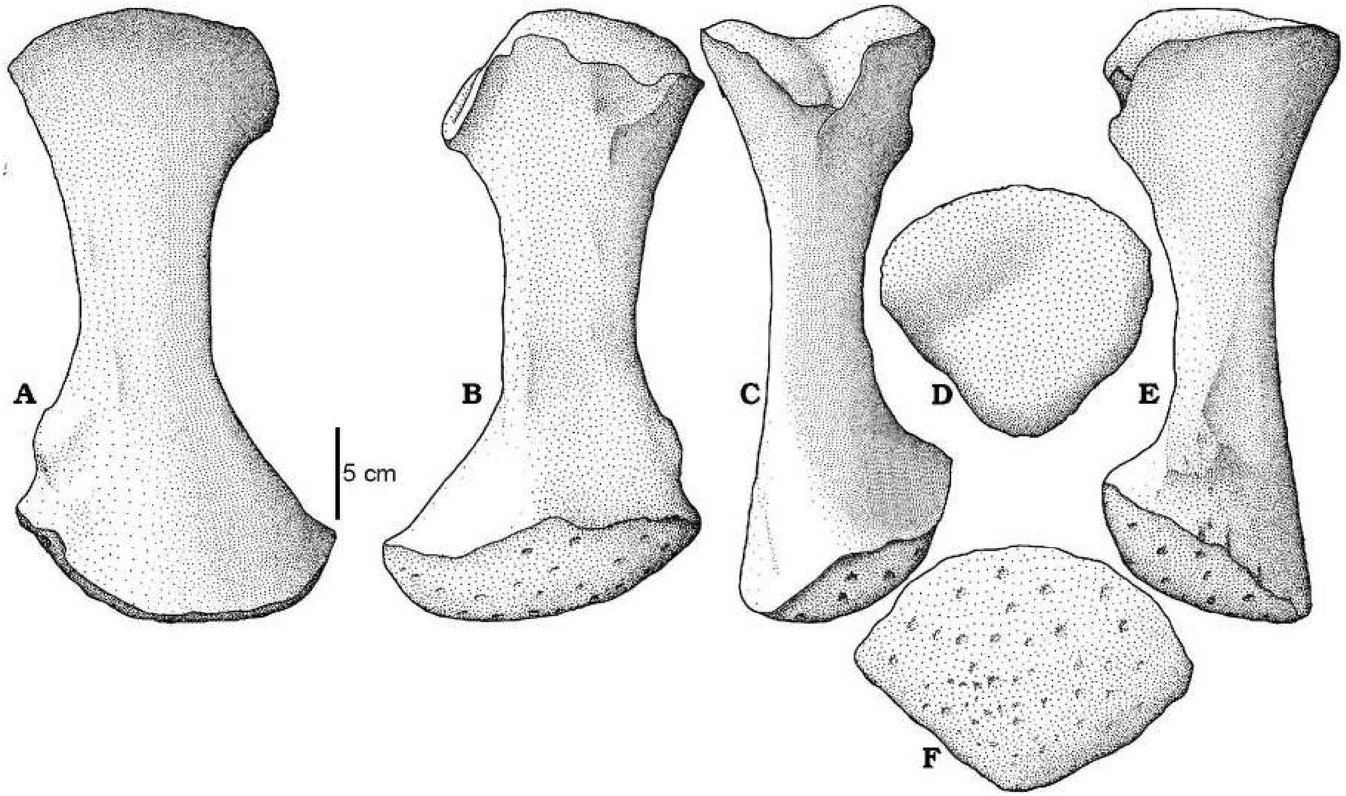

Fig. 34. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Reconstruction of radius based on ZPAL V. 33/665, in posterior (A), anterior (B), medial (C), lateral (D), and distal (E) views.

demanding modified reconstruction (Fig. 46). The main difference with respect to previous ones is the position of the lacrimal. This bone was depicted as vertical in previous reconstructions but, based on the shape of the nasal and the maxilla, its position should be horizontal. In the new reconstruction the bone is located very low in lateral view. A similarly low lacrimal is clearly visible in *Jachaleria candelariensis* and *Rabidosaurus cristatus*. This, in turn, demands a more sloped nasal, similar to *Ischigualastia jenseni*. Additional difference concerns the suture between the frontal and the parietal. The specimen UCMP 27379 shows that the frontal has a posterior process that forms sutures with the parietal and postorbital, similar to *Ischigualastia jenseni*.

The snout proportions are based on the new material of the Carnian *Woznikella triradiata* (Sulej *et al.* 2011, Szczygielski and Sulej 2023). The main problem with *P.* '*gigas*' is the position of the quadrate; it is inferred from fragments of the squamosal UCMP 32458.

In the reconstruction of *Placerias* '*gigas*' proposed here, the interparietal (postparietal) is shorter than interpreted previously, based on the specimen UCMP 27721. Also, the supraoccipital is closer to the parietal, as in *Rabidosaurus cristatus*, which has a similar morphology of these bones. The supraoccipital is shorter and lower than in the reconstruction of Cox (1965), which is visible in the cross-section of the skull. The frontal in lateral view is much lower above the orbits. The specimen UCMP 27379 shows that it was 0.5 cm above the orbit, and the postorbital has the posterior process lateral to the parietal, so this bone is not well exposed in lateral view.

In the UCMP material, there is a large collection of postorbitals, basisphenoids, and squamosals. The variability of postorbitals was illustrated by Camp and Welles (1956: fig. 14). They represent a sequence from small and narrow to large and wide (UCMP 26679). Specimens from older individuals are thicker but not longer. It seems that the termination of growth was present in *Placerias* '*gigas*' and later in ontogeny the bones grew only in their width. Probably this allometry also concerns the premaxilla. In the specimen UCMP 2761, the relationship of its length to width is 16.0 cm × 9.5 cm, but in the larger UCMP 27830, it is 16.5 cm × 11.5 cm, which means that its length increased 3% but width 21%. More increase of width than length was observed also in *Stahleckeria potens* (see figures of juvenile skull in: Vega-Dias 2005). Based on this proportion, the frontal in the 3D model in UCMP 2761 (Camp and Welles 1956: pl. 32) is too long. In the specimens UCMP 26674 and UCMP 28384, the proportion of length to width is 10.8 cm × 7.25 cm, but in the model reconstruction it is 13.0 cm × 8.5 cm, which implies an increase of length 20% and width 13%. In the reconstruction presented here, the frontal is relatively shorter than in the 3D reconstruction in UCMP.

Probably the most complete postorbital of *Placerias* '*gigas*' is GPIT-PV-108381 in the collection of the University of Tübingen, almost identical with not so complete specimens from UCMP. The lateral edge of the squamosal can be reconstructed based on the specimen UCMP 32458. The size of the quadrate in the reconstruction of Cox (1965: fig. 28) seems a little too small. The maxilla of *P.* '*gigas*' has two morphotypes that are well exemplified by the specimens UCMP 27539 (short) and UCMP 27551 (long); the difference in length is 1.7 times whereas the proportion of width is 1.16 times. According to Camp and Welles (1956) they represent sexual dimorphism.

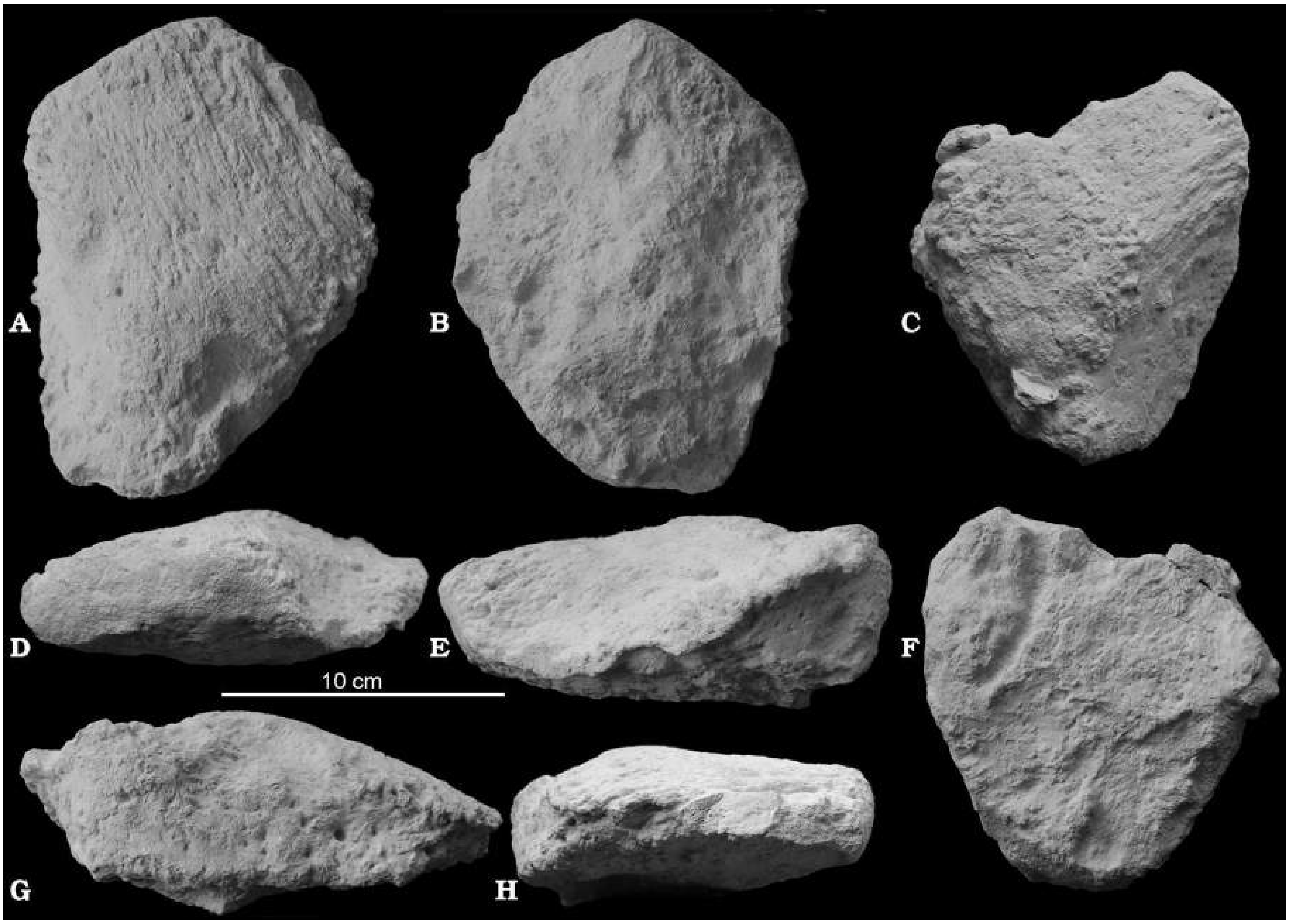

Fig. 35. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Ulnare ZPAL V. 33/716 (A, B, D, E, G, H) and V. 33/758 (C, F) respectively in proximal (A, C), distal (B, E), anterior? (D), medial? (E), lateral (G), and posterior (H) views.

Mandible

All elements of the mandible of *Placerias* '*gigas*' are known but most of them are strongly damaged. Especially the dentaries are broken. The best-preserved dentary, UCMP 27553, has a complete anterior part. The posterior process of the dentary is the best preserved in UCMP 24140, although the bone is deformed, with missing posterior tip and ventral part. The reconstruction of the lateral view was based on UCMP 27553 (as in: Camp and Welles 1956) but the length was taken from UCMP 24140 (of the same width as UCMP 27553). It was assumed that the main body of the dentary has similar proportions and an elongated posterior process as in *Wadiasaurus indicus* (Bandyopadhyay 1988: fig. 4) and *Woznikella* (Szczygielski and Sulej 2023). The general proportions of the mandible were taken from *W. indicus* (Fig. 46).

The splenial of *Placerias* '*gigas*' (UCMP 32104) was originally visible under the dentary in the lateral view of the mandible, as in *Kannemeyeria simocephalus* in Camp and Welles (1956: fig 43). The largest mandible has the dentary with height 13 cm in the middle part, and the skull could have a length of 75 cm.

Postcranial elements

Despite the thorough examination of the *Placerias* '*gigas*' material in the UCMP and GPIT museums' collections, no reliable remnant similar to the clavicle of the Carnian *Woznikella triradiata* (Szczygielski and Sulej 2023) or *Parakannemeyeria youngi* was encountered. The bones labelled as clavicles are similar rather to the pectoral ribs of *P. youngi* and *Lisowicia bojani*. However, the large acromion process of *P.* '*gigas*' suggest that it had a clavicle.

The humerus specimen UCMP 32460 represents bone pieces that were mounted into one individual [described by Camp and Welles (1956: fig. 30)] in different ways than in complete humeri of other dicynodonts. The most complete humerus of *Placerias* '*gigas*' is that in Tübingen (GPIT-PV-108382). In the mounted specimen UCMP 32460, the distal head should be rotated to make the articulation surface for the ulna much lower. In the other specimen, UCMP 32459, the fragment with the ectepicondyle is located in too low of a position.

Reconstruction of the *Lisowicia bojani* skeleton

Skull

The reconstruction of the skull of *Lisowicia bojani* (Fig. 47) is based on bones coming from a few individuals. They represent parts of the skull roof (ZPAL V. 33/MB/18), braincase (ZPAL V. 33/531), and single bones (maxilla ZPAL V. 33/85, postorbital ZPAL V. 33/708, parietal ZPAL V. 33/741, stapes) or their fragments from different individuals: the premaxilla, paroccipital.

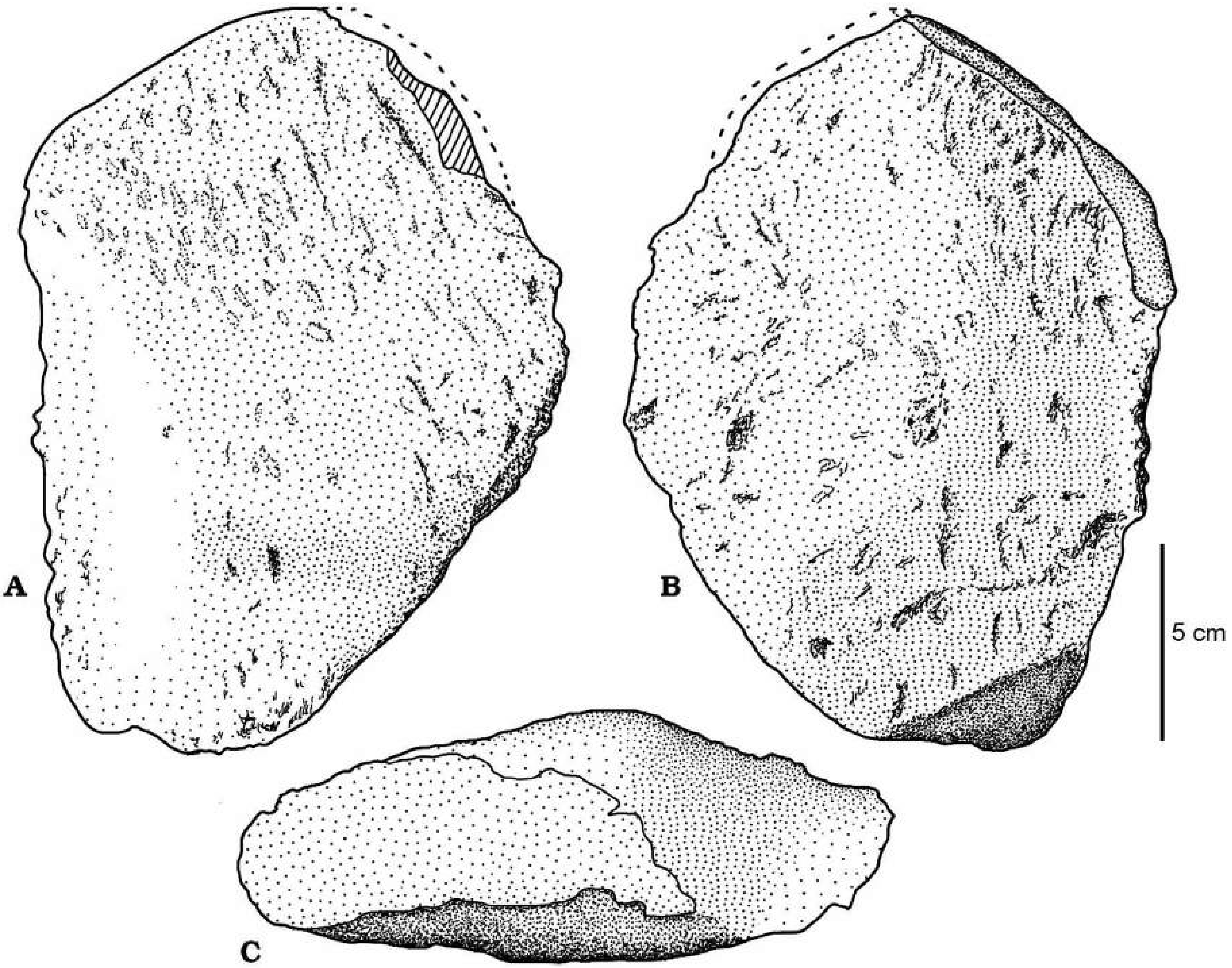

Fig. 36. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. The reconstruction of ulnare based on ZPAL V. 33/716 in proximal (A), distal (B), and anterior? (C) views.

