

BIOCHRONOLOGICAL SIGNIFICANCE OF LATE TRIASSIC TETRAPODS FROM KRASIEJÓW, POLAND

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Abstract—The Krasiejów locality in the Upper Triassic of southern Poland yields the tetrapod taxa *Cyclotosaurus robustus* (= *C. intermedius*), *Metoposaurus diagnosticus* (we reject proposed subspecies of this species), *Stagonolepis robertsoni*, *Teratosaurus suevicus* (= *T. silesiacus*), *Parasuchus bransoni* and *Silesaurus opolensis*. The occurrences of *Parasuchus* and *Metoposaurus* indicate the Krasiejów assemblage is of Otischalkian age, and the presence of *Stagonolepis* at Krasiejów expands its temporal range to Otischalkian-Adamanian. Previous non-vertebrate biostratigraphic correlation of the Krasiejów locality to the German Lehrberg Schichten is confirmed by vertebrate biostratigraphy and provides a good example of how a newly discovered tetrapod assemblage (at Krasiejów) demonstrates the utility of the global Triassic tetrapod biochronology.

INTRODUCTION

One test of a biostratigraphic (biochronologic) framework is how well it accounts for new discoveries. The discovery of an Upper Triassic tetrapod locality at Krasiejów in southern Poland (Fig. 1) provides just such a test of the Late Triassic tetrapod biochronology proposed by Lucas and collaborators (Lucas and Hunt, 1993; Lucas et al., 1997; Lucas, 1998, 1999). The Polish Triassic tetrapod assemblage contains Otischalkian index taxa and comes from a part of the Keuper section that is this age based on other data. Here, we review the Krasiejów tetrapod assemblage and its biochronological significance. In this paper, PAN refers to specimens in the collection of the Paleontological Institute, Polish Academy of Sciences, Warsaw.

PREVIOUS STUDIES

Dzik et al. (2000) provided initial information on what they referred to as “a new *Paleorhinus* fauna” from Krasiejów. They listed the tetrapod assemblage as consisting of a capitosaur, *Metoposaurus diagnosticus*, *Paleorhinus* sp., an aetosaur and a dinosaur. Subsequently, the capitosaur (Sulej and Majer, 2005), metoposaur (Sulej, 2002) and phytosaur (Dzik, 2001) were documented, as was a raiusuchian (Sulej, 2005) and a dinosauromorph (= the “dinosaur” of Dzik et al., 2000; Dzik, 2003). Dzik (2001) illustrated a jaw fragment and tooth of an aetosaur, stating that it is very similar to *Stagonolepis*. Zaton et al. (2005) documented charophytes from the Krasiejów locality, and provided a description of the geological context of the site.

GEOLOGICAL CONTEXT

At Krasiejów (Fig. 1), Triassic tetrapod bones are present in a mudstone-dominated section in a cement plant clay pit. Two beds produce bone, but their close stratigraphic proximity (~7 m) and shared taxa indicate they represent a single biostratigraphic assemblage. The bone-bearing strata have been correlated to the subsurface Drawno Beds, and are estimated to be ~80 m above the top of the Reed Sandstone, the local equivalent of the German Schilfsandstein (Dzik, 2001, 2003; Sulej, 2002; Zaton et al., 2005). The Polish workers thus consider the Drawno Beds correlative to the German Lehrberg Schichten, and conchostracan-based correlations support this conclusion (H. Kozur, written commun., 2007).

TETRAPOD ASSEMBLAGE

Amphibians

Cyclotosaurus

Sulej and Majer (2005) named a new species, *Cyclotosaurus intermedius*, for cranial and postcranial material from both bonebeds at



FIGURE 1. Location map of the Krasiejów tetrapod locality in southern Poland (after Sulej, 2002).

Krasiejów. This material includes a complete skull with associated mandible (the holotype), two incomplete mandibular rami, various disarticulated skull bones, a humerus, a scapulocoracoid, a nearly complete clavicle, a cleithrum and two interclavicles.