The general proportion of the skull was taken from the new reconstruction of *P.* '*gigas*'.

Cranium: The relationship of the frontal to postorbital is clearly visible in the specimen ZPAL V. 33/MB/18. A parietal foramen forms a canal the shape of which can be recognized in this specimen and in the whole parietal (specimen ZPAL V. 33/741). The dorsal edge of the frontal and parietal are visible in lateral view, the latter only slightly raised. The positions of the lacrimal and maxilla are based on *Jachaleria candelariensis*, *R. cristatus*, and *P.* '*gigas*'. The setting of the squamosal was reconstructed according to morphology of this element in *P.* '*gigas*'.

Mandible: The posterior part of the mandible is preserved in two specimens, ZPAL V. 33/735 and ZPAL V. 33/736. They consist of the articular, surangular, and prearticular. The angulars are also preserved, but always as isolated elements. The dentary and splenial are missing. The reconstruction of the posterior part of the mandible is based on general proportions in other Triassic dicynodonts and on the fit with known elements. The shape of the elongated dentary was based on an extremely elongated bone in *Woznikella triradiata* (length/deep—16.6 cm × 6.2 cm = 2.67, probably the ancestor of *Lisowicia* in Europe).

Postcranial skeleton

The limb postures of kannemeyeriid dicynodonts were studied by Walter (1986) and Fröbisch (2006). Most of the material of Middle and Late Triassic dicynodonts consists of disarticulated skeletons or their parts. Rare articulated skeletons represent different groups of Triassic dicynodonts. These are: *Shansiodon wangi* Yeh, 1959, *Shansiodon wuhsiangensis* Yeh, 1959, *Tetragonias njalilus* von Huene, 1942, and *Angonisaurus cruickshanki* among Shansiodontini (Cox 1965) and *Kannemeyeria simocephalus* among Kannemeyeriini (Lehman 1961). The most complete are *Parakannemeyeria youngi*, *Xiyukannemeyeria brevirostris* Liu and Li, 2003, *P. xingxianensis*, *Sinokannemeyeria yingchiaoensis*, *Dinodontosaurus tener*, *Rhadiodromus klimovi*, and *Ischigualastia jenseni*.

Two species were selected as the reference standard for the reconstruction of the skeleton of *Lisowicia bojani*: *Parakannemeyeria youngi* and *Sinokannemeyeria yingchiaoensis*.

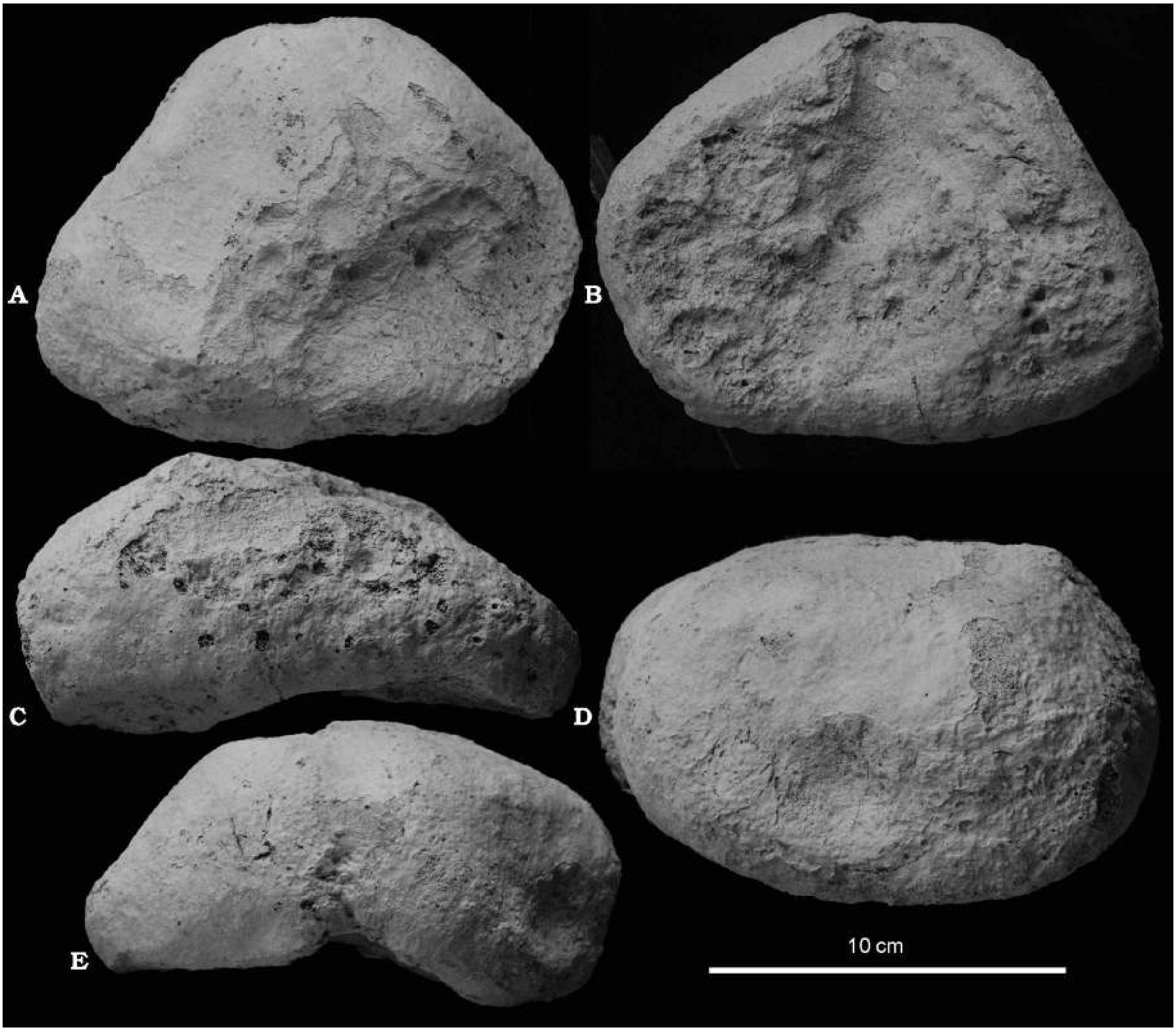

Fig. 37. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. The radiale ZPAL V. 33/453 in proximal? (A), distal? (B), posteriori? (C), Lateral? (D) and anterior? (E) views.

Their humeri, ulnae, and radii have proportions closely similar to the bones of *L. bojani*, despite different construction of the forelimb. Other dicynodonts differ substantially from *L. bojani*, for instance adult *Dinodontosaurus tener* material from Harvard has a very short scapula in relation to the length of the humerus (Cox 1965: fig. 11).

The vertebral spine of *Lisowicia bojani* and its relationship to the pelvis was based on the fit of bones in the individual ZPAL V. 33/720. The proportions of the pectoral girdle and forelimb were based on the proportions in the *Parakannemeyeria youngi* specimen IVPP V. 979; with respect to the length of scapula vs. length of the humerus, it is 1.25, and the length of the humerus vs. length of the ulna is 1.10. The length of the scapula vs. length of the sternum is 1.61 in *Sinokannemeyeria yingchiaoensis* specimen IVPP V. 974. The length of the ulna vs. length of the radius is 1.88 in *S. yingchiaoensis* specimen IVPP V. 974 (measurements from: Sun 1963).

Pelvic girdle and forelimb: The position of the humerus and scapulocoracoid in *Lisowicia bojani* is similar to that in large mammals, such as rhinoceroses and hippopotami, as well as quadrupedal dinosaurs, such as the ceratopsians (Sulej and Niedźwiedzki 2019). In most Triassic dicynodonts the scapula was *set al*most vertical and humerus almost horizontal. Such articulation would be difficult to maintain by an animal of *L. bojani* size. Also, the trackway of some dicynodont shows the manus and pes in the same line (Hunt *et al.* 1993) and thus contradicts the traditional reconstruction of their forelimb. The disposition proposed for *Triceratops horridus* Marsh 1889 (Fujiwara 2009) with a more horizontal scapula and vertical humerus (very similar to *L. bojani*) seems more realistic. The size of the joint for the scapula on the posterior side of the humerus corresponds to the position of this bone. Large *Stahleckeria potens* that had area of the articulation with the scapula small probably represents an intermediate stage between the horizontal humerus of

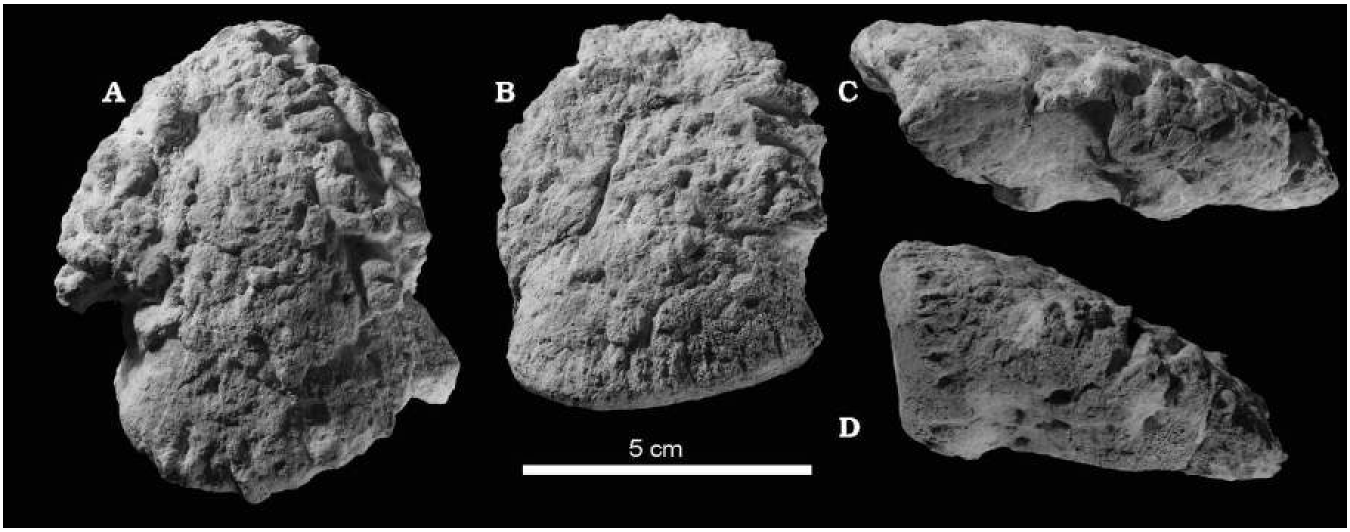

Fig. 38. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Last digits ZPAL V. 33/749 (A, C), ZPAL V. 33/744 (B, D), respectively, in dorsal (A, B), and lateral (C, D) views.

small dicynodonts with a small joint for the scapula (for instance *Oudenodon bainii* Kammerer *et al*., 2011 (earlier *Dicynodon halli*) and *Placerias* '*gigas*' that had an already large posterior joint for the scapula. An advanced stage with the vertical position of the humerus is represented by *L. bojani*, which has a non-rotating humerus with a very large joint for the scapula.

The shift of the humerus to a vertical position should be related to some changes in its articulation with the ulna and radius. The published illustrations of the dicynodont radii are too superficial to enable comparison with that of *Lisowicia bojani*. This makes the well-preserved proximal part of the quite well-preserved radius from New Mexico NMMNH P-13002 important. This bone and associated femur, part of scapula and axis were described as *Ischigualastia jenseni*? by Lucas and Hunt (1993) but Kammerer *et al.* (2013) assigned it to Stahleckeriidae indet. based on the shape of the femur.

The scapula NMMNH P-13003 is a distal part of the bone showing the scapular spine and acromion process (nomenclature from: Vickaryous and Hall 2006). It seems that the scapula was very similar to that of *Placerias* '*gigas*'. The radius has a well-visible head bent outward, which is distinct also in *Ischigualastia jenseni*, *Jachaleria candelariensis*, and *Lisowicia bojani* (all with not preserved clavicles and a small acromion process) and not known in other dicynodonts [illustration of *Pristerodon mackayi* Huxley, 1868 earlier *Diaelurodon whaitsi* in Watson (1917: fig. 13) suggests that it was present in this species]. But the bending has a different position in the radius from New Mexico then in *I. jenseni*, *J. candelariensis*, and *L. bojani*. In these dicynodonts it is situated in the posterior part of the head, whereas in the New Mexico specimen it is in an anterior position, like *D. whaitsi*, which had a horizontal position of the humerus.

The articulation of the coracoid and anterior part of the sternum occurs in the *Struthio camelus* Linnaeus, 1758, *Diplodocus* Marsh, 1878 (Hohn *et al.* 2011), *Alligator* Cuvier, 1807, *Tachyglossus* Illiger, 1811, and *Ornithorynchus* Blumenbach, 1800 (Gregory and Camp 1918). In *Lisowicia bojani*, the coracoid has a large joint with the anterior part of the sternum. In the coracoid of *Placerias* '*gigas*' UCMP 32449, the area for attachment with the sternum is clearly visible.

Sternum: The latest Triassic *Lisowicia bojani* has an articulation area on the sternum in its posterior part. The sternum of the Anisian (Liu *et al.* 2017) *Sinokannemeyeria yingchiaoensis* has an articulation for the coracoid and first dorsal rib in the middle of its length. Cox (1965), based on the specimen MCZ 3120, depicted the sternum of *Ischigualastia jenseni* with an articulation area in its posterior part. It is the only specimen in the Harvard collection with all bones of the pectoral girdle articulated, although not all are in anatomical positions. The problem with the sternum is that it is strongly compressed, and no articulation surface is visible. The Cox (1965) interpretation was based only on the general shape of the bone.

Romer (1956) showed the sternum of *Kannemeyeria simocephalus* posterior to the scapulocoracoid. In the skeleton reconstruction of *Dinodontosaurus brevirostris* at Harvard, the interclavicle is at the level of the procoracoid, and the sternum is more posterior than in the specimen MCZ 3120. In such a probably correct position, the articulation area on the sternum can contact the posterior process of the coracoid (Sulej and Niedźwiedzki 2019).

Clavicle: An intriguing problem is the presence of the clavicle and interclavicle in *Lisowicia bojani*. It was hypothesized by Sulej and Niedźwiedzki (2019: fig. 1), but the very small acromion process on the scapula, which in other dicynodonts was much larger and designed for articulation with the clavicle, contradicts its presence (Fig. 48). On the other hand, the anterior lower part of the scapula in *L. bojani* is much larger and the sternum is much higher than in most dicynodonts. This difference suggests different functioning of the whole girdle. Sulej and Niedźwiedzki (2019) showed that *L. bojani* had erect forelimbs, unlike all other dicynodonts. Instead of them, *Triceratops* or the rhinoceros may serve as the analogues for the construction of the shoulder girdle. They do not have clavicles because of the erect position of the forelimb. Probably

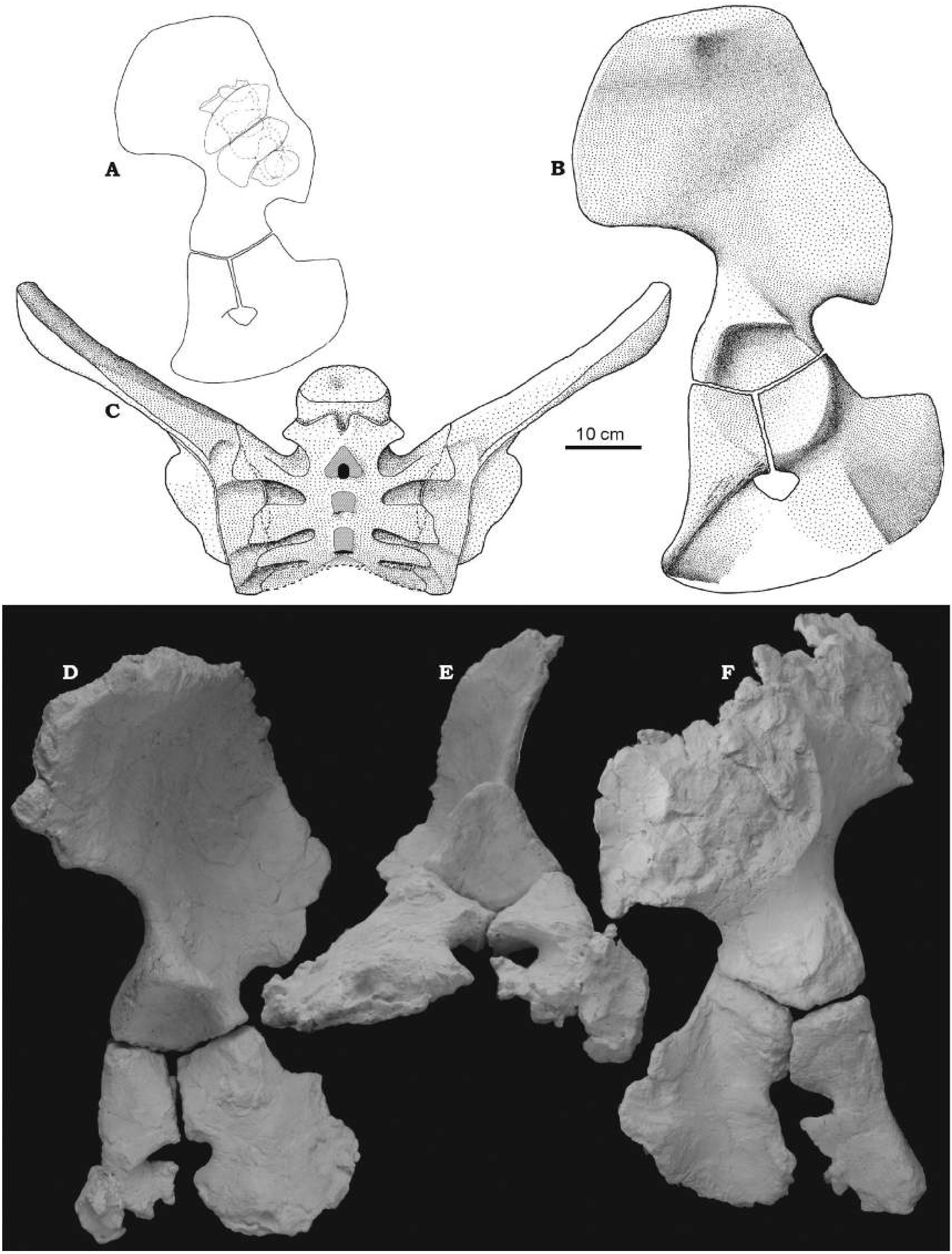

Fig. 39. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Pelvis ZPAL V. 33/720 and reconstruction of pelvis based on ZPAL V. 33/720, in medial (A, F), lateral (B, D), dorsal (C) and (E) ventral views.

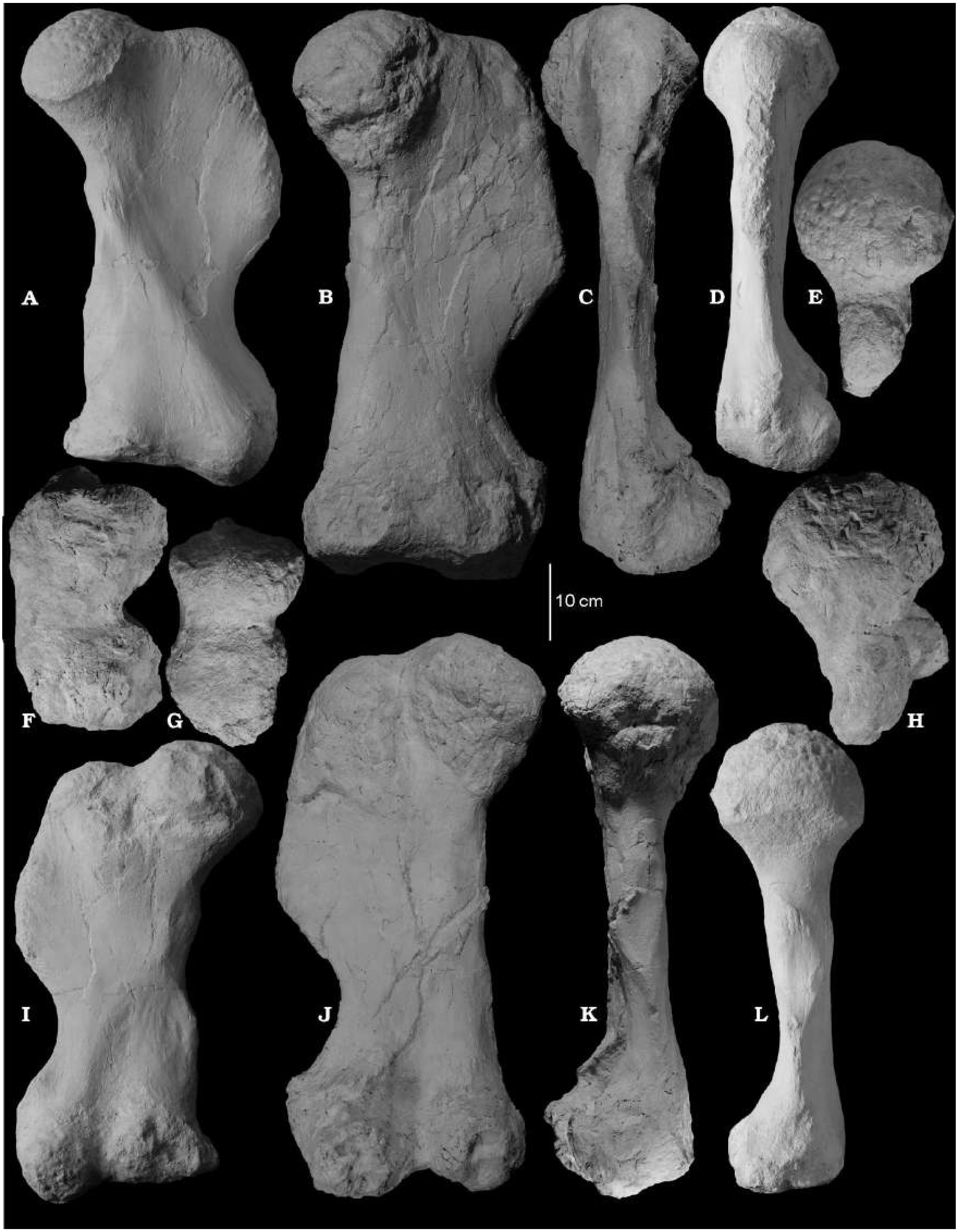

Fig. 40. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Femur ZPAL V. 33/75 (A, D, E, G, I, L) and ZPAL V. 33/763 (B, C, F, H, J, K) in anterior (A, B), lateral (C, D), proximal (E, H), distal (F, G), posterior (I, J), and medial (K, L) views.

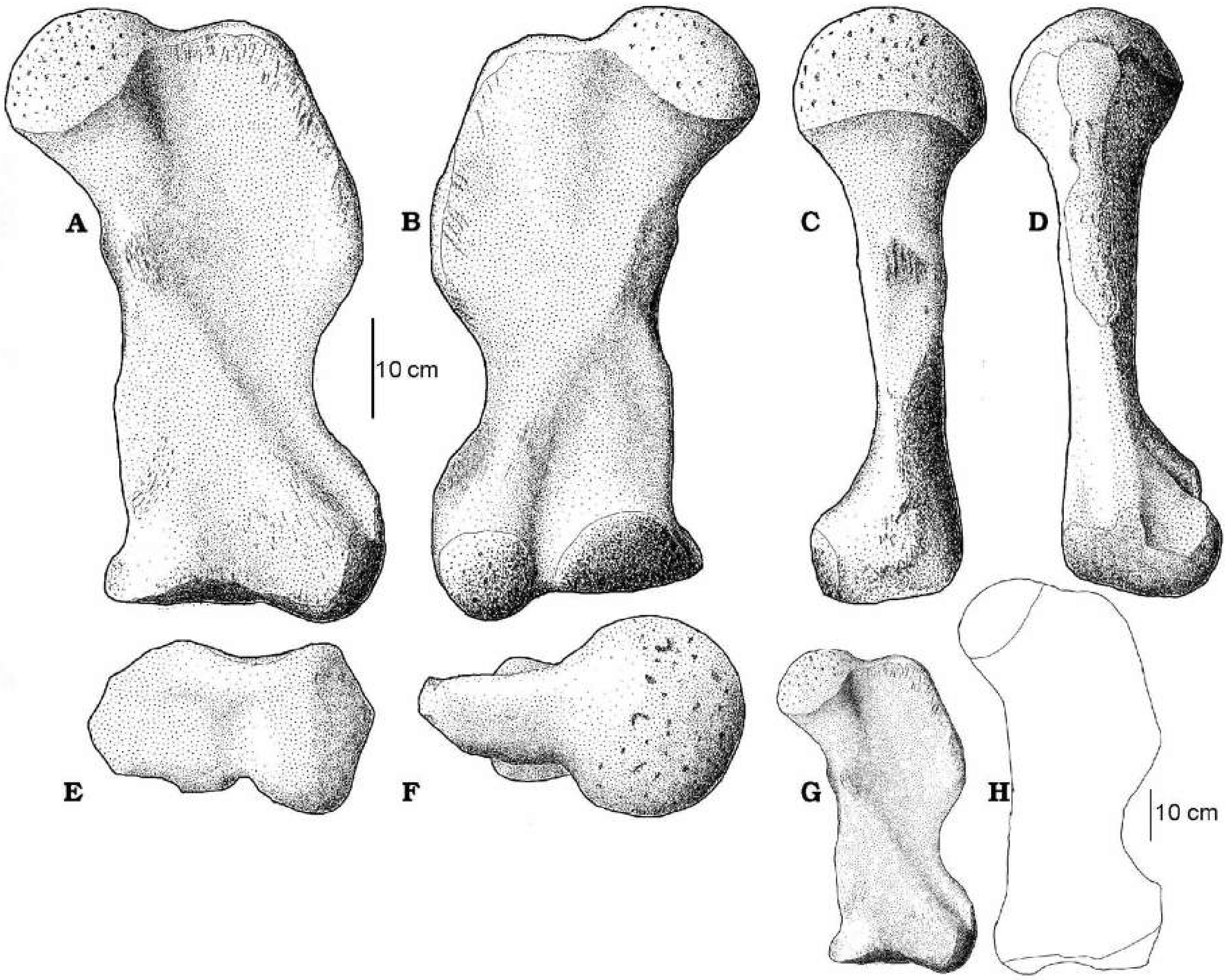

Fig. 41. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Reconstruction of femur based on ZPAL V. 33/75 (A–G) and ZPAL V. 33/763 (H) the largest in the same scale as (G), in anterior (A, H), posterior (B), medial (C), lateral (D), distal (E), and proximal (F) views. Note identical shape of curve of the small and large specimen (G and H).

a similar situation was in *L. bojani*. The loose connection of the olecranon process with the main body of the ulna in its skeleton is probably related with the position of the forelimb. In most large dicynodonts the olecranon is fused with the ulna (*Wadiasaurus*, *Stahleckeria*, *Jachaleria*, and *Sinokannemeyeria*), and that was related to a sprawling posture. The m. triceps attached to the olecranon process, the humerus, and the scapula was among the muscles responsible for keeping the animal in that position. When the humerus was rotated posteriorly to support the erect posture, other muscles became responsible for it. Among them were m. pectoralis, m. supracoracoideus (with a much larger area for articulation on the scapula than in other dicynodonts) and m. coracobrachialis (Sulej and Niedźwiedzki 2019). The loose olecranon process is known also in *Placerias* '*gigas*' (Camp and Welles 1956), but in this species the acromion was of the standard shape and it remains unknown how the rotation of the humerus took place. Presumably *Placerias* represents an early stage of the evolution towards the erect posture.

DISCUSSION

Lisowicia mode of life

Traditionally dicynodonts are depicted with abducted (directed to outside) forelimbs and nearly adducted (oriented towards the body axis) hindlimbs (Fröbisch 2006, Ray 2006). However, the trackways of a large dicynodont from the Middle Triassic named *Pentasauropus argentinae* make such posture questionable (Hunt *et al.*1993, Lagnaoui *et al.* 2019). This track is believed to have been left by a kannemeyerid dicynodont that was a sprawling limbed trackmaker with an abducted posture for the forelimbs and at least a semi-abducted posture for the hindlimbs (Abdelouahed *et al.* 2019). Sulej and Niedźwiedzki (2019) proposed that the giant *Lisowicia bojani* had also adducted its forelimbs. This has also been discussed for pelycosaur tracks, which have a much more narrow gauge than the skeleton would seem to indicate. Twisting of the body and/or limbs while walking might explain how this happens (Hunt and Lucas 1998, Hopson 2015).