C. intermedius is remarkably similar to *C. robustus* from the German Schilfsandstein (Fraas, 1889, 1913; Schoch and Milner, 2000), so we consider *C. intermedius* synonymous with *C. robustus*. Sulej and Majer (2005) listed the following putative differences between the two species: (1) orbits more laterally positioned in *C. intermedius*; (2) interchoanal tooth row gently curved posteriorly (not straight) in *C. intermedius*; (3) para- and interchoanal teeth broadly separated (not a single arcade) in *C. intermedius*; (4) shagreen of denticles on palate in *C. intermedius*; (5) quadrate projects behind margin of skull roof in *C. intermedius*; and (6) *C. robustus* has a wider skull with a more concave

posterior border. However, differences (1) and (6) are not metrically significant (see Sulej and Majer, 2005, table 1), and difference (5) is arguably the result of diagenetic distortion (a feature present in some material from the quarry, such as an aetosaur sacral vertebra; see below). Difference (2) can be rejected because Fraas (1889, pl. 10) illustrates a skull of *C. robustus* in which the interchoanal tooth row is curved posteriorly, as in *C. intermedius*. Differences (3) and (4) are apparently real, but we hesitate to make them a basis for species-level distinction because variation in the interchoanal and palatal teeth is common among stereospondyl taxa (e.g., Hunt, 1993).

Metoposaurus

Metoposaurid skulls (Fig. 2) and postcrania are common at the Krasiejów locality, and Sulej (2002) listed the following metoposaurid material: eight complete skulls, four nearly complete skulls, one skull preserving the postorbital region, two skulls preserving portions of the preorbital region, one complete and five incomplete interclavicles and three incomplete and two nearly complete clavicles. Sulej (2002) described the specimens and used them to subdivide *Metoposaurus diagnosticus* into two subspecies – *M. d. diagnosticus* and *M. d. krasiejowensis* – based on a supposed shorter prepineal portion of the parietal in the latter and putative differences in parietal shape between the two nominal subspecies.

However, we find subspecies attributions particularly inappropriate for the *Metoposaurus* sample analyzed by Sulej (2002) because it is a small sample of fewer than 20 individuals, not large enough to gauge variation within one or between multiple populations, let alone within a species. Furthermore, it is clear that Sulej's subspecies are actually "little species," an inappropriate use of subspecies (e.g., Simpson, 1961). Instead, subspecies should be used to subdivide a range of variation within

a species (cline) so that "at least a minimum proportion, now usually set at 75 per cent, of individuals of adjacent subspecies will be unequivocally determinable" (Simpson, 1961, p. 173, 175; also see Amadon, 1949).

The differences in the length of the parietal anterior to the pineal foramen used by Sulej (2002) to distinguish the "subspecies" of *M. diagnosticus* are clearly size related: there is a strong correlation between skull size and the length of the parietal anterior to the pineal foramen evident in Sulej's (2002, fig. 10B) data. The differences in the parietal angle used by Sulej to distinguish the subspecies of *M. diagnosticus* are also size related and do not convincingly separate the sample into two discrete morphotypes (Sulej, 2002, fig. 10A). Therefore, we do not recognize the subspecies of *M. diagnosticus* proposed by Sulej (2002) and simply refer the Krasiejów metoposaurs to *Metoposaurus diagnosticus*.

Another important point to address is Sulej's (2002) claim that the lacrimal enters the orbit in the Krasiejów metoposaur skulls (contrary to the normal condition in *Metoposaurus*: Hunt, 1993). Indeed, he illustrates the holotype of *Metoposaurus diagnosticus krasiejowensis* (PAN ZPAL AbIII 358) with the lacrimal entering the orbit (Sulej, 2002, fig. 4). However, our close examination of this skull (Fig. 2A) and other metoposaur skulls from Krasiejów does not confirm his claim. Either preservation is too poor to discern the lacrimal in its entirety or it is clear (as is the case in PAN ZPAL AbIII 11) that the lacrimal does not enter the orbit (Fig. 2B-C).

Reptiles

Stagonolepis

The aetosaur *Stagonolepis* is a common constituent of the Krasiejów bonebeds, and previous publications have stated that the