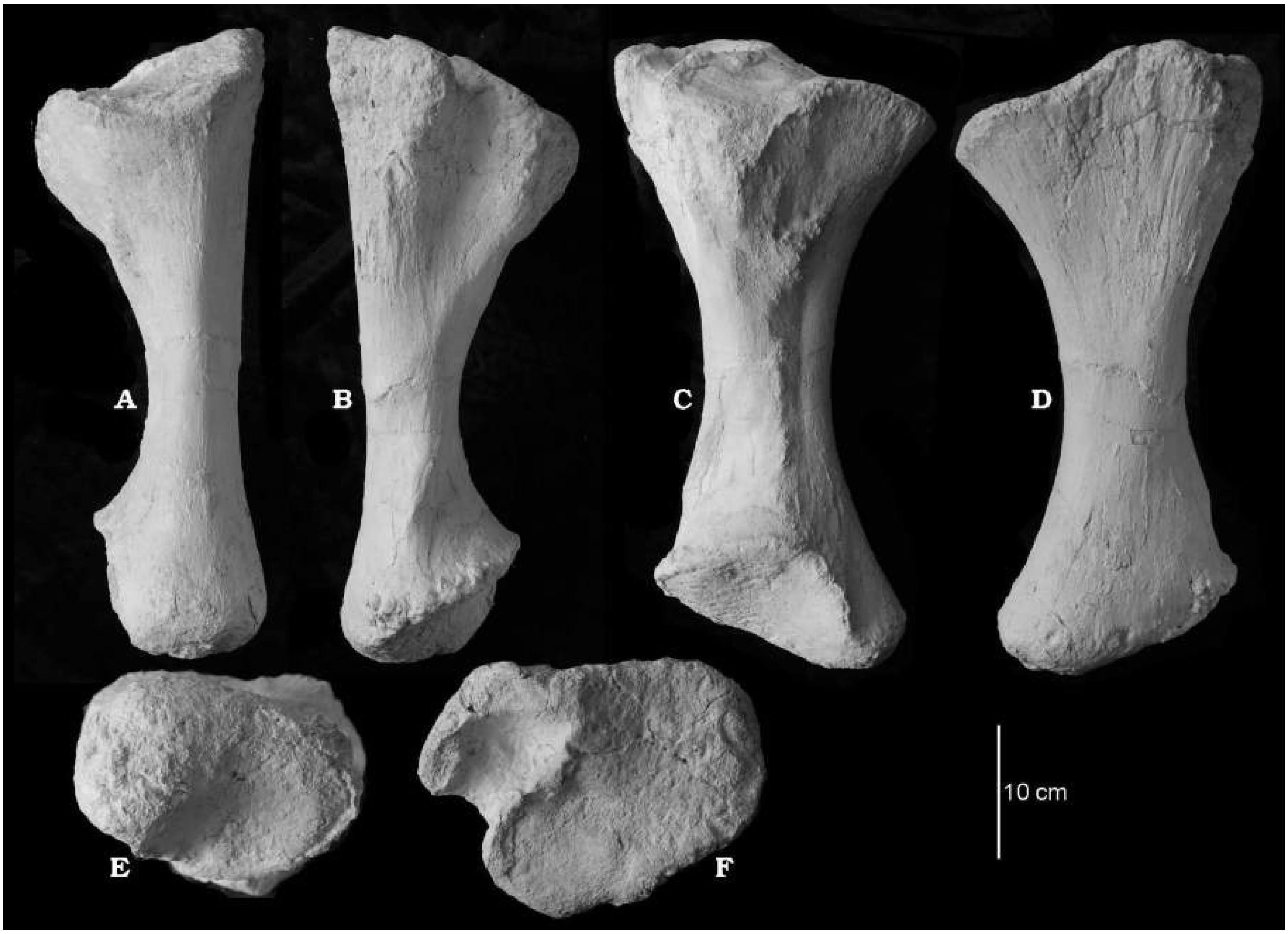

Fig. 42. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Tibia ZPAL V. 33/75 in medial (A), lateral (B), posterior (C), anterior (D), distal (E), and proximal (F) views.

The analysis of sediments (or bones) from Lisowice shows that *Lisowicia* lived in an environment near rivers with a lot of oxbow lakes (Dzik *et al.* 2008). Also, the similarities of coprolites of *Lisowicia* to *Hippopotamus amphibius* Linnaeus, 1758 suggest its affiliation with such an environment (Bajdek *et al.* 2014, 2019). In the case of *Placerias*, its bone microstructure suggests even an aquatic style of life (Fiorillo *et al.* 2000). If they lived in or close to the swamp, they probably could use the soft plants as a food (Bajdek *et al.* 2014), abundant in such environments. Such an interpretation is not in conflict with the architecture of their skulls.

There is little doubt that all the Triassic dicynodonts were herbivorous, but there are various views on the method by which they collected the food (see: Surkov and Benton 2004). According to Cruickshank (1978), *Dinodontosaurus*, *Stahleckeria potens*, *Dolichuranus* Keyser, 1973, *Tetragonias*, *Rhinodicynodon*, *Zambiasaurus*, *Sinokannemeyeria*, and *Vinceria* Bonaparte, 1969 were browsers, whereas *Placerias*, *Jachaleria*, *Ischigualastia jenseni*, *Kannemeyeria*, *Uralokannemeyeria* Danilov, 1971, *Rabidosaurus*, *Rhadiodromus*, and *Wadiasaurus indicus* were grazers (in the meaning that they ate low-growing plants). Originally, Cox (1965) made this distinction based mainly on the shape of the snout and the orientation of the occipital region of the skull. Ordoñez *et al.* (2019), based on principal component analyses (PCA) of skulls from South America, showed that the adaptation of *Stahleckeria potens*, *I. jenseni*, and *J. candelariensis* to feeding on the vegetation was characteristic of an arid climate, although the palaeoclimate was seasonal semi-arid when they lived (Mancuso *et al.* 2021). The new material from Poland calls for reconsideration of this question.

Most authors discussing the dicynodonts mode of life have focused on their sexual dimorphism (Owen 1876, Camp and Welles 1956, Barry 1957, Cruickshank 1967, Cox 1969, Bandyopadhyay 1988, Sullivan *et al.* 2003). The differences between males and females were proposed to be expressed mainly in the presence of the tusks or maxillary horns in males. The lack of conclusive material excludes *Lisowicia bojani* from these inquires. Most authors agree that the canine tusks or elongated maxillary processes were used in food gathering and fighting (Camp and Welles 1956, Rowe 1979, Bandyopadhyay 1988). Many authors have discussed the mode of feeding of dicynodonts (Cox 1969, Cruickshank 1978, Walter 1985, Hotton 1986), summarized by Defauw (1989), who recognized five dicynodont feeding types: invertebrate collecting specialists, grubbers, browsers, forest litter foragers, and flexible foragers. The functional morphology of the dicynodont masticatory

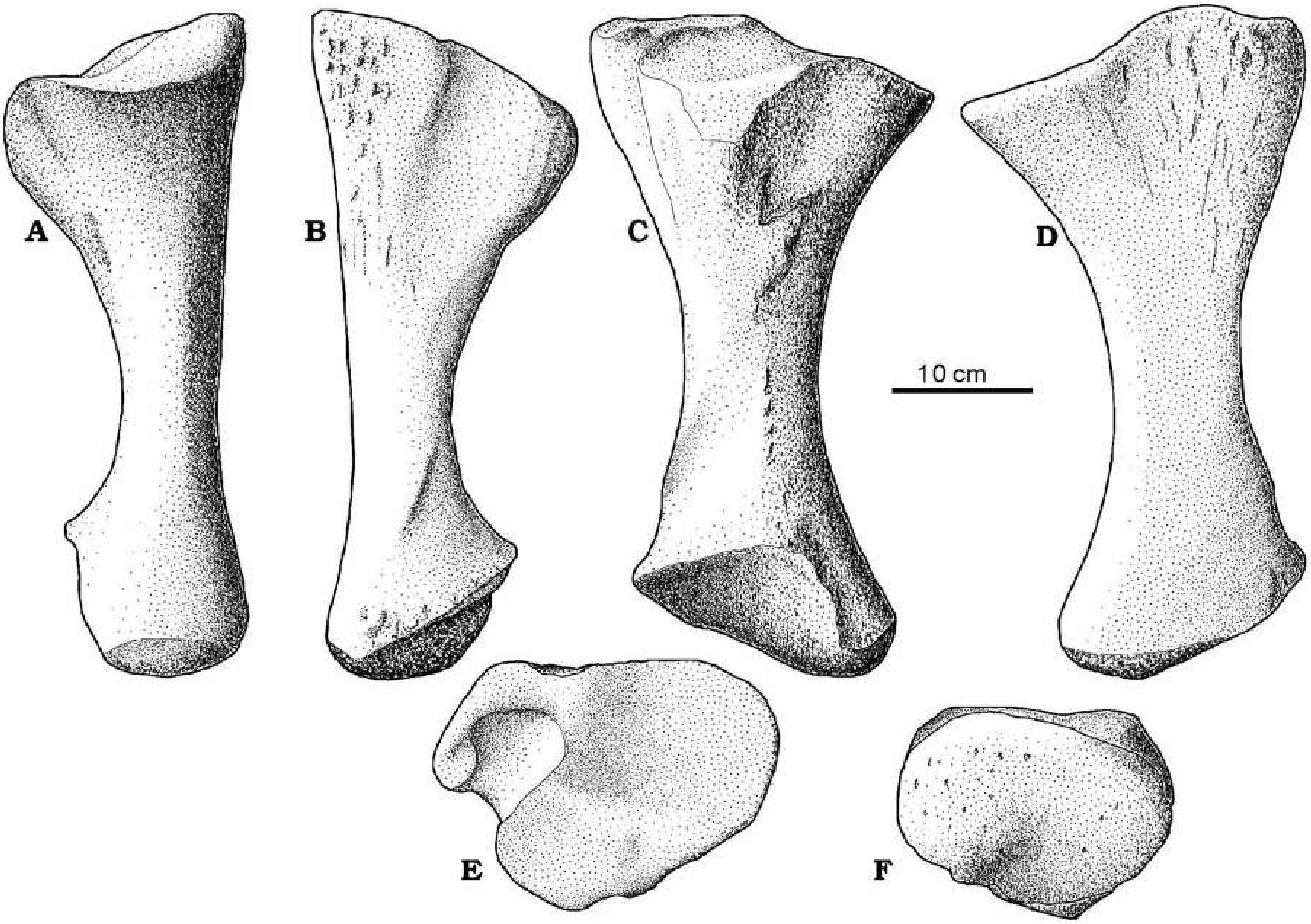

Fig. 43. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Reconstruction of tibia based on ZPAL V. 33/75, in medial (A), lateral (B), posterior (C), anterior (D), proximal (E), and distal (F) views.

apparatus was studied by Crompton and Hotton (1967), King *et al.* (1989), Cox (1998), Jasinoski *et al.* (2009, 2010), and Ordoñez *et al.* (2019).

Niedźwiedzki *et al.* (2011, 2012) showed that the archosauriform *Smok wawelski* Niedźwiedzki *et al.*, 2012 was feeding on dicynodonts in the Late Triassic but probably dicynodonts escaped this predation by evolving into giant size, already in the Middle Triassic. The most numerous preserved bones of the skull of *Lisowicia bojani* and *Placerias* '*gigas*' are postorbitals and basisphenoids, unlike the nasals that are very rare in the case of *P.* '*gigas*' and unknown in *L. bojani*. This may mean that the snout was a structurally weak portion of the skull that was the first to disarticulate during rotting of the carcass or the dorsal part of the snout was an attractive target for predators, whereas the postorbital was too massive for them.

Phylogeny of the Triassic dicynodonts

The phylogeny of the Triassic dicynodonts has been discussed by many authors, e.g. Camp (1956), Cruickshank (1978), Keyser and Cruickshank (1979), Cooper (1980), King (1988, 1990), Angielczyk (2001), Maisch (2001), Surkov and Benton (2004), Vega-Dias *et al.* (2004, 2005), Ray (2006), Damiani *et al.* (2007), Fröbisch *et al.* (2010), Kammerer *et al.* (2013), Ruta *et al.* (2013), Maisch and Matzke (2014), Sulej and Niedźwiedzki (2019), Griffin and Angielczyk (2019), Kammerer and Ordoñez (2021), Liu (2022), and Szczygielski and Sulej (2023).

Some trends in the evolution of Triassic dicynodonts are apparent. Keyser (1974) noticed an increase in the body size, the relative length of the snout and secondary palate, reduction in the length of the fenestra medio-palatinalis, shortening and dorsal expansion of the intertemporal region, fusion of elements of braincase, posterior migration of the reflected lamina of the mandible, and disappearance of the quadrate foramen. Cox and Li (1983) classified the Triassic dicynodonts into three families, Kannemeyeriidae, Stahleckeriidae, and Shansiodontidae, based on their skull proportions. According to the cladistic analysis by Surkov *et al.* (2005) *Dinodontosaurus*, *Stahleckeria*, and *Ischigualastia* form a distinct clade, whereas *Placerias* is close to *Wadiasaurus* and *Kannemeyeria*. According to Kammerer *et al.* (2011) and Vega-Dias *et al.* (2004), *Ischigualastia* and *Jachaleria* are closely related. According to Lucas and Wild (1995) and Lucas *et al.* (2002) they even represent the same species. Damiani *et al.* (2007) showed that *Stahleckeria* and *Ischigualastia* are closely related. Maisch and Matzke (2014) proposed *Placerias* to be close to the Early Triassic *Sungeodon*. Kammerer *et al.* (2013), Sulej and Niedźwiedzki (2019) and Szczygielski and Sulej (2023) showed that *Eubrachiosaurus* was closely related to *Ischigualastia* and *Jachaleria*. Still, despite these efforts

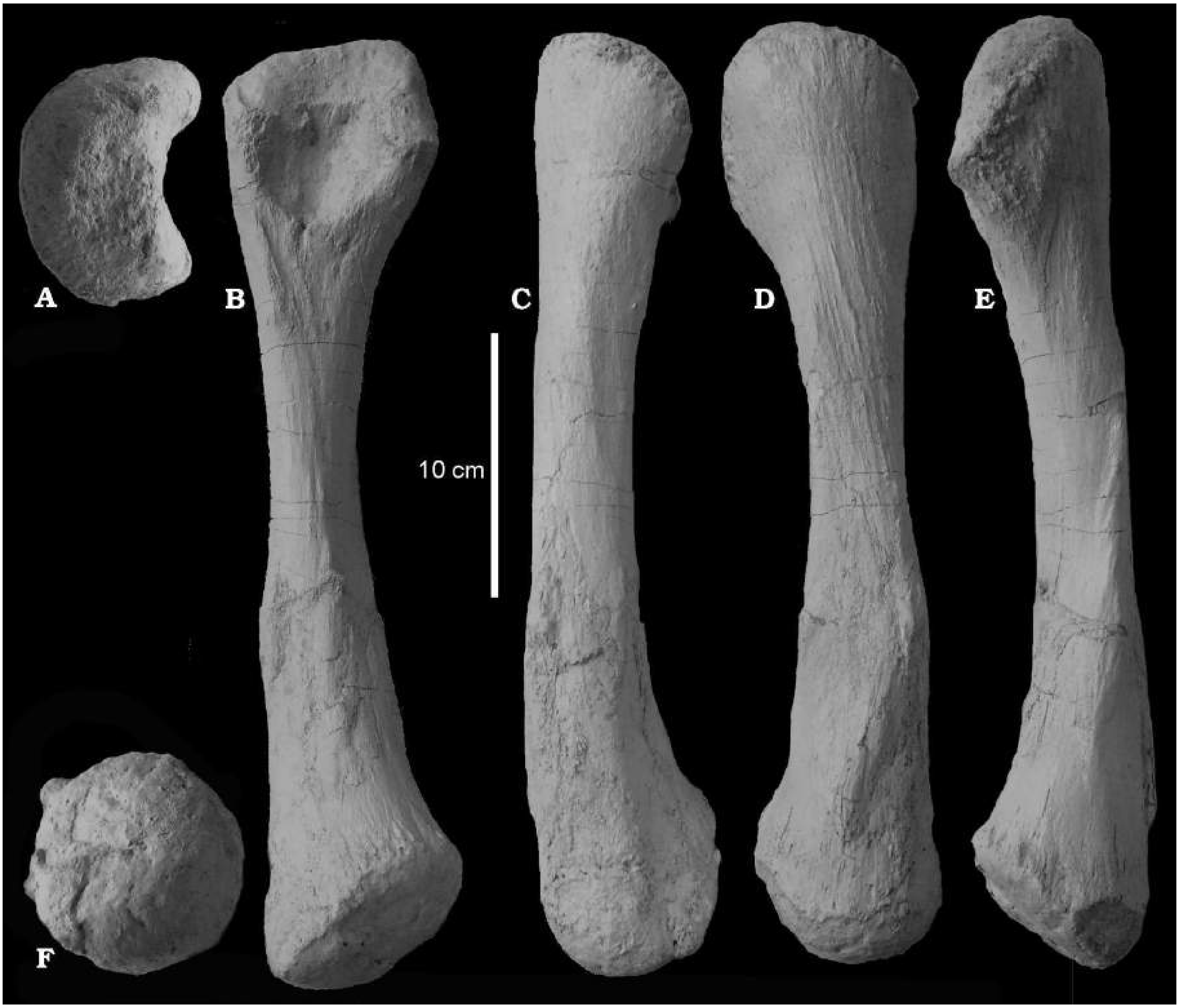

Fig. 44. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Fibula ZPAL V. 33/75 in proximal (A), medial (B), posterior (C), lateral (D), anterior (E), and distal (F) views.

there is no consensus regarding relationships of the Late Triassic dicynodont genera.