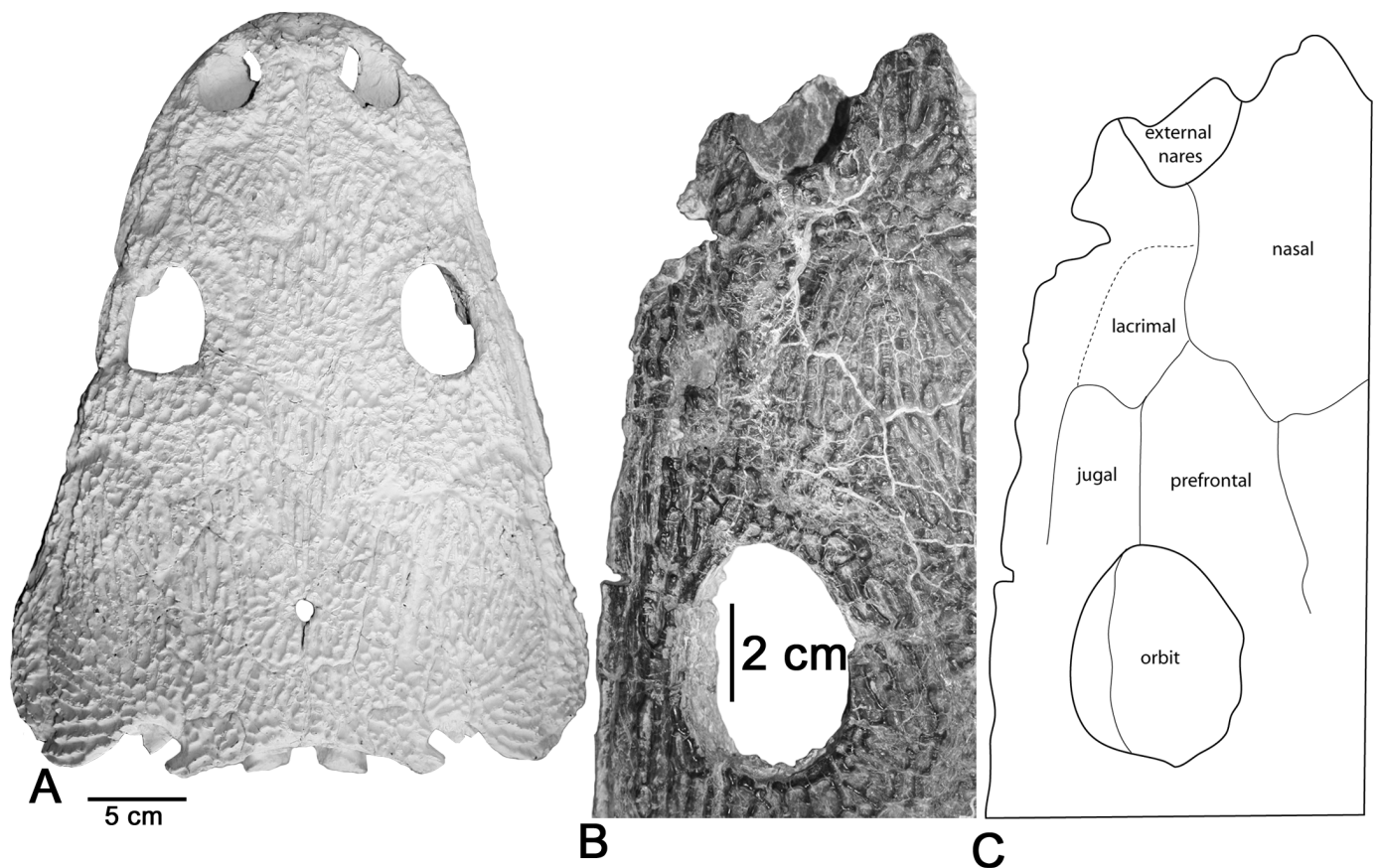


FIGURE 2. A, *Metoposaurus diagnosticus*, PAN ZPAL AbIII 358, complete skull in A, dorsal view (holotype of *M. diagnosticus krasiejowensis*). B-C, PAN ZPAL Ab III 11, dorsal view close-up of the preorbital region of an incomplete skull showing exclusion of the lacrimal from the orbit margin.

Polish specimens represent a new species. However, material of *Stagonolepis* we were able to examine in the Warsaw collection cannot be distinguished from *S. robertsoni* (sensu Heckert and Lucas, 2000). The aetosaur material from the Krasiejów bonebeds we examined consists of an isolated dorsal vertebra (Fig. 3A-B), a sacral vertebra (Fig. 3E-H), a rib (Fig. 3C-D), a cervical or caudal paramedian osteoderm (Fig. 4D-F), a dorsal paramedian osteoderm (Fig. 4A-C), an incomplete left scapulocoracoid (Fig. 5A-D), a left humerus (Fig. 5E-J), a left ulna (Fig. 6A-D), a metapodial (Fig. 6E-H), an incomplete left femur (Fig. 7A-D) and a left tibia (Fig. 7E-J).