Regrettably, the phylogenies proposed by various authors are hardly compatible. New data on the latest Triassic dicynodont, *Lisowicia bojani*, may enable refining and testing these interpretations but this calls for a different methodological approach to inference on the evolution of dicynodonts. Here, as an alternative to the cladistic view on the phylogeny of Triassic dicynodonts, I try to use stratigraphic and geographic aspects of the dicynodont fossil record, which is the chronophyletic approach to the subject. It implies hypothesizing in terms of anagenetic relationships between ancient populations represented by fossils having objective time and space coordinates instead of estimating morphological distances between taxa.

An intriguing aspect of the dicynodonts is their seemingly bipolar distribution. The similar bipolar distribution was observed also in Late Triassic dinosaurs (Griffin *et al.* 2022), although in the case of dicynodonts there were periods of wide migrations, when species from Asia and Europe gave origin to southern lineages. A closer look at their fossil record allows us to distinguish their separate lineages evolving in specific geographic contexts. It is also possible that dicynodonts were probably cosmopolitan in distribution in the Triassic; the issue is with outcrop area, not their actual biogeography.

The dicynodonts from the Triassic tribes Placerinii and Stahleckerini (King 1988, 1990) can be distinguished based on the shape of the frontal and parietal (Fig. 49). The differences between various species were already noticed by Camp (1956). Especially the cross-section in the midline of these bones is very characteristic. This part of the skull surrounds the brain and probably is strictly controlled by natural selection. It is probably the most important character that may be used to trace the evolution of this group. The dicynodonts from South America (*Stahleckeria* and younger), *Sinokannemeyeria* from China, and *Rhadiodromus* from Russia have the parietal with its ventral part extended. In cross-section their parietal is less or more round or

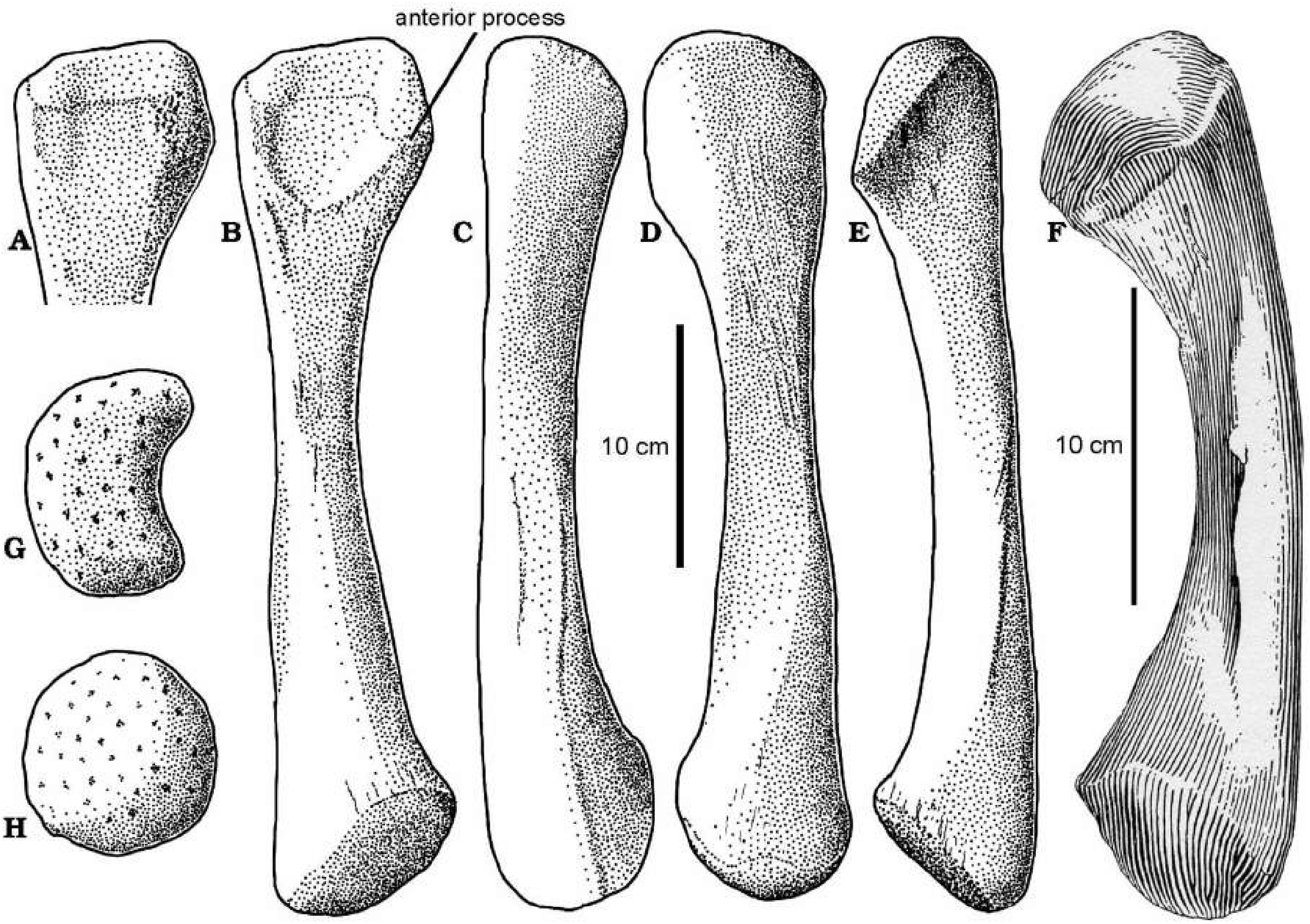

Fig. 45. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Reconstruction of fibula based on ZPAL V. 33/75 (B–E, G, H), and ZPAL V. 33/475 (A, proximal head). Fibula of *Placerias* '*gigas*' UCMP 32446 (F) from (Camp and Welles 1956: fig. 37). All in medial (A, B), posterior (C), lateral (D), anterior (E), anteromedial (F), proximal (G), and distal (H) views.

oval (see Fig. 46 with citations). The situation in *Ischigualastia* is visible in the specimen MCZ 3119 where the parietal is almost round in medial section, and the postparietal is very massive. In *Jachaleria* and *Stahleckeria*, the medial section of the parietal is more or less similar, it is always a large area, and it is never a vertically elongated triangle as in *Placerias* and *Lisowicia*.

The situation in *Stahleckeria* is different from that in *Shaanbeikannemeyeria*, *Rabidosaurus*, *Placerias*, and *Lisowicia*. In these genera the ventral part of the parietal is very short. The bone is almost pointed ventrally. This results in the medial section of the bone being elongated vertically (Fig. 49). It seems that the occipital part of the skull elongated vertically in the evolution of this lineage, so the braincase had a very low position in these dicynodonts. Their braincase (it is clearly visible only in *Placerias* '*gigas*') is oblique to the plane of the palate. These dicynodonts have a different skull roof as well.

Shaanbeikannemeyeria, *Rabidosaurus*, *Placerias*, and *Lisowicia* have the parietal foramen very close to the posterior surface of supraoccipital. In *Stahleckeria*, *Ischigualastia*, and *Jachaleria*, the situation is very different. The parietal foramen is distant from the posterior surface of the supraoccipital (e.g. Maisch 2021). Also, the shape of the dorsal side of the frontals strongly differentiates these groups. The frontal is very elongated anteriorly in *Placerias* and *Lisowicia* and it forms a large part of the orbital margin. A large part of the orbit is also visible in dorsal view. The opposite situation is in *Stahleckeria*, *Ischigualastia*, and *Jachaleria*. Their frontals are short and the trend to moving away from the orbit margin might be observed (Fig. 49). The orbit orientation (which might be related somehow with differences in the frontal construction) suggests that the sight of both *Placerias* and *Lisowicia* was directed more dorsally, or that they have their heads oriented strongly ventrally and looked forward with a leaning head. But, *Stahleckeria*, *Ischigualastia*, and *Jachaleria* had the most horizontal position of the head and they looked more laterally. *Kannemeyeria*, *Acratophorus*, and *Dinodontosaurus* have orbits directed partly dorsally. They probably represent a separate lineage with the parietal in cross-section, similar to that in Stahleckerini and the wide anterior part of frontal, which became narrower.

Some evolutionary trends in Triassic dicynodonts were already recognized by Ray (2006) and earlier authors. She stated that 'in Triassic dicynodonts evolutionary changes in the pectoral girdle and forelimb morphology of the included increasing robustness of the deltopectoral crest, a change in humeral orientation from

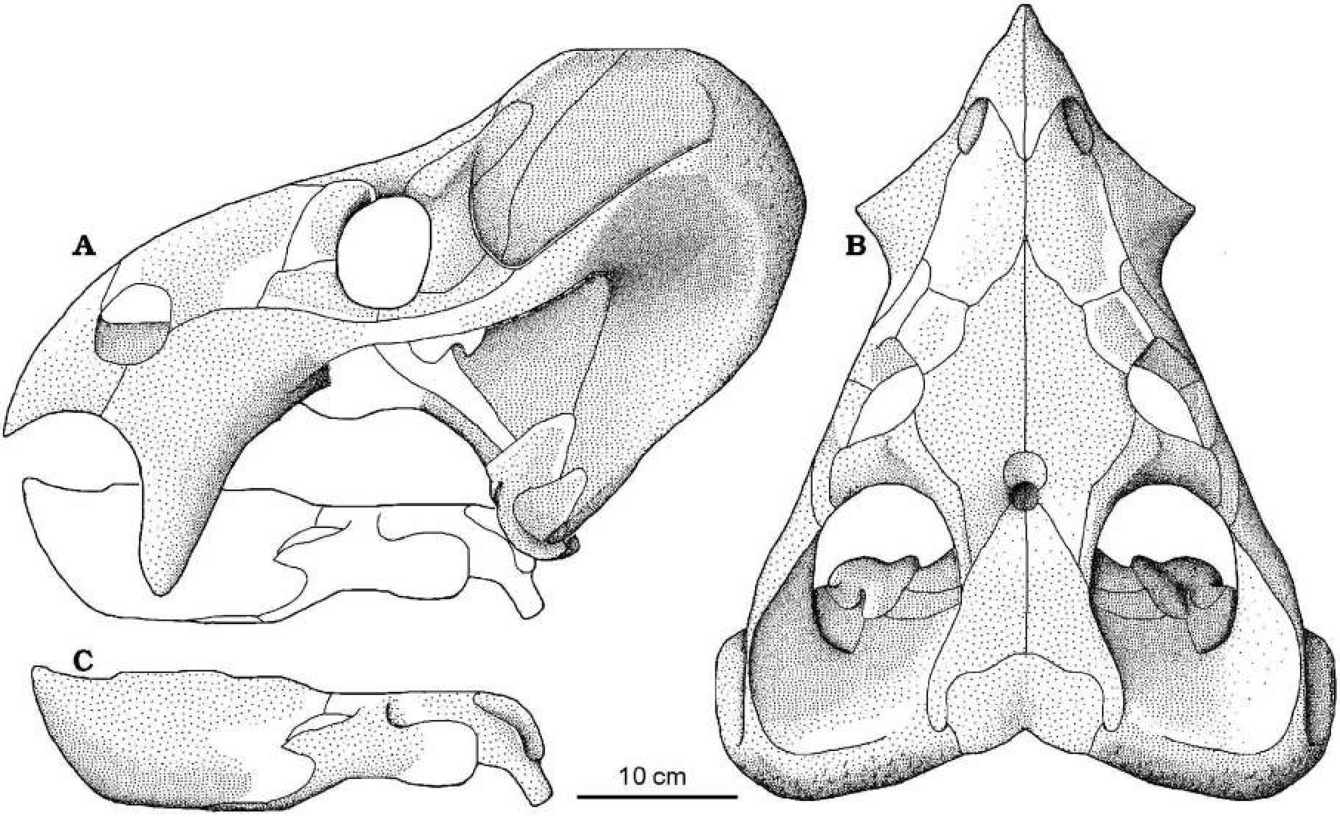

Fig. 46. *Placerias* '*gigas*' Camp and Welles, 1956 from Placerias Quarry, Chinle Formation of Arizona. Reconstruction of skull (A, B) and mandible (C) based on many elements described in text, in lateral (A, C), and dorsal (B) views.

lateral to caudolateral, increasing prominence and asymmetry of the radio-ulnar facet, and increasing robustness of the radius and the ulna. Changes in the pelvic girdle and hindlimb structure included preacetabular iliac expansion resulting in increased cross-sectional area for m. ilio-femoralis and m. ilio-tibialis, a decrease in postacetabular iliac expansion, increased dorsoventral iliac expansion, a change in the shape of the pubis from flat and plate-like to small and rod-like with a cranial process, a change in acetabular orientation from lateral to caudolateral, a shift of the femoral head from cranioproximally positioned to dorsally pronounced and offset from the body, increasing robustness of the trochanter major, and increasing flattening of the femoral midshaft. Changes in the axial skeleton included stiffening of the centrum to reduce lateral undulation, increasing dorsoventral flexion, and increasing sacral vertebral count, which can be correlated with the expansion of the preacetabular iliac process' (Ray 2006: 1281).

These changes in morphology were more or less restricted to particular regions of the Triassic world and have their record in strata of different geological ages. Three such lineages confined to regions have been identified. The Gondwanan lineage *Kannemeyeria simocephalus* → *Dinodontosaurus brevirostris* is characterized by an initially short frontal and two articulation surfaces on the sternum. The Laurasian–Gondwanan *Rhadiodromus klimovi* → *Jachaleria candelariensis* lineage show an initially elongated anterior frontal, large number of sacral ribs, and two articulation surfaces on the sternum. The Laurasian lineage *Shaanbeikannemeyeria xilougouensis* → *Lisowicia bojani* is characterized by a triangular parietal, initially elongated frontal, and fused facet on the sternum.

The Laurasian–Gondwanan *Rhadiodromus klimovi* → *Jachaleria candelariensis* lineage

Middle Triassic European dicynodonts are known from Russia. *Rabidosaurus cristatus* and *Rhadiodromus klimovi* and *Rhadiodromus mariae* (Surkov 2003) are there represented by the most complete materials (Surkov 2003) from the Donguz and Bedyanka localities of the Lower and Upper Donguz formations, respectively, which is dated as Anisian (Tverdokhlebov *et al.* 2003, Ivakhnenko 2008). *Parakannemeyeria youngi* Sun, 1960 and *Shaanbeikannemeyeria xilougouensis* Cheng, 1980 from the Early Anisian Ermaying Formation in China (Sun 1963, Liu *et al.* 2017) may be their relatives. Angielczyk *et al.* (2018) showed that *Sangusaurus parringtonii* from the upper Ntawere Formation in Tanzania and Zambia is a stahleckeriid. *Stahleckeria potens* from the Santa Maria Formation in Brazil is dated as Ladinian (or Carnian? according to: Lucas 1998b, Rayfield *et al.* 2005, Ordoñez *et al.* 2020; see also: Schultz *et al.* 2000). The new *Stahleckeria* sp. indet. material was reported from the Carnian Chañares Formation of the Ischigualasto-Villa Unión Basin by Escobar *et al.* (2021). *Ischigualastia jenseni* is known only from the lower third of the Ischigualasto Formation (Bonaparte 1970, Rogers *et al.* 1993, Zerfass *et al.* 2003, Martinez *et al.* 2011). The latter authors dated the formation as 227.8 ± 0.3 Mya, i.e. Late Carnian. Fröbisch (2009; based on: Lucas 1998b) considered it to represent the upper part of Adamanian, but according to

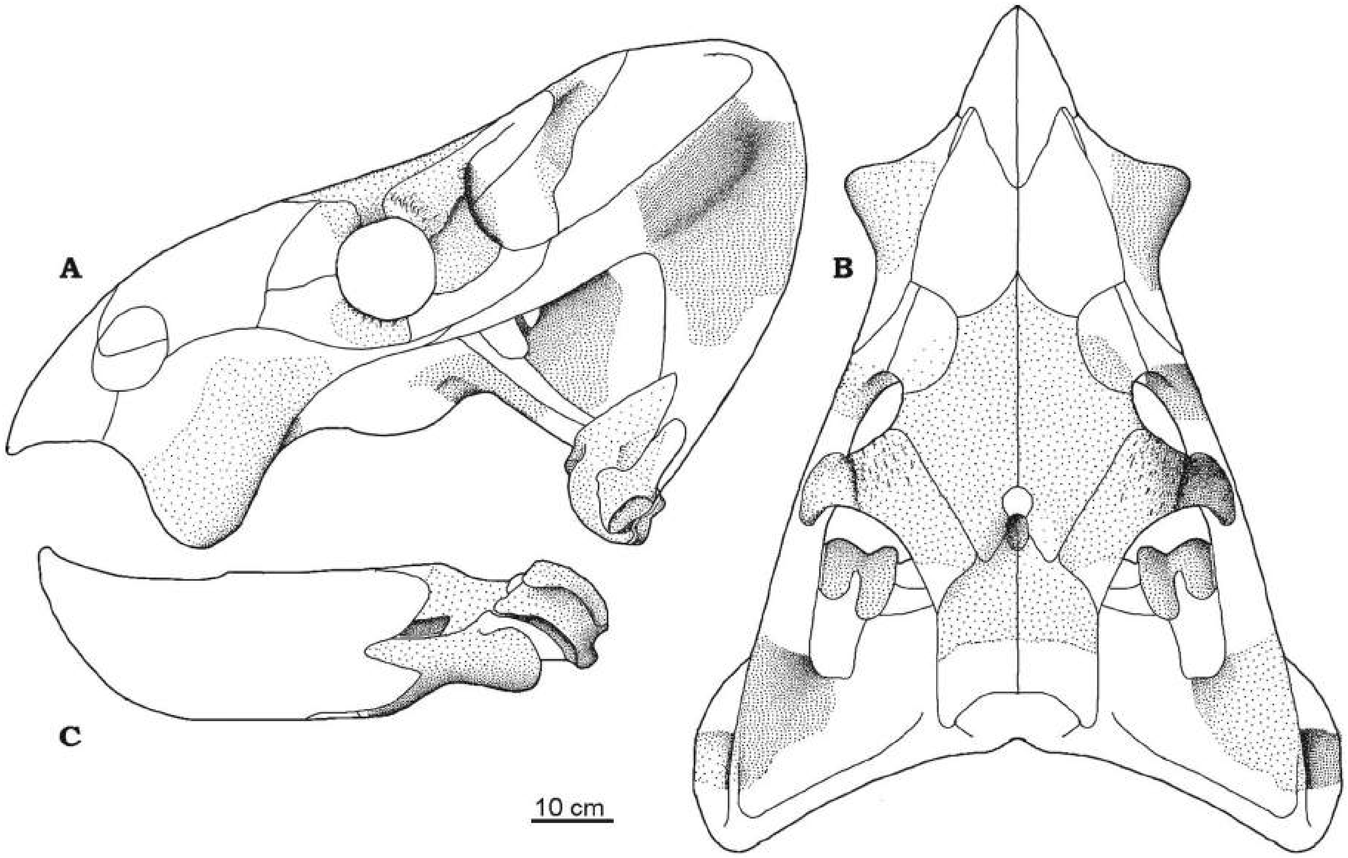

Fig. 47. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. Reconstruction of skull (A, B) and mandible (C) based on many elements described in text, in lateral (A, C), and dorsal (B) views.

Langer (2005b) it is older than Adamanian. He also showed that probably *I. jenseni* is older than *Eubrachiosaurus browni* Williston, 1904 from the Popo Agie Formation [contrary to Lucas and Hunt (1993), the relative ages of these two taxa is highly uncertain in the absence of precise radiometric dates for the Popo Agie Formation].

According to Ramezani *et al.* (2014), the lower third of the Ischigualasto Formation represents the boundary between the Carnian and Norian. The youngest dicynodonts from South America are *Jachaleria colorata* from the Norian Los Colorados Formation of Argentina, which is a fluvial–lacustrine siliciclastic (Bonaparte 1971, 1978, Vega-Dias and Schwanke 2004), and *J. candelariensis* (Vega-Dias and Schultz 2004) that originated from the Norian Caturrita Formation (Araújo and Gonzaga 1980, Langer *et al.* 2018). The close relationship of *Stahleckeria*, *Eubrachiosaurus*, *Jachaleria*, and *Ischigualastia* was supported by the cladistic analysis published by Kammerer *et al.* (2013) and Szczygielski and Sulej (2023).

These dicynodonts experienced a mosaic evolution, with modifications of particular bones not necessarily correlated with each other. This refers especially to the bones of the cranium.

Evolution of the cranium: The position of the dicynodont orbits is correlated with the shape of the postorbital. This bone is perpendicular to the zygomatic arch in *Rhadiodromus klimovi*, the oldest member of the lineage, and in subsequent evolution became more and more oblique anteriorly. The extreme state of this trait is that in *Jachaleria candelariensis*. In *J. candelariensis* and *Ischigualastia jenseni* the orbits are located above the posterior margin of the maxillary horn and the temporal opening is very large.

The route of the evolution of the frontals was different in the lineage represented in South America by *Stahleckeria*, *Ischigualastia*, and *Jachaleria*. The anterior part of the bone became shorter, and the narrow edge of the orbital margin almost disappeared and moved outside. The original shape of the frontal may be shown by *Rhadiodromus mariae* Surkov, 2003. In its very wide anterior part, *R. mariae* is more similar to *Stahleckeria*. Also, the large number of sacral ribs of *Rhadiodromus klimovi* is typical for the Middle Triassic dicynodonts from South America. It seems that *Rabidosaurus* and *Rhadiodromus* are genera that gave the beginning to different lineages.

Probably in the Ladinian, the tusks vanished from the maxillae in the South American members of the lineage, although they were present until the Carnian in *Dinodontasurus brevirostris* in the other Gondwanan lineage and until the Norian in the Laurasian lineage.

Some changes can be also observed in the disposition of the adductor externus lateralis and externus medialis muscles, which are attached to the zygomatic arch (Ordoñez *et al.* 2019). In most Early and Middle Triassic dicynodonts the zygomatic arch in dorsal view is directed anteriorly (Fig. 49). In *Stahleckeria*, the zygomatic arch is directed antero-medially at its base. From *Ischigualastia* to *Jachaleria* it became directed more and more laterally. The changes in the shape of the zygomatic arch are correlated with the shape of the occiput. The lateral edge of the occipital

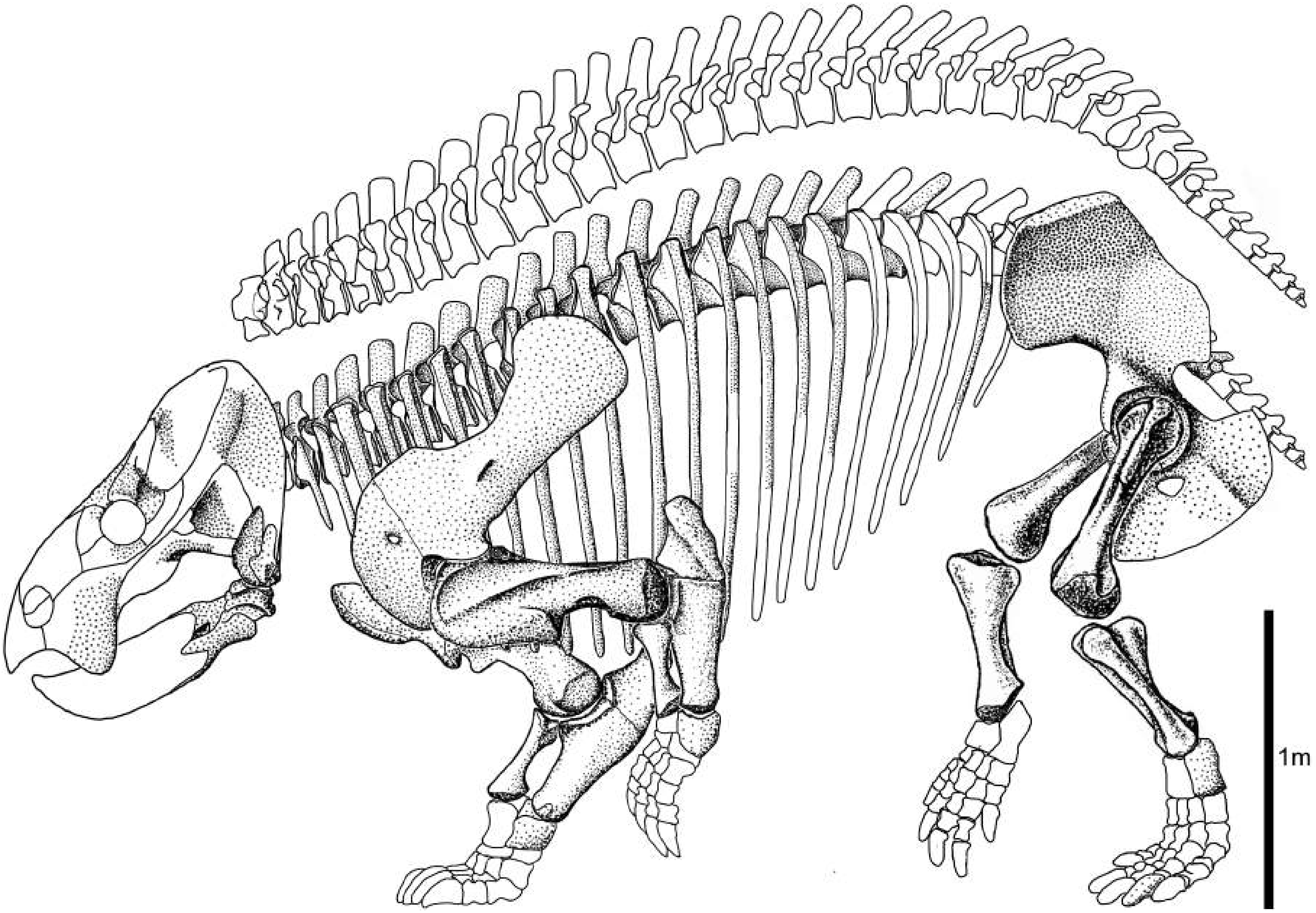

Fig. 48. *Lisowicia bojani* Sulej and Niedźwiedzki, 2019 from Lisowice-Lipie Śląskie. A, reconstruction of skeleton in lateral view. The proportions from *Parakannemeyeria chengi*, and the shape of the manus and foot are based on Camp and Welles (1956). B, reconstruction of vertebral column in lateral view.

plate (posterolateral wing of the squamosal) in most Triassic dicynodonts had an apparent posterior edge (in lateral view) and forms a large attachment area for muscles (Figs 49, 50). This area was small only in *Ischigualastia* and *Jachaleria*, in which the lateral edge of the occipital plate in lateral view is vertical. This characterizes both species of the genus, *J. colorata* (Bonaparte 1978, Vega-Dias and Schwanke 2004) and *J. candelariensis* (Vega-Dias and Schultz 2004). The slope of the lateral edge of the occipital plate resulted in a different orientation of the adductor muscles with respect to the mandible. The external adductor attachment was enlarged due to the horizontal position of the zygomatic arch. It seems that *J. candelariensis* had enormously strong adductors, probably to feed on hard food. The morphology of the occipital is strongly correlated with the slope of the whole skull.

Already Surkov and Benton (2004) and Kalandadze and Kurkin (2000) interpreted proportions of the occipital plate and the whole skull in the context of feeding adaptations. However, their ‘occipital index’ mixes proportions of the occipital plate and the length of the skull. Proportions of the occipital plate in Middle and Late Triassic dicynodonts exhibit two separate types. *Stahleckeria*, *Dinodontosaurus*, and *Rabidosaurus* have very low and wide occipitals, whereas *Ischigualastia*, *Jachaleria*, and *Placerias* have high and relatively narrow occipitals. It seems that increasing skull height and narrowing evolved in parallel in both lineages.

In both species of *Jachaleria* the occipital condyles were directed posteriorly. In the resting position of the skull the orbits were directed frontolaterally.

The shape of the mandible is variable in Triassic dicynodonts, and it is difficult to identify any evolutionary trend in its morphology. Only the shape of the dentary seems to differentiate the lineages. In *Stahleckeria* (Abdala *et al.* 2013), *Dinodontosaurus*, and *Ischigualastia* it is high and short, unlike *Placerias*.

Evolution of postcranial skeleton: Although most aspects of the postcranial skeleton are variable in Triassic dicynodonts, some trends are identifiable. The most important changes concern the pectoral girdle. Regrettably, the scapula of dicynodonts from the Anisian of Russia remains unknown. The increase in size of the acromion process of the scapula characterizes the evolution of the longest lasting lineages. In *Stahleckeria* (Escobar *et al.* 2021), the acromion process was elongated into a ridge (scapular spine) that extended almost to the upper end of the scapula. In *Ischigualastia*, only the base of the ridge was preserved. *Jachaleria* had a very small acromion process and a distinct attachment for the triceps scapularis (Araújo and Gonzaga 1980). According to Surkov *et al.* (2005), the general trend to widening of the scapula blade is observed already in the Permian dicynodonts (Rubidge *et al.* 1994), and the reversal of this trend occurred in Late Triassic species (Fig. 50). The Late Triassic dicynodonts

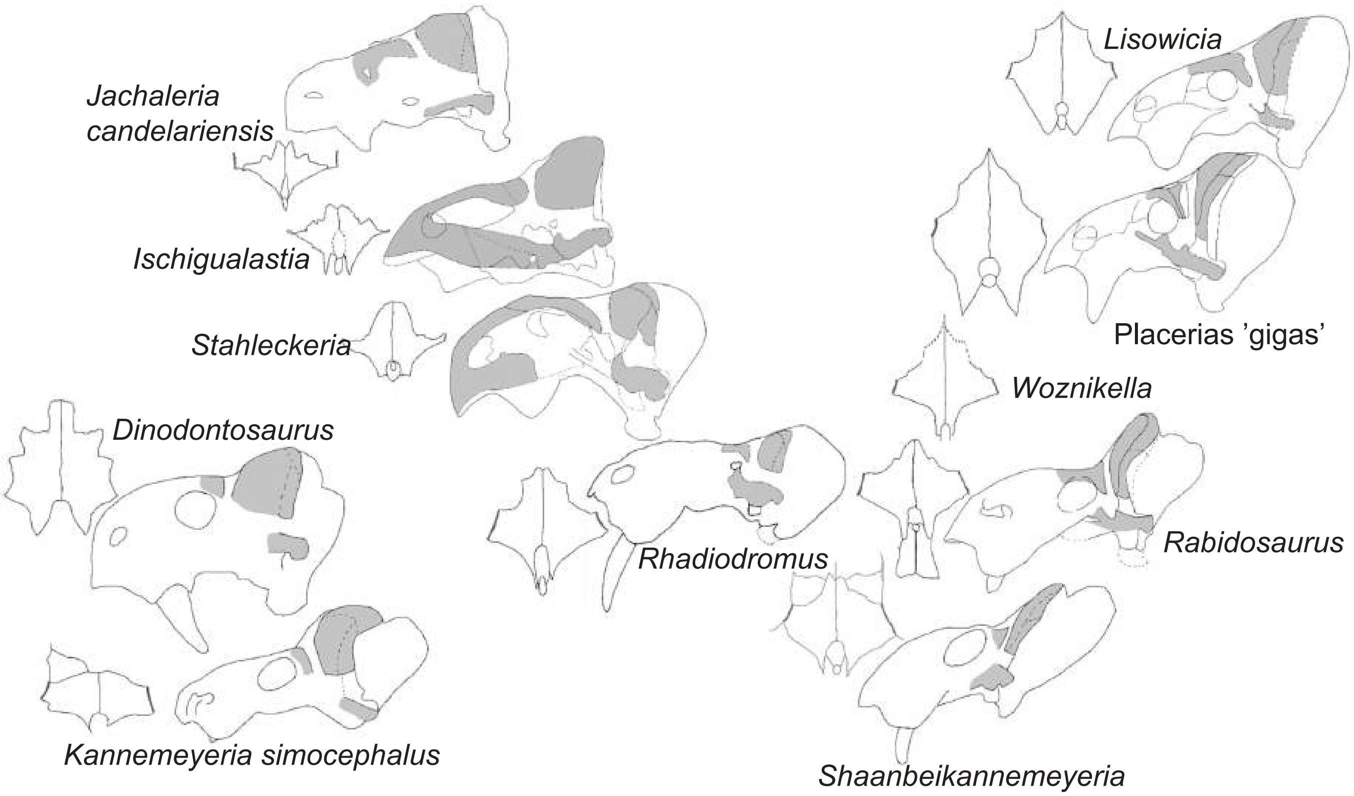

Fig. 49. Phylogeny of Triassic dicynodonts. The crania of the well-known dicynodonts in cross-sections, showing three lineages with much different shape of the parietal and braincase. *Stahleckeria* and *Ischigualastia* are based on Camp (1956).

from South America had a very wide base of the scapular blade (Kammerer *et al.* 2013). This character is conservative.