The single dorsal vertebra (PAN AbIII 502/67) is complete (Fig. 3A-B). The centrum has nearly circular anterior and posterior articular surfaces. The neural canal is elliptical, with the long axis oriented dors-oventrally. The transverse processes are bifurcate with the rectangular dorsal bifurcation projecting farther laterally than the columnar ventral half. The width of each transverse process is approximately two and one half times the length of the centrum. Heckert and Lucas (2000, 2002) diagnosed *Stagonolepis robertsoni* as having transverse processes that exceed twice the centrum length; thus, the ratio of transverse process width to centrum length supports assignment of the Krasiejów material to *S. robertsoni*. The neural spine is mediolaterally compressed, triangular in cross section and terminates dorsally with a triangular expansion of bone, a typical feature of aetosaur dorsal vertebrae. The tall height of the neural spine compares closely with *S. robertsoni*.

The sacral vertebra is complete, with some slight distortion of the anterior articular surface of the centrum (Fig. 3E-H). The ventral margin of the anterior articular surface appears compressed dorsally, resulting in a kidney-shape in anterior view; this contrasts with the undistorted posterior articular surface, which is elliptical. The neural canal is elliptical and proportionally quite small when compared to that of the dorsal vertebra. The prezygapophyses are triangular in lateral view, project anterodorsally and extend beyond the anterior margin of the centrum. The transverse processes are extensive; the width of each equals the width of the centrum. The processes are triangular in anteroposterior view and angle posteriorly ~45°. The posterior margins of the transverse processes extend beyond the posterior margin of the centrum. The postzygapophyses are triangular, project posteriorly and are approximately half the size of the prezygapophyses. The neural spine is proportionately shorter than in the dorsal vertebrae, considerably thicker, and terminates in a large, circular knob of bone.

The single rib is complete (Fig. 3C-D) and has extensive buttressing, both anteriorly and posteriorly, near its proximal end. The anterior buttress is confluent with the capitulum. The capitulum is displaced laterally from the tuberculum.

Both the left dorsal paramedian osteoderm (Fig. 4A-C) and the left cervical or caudal paramedian osteoderm (Fig. 4D-F) are complete. The dorsal paramedian osteoderm is rectangular, whereas the cervical or caudal paramedian osteoderm is nearly square. Both possess prominent anterior bars, anteroposteriorly-directed keels on the dorsal surfaces of the osteoderm that contact their respective posterior margins, and a radiating pattern of pits and grooves that extend from the dorsal keels. These features readily identify this material as *Stagonolepis robertsoni* (Heckert and Lucas, 2000, 2002).

The scapulocoracoid is nearly complete, missing the ventral margin of the coracoid (Fig. 5A-D). The scapular blade is rectangular along its height but expands both anteriorly and posteriorly at its distal end. This expansion is more pronounced posteriorly, but both expansions are triangular. The glenoid is subcircular and angled posterolaterally. The entire scapulocoracoid is angled; in anteroposterior view, a point of flexure is apparent just dorsal to the glenoid.

The left humerus is complete (Fig. 5E-J), with an expanded proximal end, a shaft that is elliptical in cross-section, and two prominent condyles distally. The shaft is asymmetrically oriented anteriorly; all these are features typical of aetosaur humeri (Long and Murry, 1995; Lucas et al., 2002).

The left ulna is complete (Fig. 6A-D) and lacks a prominent olecranon process. The proximal articulation is subelliptical in proximal view. The shaft thins distally and is anteroposteriorly compressed.

The isolated metapodial is complete (Fig. 6E-H). The proximal articular surface is a flattened ellipse, while the distal articular surface is rectangular. This distal surface also has collateral ligament pits on both sides of its distal articulation for the attachment of the extensor muscles of the digits.

The right femur is missing its head, but everything distal to its position is preserved (Fig. 7A-D). The femoral shaft is fairly massive with a rounded, pyramidal fourth trochanter and very large distal condyles. This specimen is identical to a femur Long and Murry (1995, fig. 81) assigned to *Stagonolepis*.

Like the femur, the left tibia is identical to material assigned to and illustrated as *Stagonolepis* by Long and Murry (1995, fig. 84). The tibia is mediolaterally compressed and expanded proximally (Fig. 7E-J). Additionally, a slight crest wraps around the anterior edge of the tibial shaft at its midpoint. Both the Polish specimen and the specimen illustrated by Long and Murry (1995) have elliptical distal ends and shallow sulci on their lateral edges.

Teratosaurus

Sulej (2005) erected the new species *Teratosaurus silesiacus* for disarticulated cranial and mostly disarticulated postcranial material from both bone beds at Krasiejów. He distinguished *T. silesiacus* from the type, and the only other named, species of *Teratosaurus*, *T. suevicus*, by features of the maxilla, the only bone in common between specimens of either species (Fig. 8). According to Sulej (2005), unlike *T. suevicus*, *T. silesiacus* has the medial anterior foramen on the maxilla located on its medial surface, a more strongly oblique dorsal process of the maxilla, and foramina for replacement teeth set in a straight line and not connected by a dental groove.

However, a close comparison of the maxilla of *Teratosaurus silesiacus* (Fig. 8) and that of *T. suevicus* (Galton, 1985, pl. 1) calls into question the distinctiveness of *T. silesiacus*. No obvious difference exists in the obliquity of the maxilla dorsal processes, and the alignment of the foramina for replacement teeth in *T. "silesiacus"* is not straighter than that in *T. suevicus*. There is a distinct dental groove connecting these foramina in *T. suevicus* that is present, but not as distinct, in *T. silesiacus*. The medial anterior foramen on the maxilla opens anteriorly on *T. suevicus* and more ventrally on *T. silesiacus*. This relatively minor difference, however, could be due to preservation quality and distortion. We also reject Sulej's (2005) argument that "the great distance in time of about 4 million years between these animals [*T. suevicus* and *T. silesiacus*] suggest that they probably belong to different species." Therefore, we consider *T. silesiacus* to be a junior synonym of *T. suevicus*.

Parasuchus

Dzik (2001) described a skull he identified as *Paleorhinus* sp. from Krasiejów that we assign to *Parasuchus bransoni* (cf. Hunt and Lucas, 1991). Note that creation of a diagnostic neotype for *Parasuchus hislopi* by the International Commission on Zoological Nomenclature in 2003 (opinion 2045, case 3165) renders *Paleorhinus* a junior subjective synonym of *Parasuchus*.

The *Parasuchus* material present from the Krasiejów locality includes two nearly complete skulls and an incomplete, associated torso in a matrix block. One skull (Fig. 9A-D) is nearly complete, missing only part of its left squamosal, and its snout exhibits separation along the midline. The other skull (Fig. 9F-G) is nearly complete, missing a portion of its snout and having its postorbital region partially disarticulated. This skull preserves its lower jaws in articulation with the rest of the skull and has a large percentage (>80%) of its maxillary dentition intact (Fig. 9F). Both skulls have nasal openings anterior to their antorbital fenestrae, dorsally directed orbits, dorsal margins of the nares that are