Stahleckeria and *Ischigualastia* had a small groove on the anterior edge of the scapular blade. This seems important as *Placerias* and *Lisowicia* did not have such a structure. It is interesting that the share of the coracoid in the formation of the glenoid is low in *Stahleckeria*, in contrast to *Ischigualastia*. In both lineages also the direction of the glenoid changed in parallel. At the beginning it is directed laterally, as in all Middle Triassic dicynodonts, but it changed to a more posterior direction. The role of the triceps brachii muscles probably changed in the Late Triassic dicynodonts. In advanced form, like *Jachaleria*, the attachment area for these muscles on the scapula is very large.

It seems that in *Stahleckeria* and *Jachaleria* the sternum had two articulation surfaces on each side. This character is not known in older representatives of the lineage.

The shape of the ilium is variable in dicynodonts, and only the number of sacral ribs and the length of the posterior process may allow identification of evolutionary trends (Fig. 50). The Middle Triassic *Rhadiodromus* had many sacral ribs (seven to eight?). The trend to decrease their number characterizes South America dicynodonts. *Stahleckeria* had seven to eight sacral ribs, *Ischigualastia* six to seven? [uncatalogued specimen in Instituto Miguel Lillo in Tucuman; contrary to Griffin *et al.* (2019)], and *Jachaleria* only five sacral ribs. It seems that small Permian dicynodonts had four sacral vertebrae, but as they grew in size they had to increase the number of sacral vertebrae so that the pelvis could support larger weight (*Rhadiodromus* and *Stahleckeria*), but then when the forelimbs started to be displaced under the shaft, this was no longer necessary and the number of sacral vertebrae decreased. In *Jachaleria* and *Ischigualastia*, two or three sacral ribs are in front of the acetabulum.

The femur from the Los Esteros Member of the Santa Rosa Formation in New Mexico, is more similar to *Stahleckeria* than to *Placerias* (Kammerer *et al.* 2013) and suggests that some representative of the Gondwanan lineages came to live in North America. *Eubrachiosaurus* may be such an immigrant. The distinction between South and North American lineages of dicynodonts is especially well expressed in the morphology of the pubis and ischium, although they are known only in more advanced representatives. The notch in the ventral border of the ischium and pubis is very distinct in *Stahleckeria*. The ischium of *Jachaleria* has the vertical length very short in comparison to very long in *Lisowicia* and *Placerias*. The ischium has a posterior blade slightly curved medially in *Jachaleria*. *Jachaleria* probably represents the crown achievement of dicynodont evolution in South America. It seems that its mode of life was very different from that of *Placerias* and *Lisowicia*. Their skulls are very different. The wide snout with well-developed grooves for tearing plants, together with the very large area for attachment of muscles adducting mandible and the massive zygomatic arch, suggest that *Jachaleria* ate a hard plant food difficult to tear. The position of the quadrate that is directed ventrally (in *Lisowicia* rather anteroventrally) may be related with the mode of tearing but is difficult to explain.

The almost oval and longer than high parietal, the short and only slightly oblique posterior surface of the supraoccipital, and the almost horizontal base of the braincase suggest that *Jachaleria* kept its head horizontal and was a browser. This is consistent with the position of the orbits. They were very large and

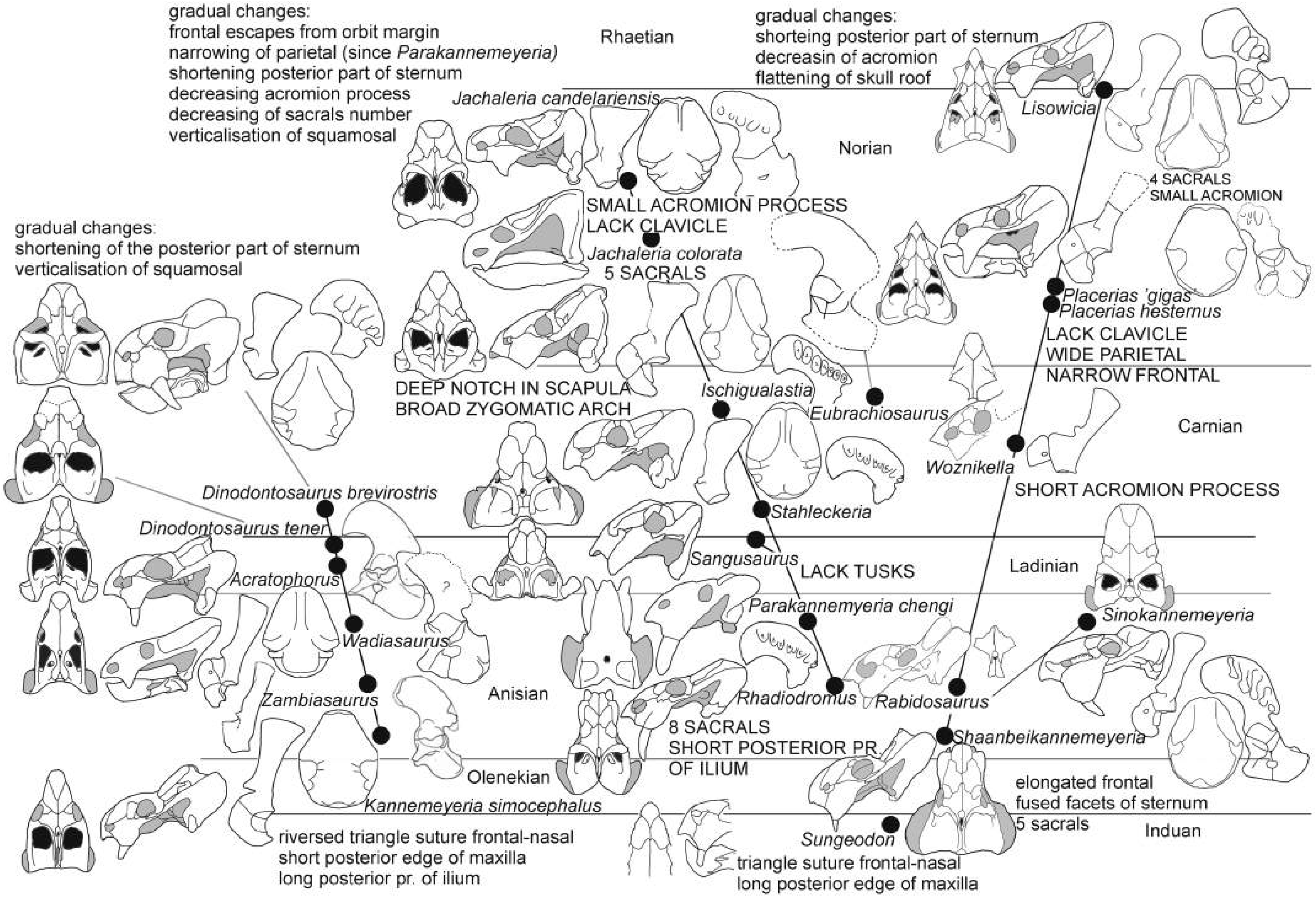

Fig. 50. Phylogeny of the well-known Triassic dicynodonts. The ilium of *Dinodontosaurus brevirostris* is based on the material from MCN [personal studies, and Kammerer and Ordoñez (2021)], ilium of *Stahleckeria potens* and all postcranial elements of *Placerias* '*gigas*' are based on Camp and Welles (1956) and modified. The skulls of *Dinodontosaurus tener* and *D. brevirostris*, their scapula and sternum are based on Kammerer and Ordoñez (2021). The skull of *Stahleckeria potens* is based on Maisch (2001), its scapula is based on personal observation of the GPIT. The sternum of *Stahleckeria* is based on Cox (1965). The scapula of *Ischigualastia jenseni* is based on personal studies of MCZ materials. The rest of the *Ischigualastia jenseni* bones are based on Cox (1965) and modified. The scapula of *Jachaleria candelariensis* is based on Araújo and Gonzaga (1980), skull and other bones are based on Vega-Diaz and Schultz (2004) and modified based on personal studies. *Jachaleria colorata* is based on Bonaparte (1978). *Acratophorus argentinensis* is based on Kammerer and Ordoñez (2021). *Kannemeyeria simocephalus* is based on Cox (1965) and Renaut and Hancox (2001). *Rhadiodromus mariae* is based on Surkov (2003), *Rabidosaurus cristatus* is based on personal observation, *Wadiasaurus indicus* is based on Bandyopadhyay (1988) and modified based on personal observations. *Parakannemeyeria youngi* skull and *Sinokannemeyeria yingchiaoensis* scapula, ilium, and sternum from Sun (1963). *Sangusaurus* is based on Angielczyk *et al.* (2018). *Shaanbeikannemeyeria* is based on Liu *et al.* (2017). *Woznikella* is based on Szczygielski and Sulej (2023). *Zambiasaurus* is based on Cox (1969).

displaced anteriorly to be located above the maxilla. In *Lisowicia* they are much more posterior.

The question about pass of dicynodonts, from Laurasia to South America that *Rhadiodromus* and *Parakannemeyeria* could be ascendants of South American dicynodonts seems problematic, but Haq (2018) showed that in the Anisian, the sea level was very low, and later it rose until the Carnian/Norian boundary. It means that in the Anisian, large lands were accessible for migrating animals and in that time the terrestrial communication between these distant lands was possible also for dicynodonts.

The Laurasian lineage *Shaanbeikannemeyeria xilougouensis* → *Lisowicia bojani*

Until the description of the Polish dicynodonts, *Placerias* '*gigas*'occipitals were the most well-known dicynodont from the Late Triassic of Laurasia. Its diagnostic characters are elongated frontals, parietal triangular in cross-section, and maxillae with long 'tusks'. They were ignored by earlier researchers and the species was grouped together with the Gondwanan dicynodonts. According to Vega-Dias *et al.* (2004) they were closely related and may represent a lineage initiated by *Stahleckeria potens* (Damiani *et al.* 2007). King (1988, 1990) distinguished two separate 'suites': Placerinii for *P.* '*gigas*' and *Ischigualastia jenseni* with a thin, tapering snout, and Stahleckerini for *Stahleckeria potens* and *Zambiasaurus submerses* (probably juvenile). Keyser and Cruickshank (1979) discussed alternative origins for *I. jenseni* from *Dinodontosaurus* or from *Kannemeyeria simocephalus*. The close relationship of *K. simocephalus* with *S. potens* and *I. jenseni* was posited by Damiani *et al.* (2007). In many recent phylogenetic analyses, the South American taxa have been joined together (Griffin and Angielczyk 2019, Sulej and Niedźwiedzki 2019, Kammerer and Ordoñez 2021). *Lisowicia* and *Placerias* are probably not closely related to the Gondwanan ones.

Placerias '*gigas*'comes from the basal Bluewater Creek Formation at the Placerias quarry near St. Johns, Arizona, dated as Adamanian. *Placerias hesternus* is known from the stratigraphically higher Blue Mesa Member of the Petrified Forest Formation from just north-east of Cameron, Arizona (Lucas 1904, 1995, 1998a, Lucas and Hunt 1993, Lucas and Heckert 1996, Heckert and Lucas 2002) of slightly younger age (Heckert 2004). Many new studies have shown that both taxa come from the Blue Mesa Member, which is dated as ~223 to ~218 Mya (Lucas 1993, Martz *et al.* 2017, Gehrels *et al* 2020). The localities are 150 km apart, so the different exact ages are possible. These are separate species (Camp and Welles 1956) that have different humeri (contrary to: Lucas and Hunt 1993, Kammerer *et al.* 2013). The supinator process is more proximal then the entepicondylus in *P.* '*gigas*' (like in *Lisowicia bojani*), than in *P. hesternus* [compare fig. 5D and 6A in Kammerer *et al.* (2013)]. The edge above the entepicondylus is straight in *P. hesternus* and concave in *P.* '*gigas*' (similar to *Lisowicia bojani*, but not so much). The deltopectoral crest is more laterally expanded in *P. hesternus* than in *P.* '*gigas*' (clearly visible in the best preserved specimen of proximal part GPIT-PV-108382).

According to Kammerer (2018), *Pentasaurus goggai* from the lower Elliot Formation (probably Norian age) represents the latest surviving Placerinii, but the material is very poor, and similarities to *Placerias* are very weak. In some aspects it is also similar to Middle Triassic *Zambiasaurus* consistently recovered as Placerinii in recent analyses of dicynodont evolution (Kammerer 2018). In fact the most characteristic element is the distal head of the humerus, which is very different than in *Lisowicia*, and *Placerias* '*gigas*'. Any humerus of *Jachaleria* is unknown. Only the posterior part of the frontal is elongated like in *Lisowicia*, but for the most, part of the bone is lacking. If it is true that *Pentasaurus goggai* represents the latest surviving Placerinii, it will be evidence that this group is not characteristic only for Laurasia, but more specimens are needed to confirm that.

The age of the youngest member of the lineage, *Lisowicia bojani*, is close to the Norian/Rhaetian boundary (Sulej and Niedźwiedzki 2019). Its older relative, *Woznikella triradiata*, originates from the Carnian sediments from Poland and Germany (Schoch 2012, Szczygielski and Sulej 2023).

Evolution of the cranium: Placerias '*gigas*' and *Lisowicia bojani* have exceptionally small areas for muscles responsible for adducting the mandible. Moreover, the zygomatic arch to which some of these muscles are attached is very thin and delicate. The snout is very thin, and the grooves for the dentary are poorly developed, which means that the area for tearing food is rather small. These aspects of the skull anatomy are derived and opposite to those of *Jachaleria candelariensis*. In some Permian dicynodonts there was a large ridge in the anterior part of the surface for articulation with the quadrate, which was a barrier for the quadrate. It is absent in *P.* '*gigas*' and *L. bojani*. This means that the quadrate could drop anteriorly from its normal position when the mandible moved backward. Apparently, the forces acting on the jaw were much smaller than in the case of Permian dicynodonts. It seems that in the evolution of Triassic dicynodonts the shape of the frontal was strictly controlled by selection. Especially the shape of its anterior part and the morphology of the contact with the orbital margin are the most characteristic and useful for understanding the evolution of that group.

In the Laurasian lineage, the anterior part of the skull is elongated. In all species the frontals form a part of the orbital margin. It is most elongated in *Placerias* '*gigas*', similar to *Lisowicia bojani* (Fig. 48). The specimen of the older *Woznikella triradiata* (Sulej *et al.* 2011, Szczygielski and Sulej 2023) has the frontal partly preserved, but it shows a long edge forming the orbital margin and an elongation of the anterior part of the frontal is suggested by well-preserved nasals. Even older dicynodonts with a similar frontal are those from the Anisian of Russia: *Rhadiodromus klimovi* and the smaller *Rabidosaurus cristatus* (Ochev and Shishkin 1989). *Rhadiodromus mariae* is known after a complete skull but from a different locality of the same formation. They all have a very long anterior part of the frontal and a very long edge of the frontal forming the orbital margin (which is characteristic for almost all Anisian dicynodonts). Both species of *R. mariae* have orbits directed strongly dorsally and the frontal elongated anteriorly. *Rabidosaurus cristatus* has the frontals with a distinct high posterior process, and its parietals are similar to those of *P.* '*gigas*'. The slightly older *Shaanbeikannemeyeria xilougouensis* has frontals elongated anteriorly. The same type of suture between frontals and nasals is present in both species of *Rhadiodromus*.