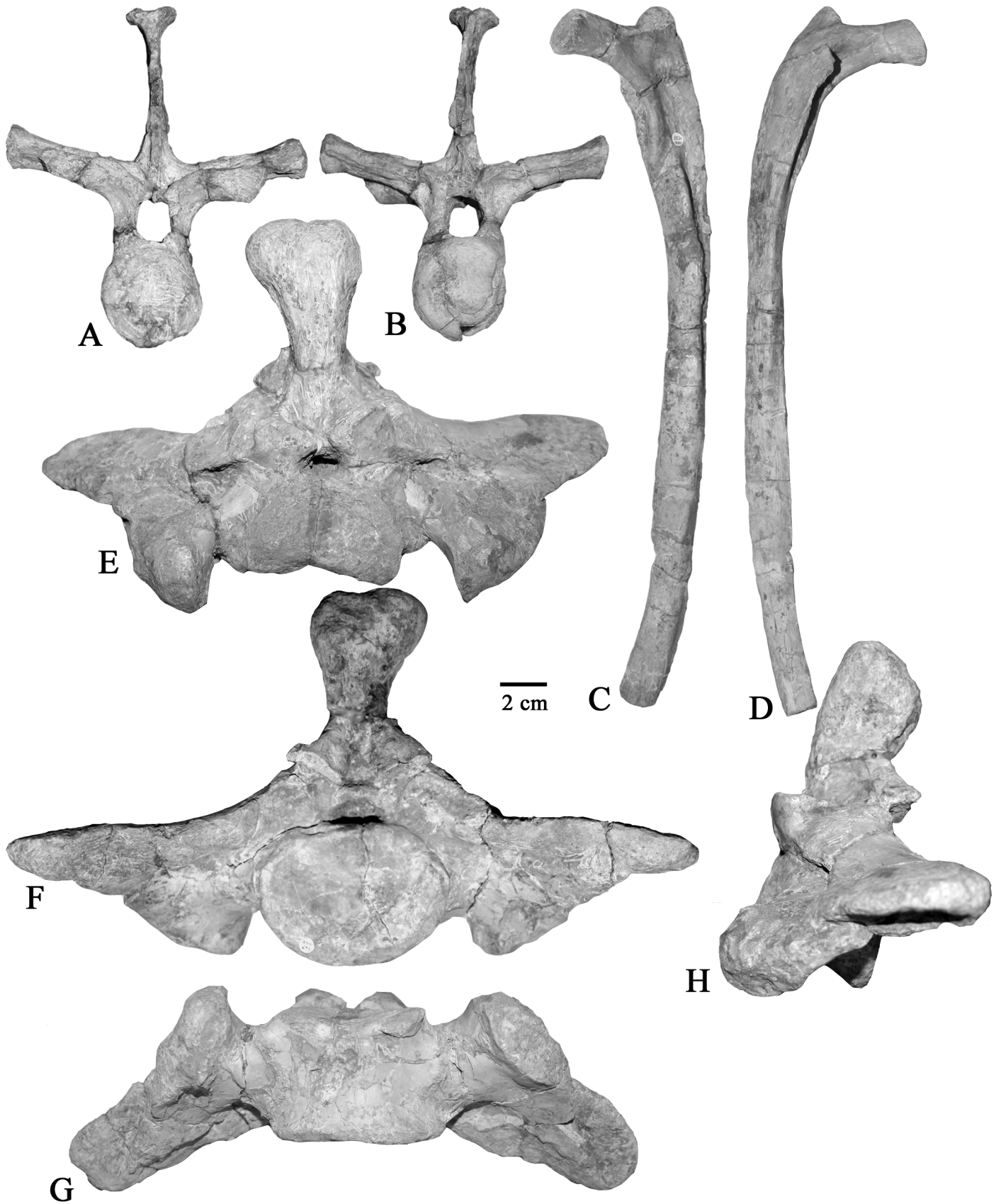


FIGURE 3. **A-B**, *Stagonolepis robertsoni*, PAN ZPAL AbIII 502/67, mid-dorsal vertebra in **A**, anterior and **B**, posterior views. **C-D**, *Stagonolepis robertsoni*, PAN ZPAL AbIII 1527, complete right? rib in **C**, anterior, and **D**, posterior views. **E-H**, *Stagonolepis robertsoni*, PAN ZPAL AbIII 1693, incomplete sacral vertebra in **E**, anterior, **F**, posterior, **G**, ventral, and **H**, left lateral views.