The position of the orbits is correlated with the shape of the postorbital. This bone is oblique posteriorly in *Placerias* '*gigas*' and *Lisowicia bojani*. In these species the orbits are located more posteriorly, and the temporal opening is smaller; it was related with the size of the external adductor muscles. The zygomatic arch morphology is not known in *P.* '*gigas*' and *L. bojani*, but preserved fragments of the squamosal suggest that it was directed slightly antero-medially. In *P.* '*gigas*' the lateral edge of the occipital plate in lateral view is strongly oblique posteriorly (to the horizontal position of the frontal). The adductor muscles were attached to the mandible more posteriorly.

In *Placerias* '*gigas*' the occipital condyles are directed ventrally, which means that in the resting position the skull was strongly oblique ventrally (Fig. 50). It is consistent with the shape of the orbits, which are opened antero-dorsally and frontally in an oblique position of the skull.

There is no evidence in the fossil material for the reconstruction of *Placerias* '*gigas*' by Camp and Welles (1956: fig. 24), with the dentary much higher than the posterior part of the mandible. Also, in *Woznikella triradiata* the dentary is relatively long and low. It is more similar to the elongated one of *P.* '*gigas*', than to any other dicynodont from South America. In *Lisowicia* the dentary is unknown but the articulation for the dentary on the angular suggests that it was high and with a concave middle edge of the mandible, almost like in *Ischigualastia jenseni*.

Evolution of postcranial skeleton: The acromion process trend to decrease is apparent in the Laurasian lineage. *Woznikella triradiata* has a scapula with the acromion process high but short. *Placerias* '*gigas*' has an elongated ridge (Camp and Welles 1956: fig. 29) and *Lisowicia bojani* has the process very small. In both species the base of the scapular blade is relatively narrow. It has a similar shape in *L. bojani*, but in this species the end of the scapular blade is very wide, probably as a result of the large size of the animal. Probably a decrease in size of the acromion process was convergent in both these long-lasting lineages.

The triceps brachii muscles probably changed their role in the Late Triassic dicynodonts. In the advanced forms like *Placerias* '*gigas*', the attachment for these muscles on the scapula is relatively small, and in *Lisowicia* it is diminutive.

Sinokannemeyeria yingchiaoensis is the oldest Laurasian form with a single articulation surface on the sternum. This continued to occur in *Placerias* '*gigas*' and *Lisowicia bojani*. The Late Triassic increase in dicynodonts general size was related to a gradual change of the position of the humerus and decrease in size of the acromion process on the scapula (Sulej and Niedźwiedzki 2019). The change in movement of the humerus affected the position of the articulation surface for the coracoid and ribs on the sternum. In both lineages this surface moved posteriorly. In the Laurasian lineage, the sternum of *Lisowicia* with extremely posteriorly set the articulation and very high ridges represents probably the last stage of evolution.

The underived humerus of *Sinokannemeyeria yingchiaoensis* and *Kannemeyeria simocephalus* have rotated distal and proximal heads, whereas in *Lisowicia* they are almost in the same plane; only the deltoid crest is curved ventrally. This decreasing of the rotation was related to changes in the orientation of the humerus relative to the scapulocoracoid. Ray (2006) stated that the humerus changed its position, and it was related to the change from the lateral orientation of the glenoid to a posterior orientation.

The size of the supinator process seems to have become gradually larger in the sequence: *Woznikella triradiata* (Szczygielski and Sulej 2023), *Placerias* '*gigas*', and *Lisowicia bojani*. Surprisingly, the humerus of *Zambiasaurus* from the Anisian already had a large supinator process similar to that in *P.* '*gigas*' (Kammerer *et al.* 2013). In the Gondwanan lineage, dicynodonts and the Chinese *Sinokannemeyeria yingchiaoensis* the entepicondyle is large, whereas it is small in *P.* '*gigas*' and even smaller in *L. bojani*. Probably also the medial epicondyle became narrower during evolution of the Laurasian lineage. Other postcranial skeletal characters seem to be more variable in the Laurasian dicynodonts. The articulation surface for the ulna on the dorsal side of the humerus is very large in *S. yingchiaoensis* and *P.* '*gigas*' but very small in *L. bojani*.

In the Laurasian lineage, the number of sacral ribs was probably small from the beginning. In *Sinokannemeyeria yingchiaoensis* there were only five, but in most genera it remains unknown. *Placerias* '*gigas*' has a rather underived ilium with five sacral ribs (Camp and Welles 1956), although only three areas for articulation are visible. *Lisowicia bojani* has only four sacral ribs, and the first sacral rib is above the acetabulum.

The North American *Eubrachiosaurus browni* probably represents a South American immigrant lineage (Kammerer *et al.* 2013). Its well-preserved pelvis shows a frontally elongated ilium with a curved lower end, with a ridge on the blade, and its pubis is very small in relation to the ischium. It is also older (Camp and Welles 1956) than *Placerias* '*gigas*' but differences in the morphology make an ancestor–descendant relationship unlikely.

The ischium of *Lisowicia bojani* and *Placerias* '*gigas*' are vertically elongated. *Placerias* '*gigas*' and *L. bojani* have their posterior blade a little curved medially. The vertically short ischium of *Parakannemeyeria chengi* probably represents an underived stage for all three lineages. In *Placerias* '*gigas*' specimens, this part of the ischium is broken but in *L. bojani* its shape suggests such a morphology.

The position of the proximal head of the femur changed during evolution to large in *Placerias* '*gigas*' and *Lisowicia bojani*, which have the proximal head directed dorsally in lateral view, thus the femur had a vertical position while resting.

Evolution of the mode of life: It is a matter of controversy whether dicynodonts were 'grazers' or browsers (Cox 1959, Kalandadze and Kurkin 2000, Surkov and Benton 2008, Ordoñez *et al.* 2019). It seems that the shape of the parietal (especially its medial section), and position of the occipital condyle and the orbits are strongly connected with the disposition of the head and the way of seeing the food. In *Placerias* '*gigas*' and *Lisowicia bojani* the angulation of the base of the braincase suggests that the skull had an oblique orientation with the snout very low above the ground. Also, the occipital condyle is low under the jaw articulation and far from the top of the skull, which is situated more posteriorly than in such dicynodonts as *Jachaleria candelariensis* or *Stahleckeria potens*.

To keep the head oblique demanded a special position of the orbits, because 'grazing' animals need to be aware of predators. This was probably the selection pressure to makes the orbits displaced to the top of the skull in *Placerias* '*gigas*' and *Lisowicia bojani*. While lowering the head the animal saw the surroundings in the horizontal plane. Present-day large herbivorous animals with orbits similarly directed or situated more dorsally are the hippopotamuses, connected with aquatic environments.

However, animals spending much of their life in water often have lighter limb skeletons, which is not the case of *Lisowicia*.

The Gondwanan lineage *Kannemeyeria simocephalus* ⟶ *Dinodontosaurus brevirostris*

In the Induan, the Gondwanan dicynodonts are represented by the single genus *Lystrosaurus* known from Antarctica, Russia, China, India, and South Africa, but it has not been reported from the Olenekian (Fröbisch 2013). *Kannemeyeria simocephalus* and *Dolichuranus primaevus* are the best known kannemeyerids from Africa. *Kannemeyeria simocephalus* is a medium to large dicynodont (Govender *et al.* 2008) from the Cynognathus Assemblage Zone of the South Africa dated as Early Anisian (Catuneanu *et al.* 2005, Hancox *et al.* 2020); however, some zircon studies of the Puesto Viejo Group (San Rafael depocenter, Argentina) suggest a Carnian age for this assemblage (Ottone *et al.* 2014). *Dolichuranus primaevus* Keyser, 1973 was described from the Omingonde Formation, Karoo Supergroup, Waterberg Basin; Middle Triassic, probably Anisian–Ladinian (Damiani *et al.* 2007, Wynd *et al.* 2018, Zieger *et al.* 2020).

The Middle Triassic kannemeyerids are represented by *Wadiasaurus indicus* and *Rechnisaurus cristarhynchus* Roy-Chowdhury, 1970 from the Anisian Yerrapalli Formation of India (Chowdhury 1970, Keyser and Cruickshank 1979, Bandyopadhyay 1988, *Bandyopadhyay* and Sengupta 2006, Ottone *et al.* 2014), which was related with South Africa at that time.

The South American Ladinian kannemeyerids dicynodonts are *Acratophorus argentinensis* Kammerer and Ordoñez, 2021 from the Rio Seco de la Quebrada Formation of Argentina (Bonaparte 1967, Lucas and Harris 1996, *Renaut* and *Hancox* 2001, Arcucci *et al.* 2004, Zavattieri and Arcucci 2007, Kammerer and Ordoñez 2021) and *Kannemeyeria aganosteus* Kammerer and Ordoñez, 2021. Based on the similarity of faunas it was correlated with the Cynognathus zone. *Dinodontosaurus brevirostris* was the most common in the Late Triassic of South America. Kammerer and Ordoñez (2021) recognized *D. tener* and *D. brevirostris* as the only valid species of the genus. *Jachaleria platygnathus* is a nomen dubium (Morato *et al.* 2006).

Evolution of the cranium: The significance of proportions of the skull was studied by Cox and Li (1983). The morphology of the cranium of dicynodonts from the Permian of South America and South Africa is well known (Ordoñez *et al.* 2020, de Simão-Oliveira *et al.* 2020). The Triassic lineage probably started from *Kannemeyeria simocephalus* (Govender *et al.* 2008). It had the orbits directed dorsally and elongated, and a narrow snout. *Acratophorus argentinensis* has a short frontal without any middle anterior process (Renaut and Hancox 2001, Domnanovich and Marsicano 2012, Kammerer and Ordoñez 2021), similar to that of *K. simocephalus*. But, in younger Ladinian and Carnian? (Kammerer and Ordoñez 2021) species of *Dinodontosaurus*, the anterior process became longer (Kammerer and Ordoñez 2021) and the whole frontal narrower. It differs from *Sungeodon kimkraemerae* in the shape of the frontal–nasal suture. In *K. simocephalus*, the nasals form the posterior process running between the frontals, but in *S. kimkraemerae* the situation is the opposite, the frontals form an anterior process running between the nasals. This shape is very similar to that of *Rhadiodromus mariae.*

Evolution of the postcranial skeleton: The sternum probably had a function related mainly to the movement of the forelimb and, unlike the skull, it was not related to diet. The oldest known Triassic sternum of kannemeyerids is that of *Kannemeyeria simocephalus* from the Karoo in which there are two surfaces for the coracoid and first dorsal rib, and it is probably the starting point of the evolution. The sternum of the Gondwanan *Wadiasaurus indicus* has two distinct surfaces, unlike the Laurasian dicynodonts having one large surface [contrary to Bandyopadhyay (1988)].

Dinodontosaurus tener has five to six sacral ribs (but juvenile ilium had six sacral ribs). In all these species (except specimen MCN-PV-1489 of *Dinodontosaurus*) the first sacral rib is sutured very far frontally on the iliac blade. According to Govender *et al.* (2008) *Kannemeyeria simocephalus* had five sacral ribs. In *Acratophorus argentinensis* the ilium is known but the number of sacral ribs was not determined. The posterior process of the ilium is very short in most Triassic dicynodonts. Only representatives of the lineage of *A. argentinensis* and *D. brevirostris* had this process elongated.

The distinction between South and North American lineages of dicynodonts is also expressed in the morphology of the pubis and ischium. The ischium of *Dinodontosaurus brevirostris* has the vertical length very short in comparison to very long in *Lisowicia bojani* and *Placerias* '*gigas*'. The ischium has the posterior blade strongly curved medially in *Dinodontosaurus*. In the Gondwanan lineages, the notch in the ventral border of the ischium and pubis is distinct (in *Kannemeyeria simocephalus* and *D. brevirostris*) but in *Wadiasaurus indicus* this notch is shallow.

In the underived *Kannemeyeria simocephalus* the proximal head of the femur is directed antero-medially in lateral view, which results in being set obliquely anteriorly. In maximum posterior position, it was set vertically.

The Chinese lineage

Only the snout is preserved in *Sungeodon kimkraemerae* from the Induan of Jiucaiyuan, China (Maisch and Matzke 2014, Tong *et al.* 2018). This species is the oldest non-lystrosaurid Triassic dicynodont and perhaps it initiated the Chinese lineage. Its diagnostic character is a short and high skull. *Shaanbeikannemeyeria xilougouensis* Cheng, 1980 from the early Anisian Lower Ermaying Formation (Cheng 1980, Liu *et al.* 2017) continued the evolution, but it is rather a representative of the lineage leading to *Rabidosaurus cristatus* and later to *Woznikella triradiata*. It may be intermediate to *Sinokannemeyeria yingchiaoensis* from the Anisian Ermaying Formation in China (Sun 1963) but a close relationship to the Laurasian *Rhadiodromus mariae* was suggested by Szczygielski and Sulej (2023) because it has the sternum with single large surface for coracoid and first dorsal rib.

CONCLUSION

Three evolutionary lineages of the Late Triassic dicynodonts are identified:

The African and South American lineage characterized by an initially short frontal and two articulation surfaces on the sternum, represented by *Kannemeyeria simocephalus*, *Wadiasaurus indicus*, *Acratophorus argentinensis*, *Dinodontosaurus tener*, and *D. brevirostris*.

The Laurasian–Gondwanan *Rhadiodromus mariae* → *Jachaleria candelariensis* lineage with initially elongated anteriorly frontal and two articulation surfaces on the sternum includes *Rhadiodromus mariae*, *Parakannemeyeria youngi*, *Stahleckeria potens*, *Ischigualastia jenseni*, and *Jachaleria candelariensis*. The characteristic aspects of the skull are an oval parietal in cross-section, a short frontal bone covering the eye socket, participating less and less in its formation (in *J. candelariensis*, it does not form the edge of the eye socket at all), the acromion decreasing in size, double attachments on the sternum, short, wide and high snout. The large number of sacral vertebrae (seven to eight) at the beginning changes into five at the end. The posterior part of the sternum becomes shorter.

The Laurasian lineage *Shaanbeikannemeyeria xilougouensis* → *Lisowicia bojani* with a single articulation on the sternum. They have a long frontal bone, decreasing acromion with a straight crest, long and low snout. They are known from China, Russia, North America, and Poland where they are represented by *S. xilougouensis*, *Rabidosaurus cristatus*, *Woznikella triradiata*, *Placerias* '*gigas*', and *Lisowicia bojani*. Trends in their evolution concern the development of a very narrow cross-section of the parietal. These aspects are mostly not related to size of the animal.

Both lineages, Laurasian and Laurasian–Gondwanan (that to *Jachaleria candelariensis*), in the Middle and Late Triassic shared the same evolutionary trends in modification of the postcranial anatomy. They probably represented a case of convergence connected with increasing body size, in response to the appearance of dinosaurs (Niedźwiedzki *et al.* 2011, Sulej and Niedźwiedzki 2019; contrary to: Sookias *et al.* 2012). The configuration of the skull roof differentiates Laurasian and Gondwanan lineages in the Middle and Late Triassic. It seems that on Gondwana there were two separate lineages, the longer existing lineage that originated in Laurasia, ranging from *Rhadiodromus mariae* through *Stahleckeria* to *Jachaleria candelariensis*, and the short ranging lineage from *Kannemeyeria simocephalus* to *Dinodontosaurus brevirostris*.

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CONFLICT OF INTEREST

None declared.

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