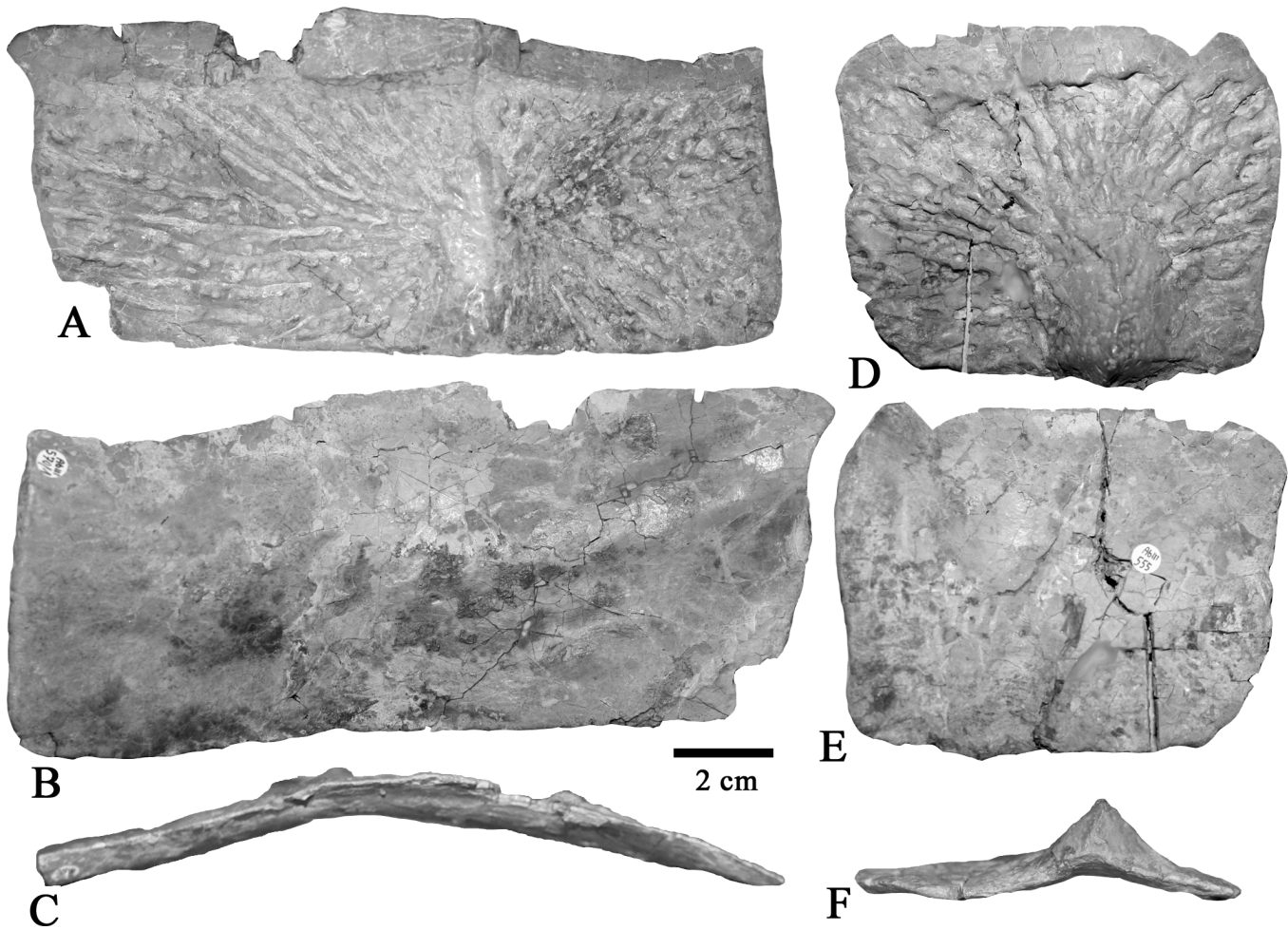


FIGURE 4. A-C, *Stagonolepis robertsoni*, PAN ZPAL AbIII 57011, left paramedian osteoderm in A, dorsal, B, ventral, and C, posterior views. D-F, *Stagonolepis robertsoni*, PAN ZPAL AbIII 535, left lateral osteoderm in D, dorsal, E, ventral, and F, posterior views.

inclined anteriorly, and large quadratic foramina, diagnostic features of *Parasuchus* (Hunt and Lucas, 1991). The associated torso is partially disarticulated but consists of numerous dorsal osteoderms, proximal rib fragments and the left scapular blade in a matrix block (Fig. 9E). The two skulls from Krasiejów show a significant range in size (total lengths are ~400 and ~610 mm) and confirm that position of the external nares relative to the antorbital fenestra (a feature diagnostic of *Parasuchus*) does not change ontogenetically.

Silesaurus

Dzik (2003) named the dinosauriform *Silesaurus opolensis* based on cranial and postcranial material from Krasiejów. This taxon is unique to the locality, and thus of little value to biochronological correlation. Indeed, *Silesaurus* is one of the youngest known non-dinosaurian dinosauriforms.

DISCUSSION

Taxonomic descriptions of much of the Krasiejów tetrapod assemblage provide a classic example of what Cooper (1982) termed “provincial taxonomy”: virtually all of the taxa described from Krasiejów were assigned to new species, not based on robust morphological differ-

ences, but mostly on their location at a new site. However, a careful review of the Krasiejów tetrapod taxa indicates that it contains only one new (and thus far endemic) taxon, the dinosauriform *Silesaurus opolensis*. *Metoposaurus* and *Parasuchus* from Krasiejów are indicators of an Otischalkian age (Lucas, 1998, 1999). The occurrence of *Stagonolepis* is particularly important because it documents an Otischalkian record of this taxon, which can no longer be considered an index taxon of the Adamanian.

Lithostratigraphic and microfossil correlations indicate that the Krasiejów locality is equivalent to the Lerhberg Schichten of the German Keuper. Tetrapod biostratigraphy indicates the Lehrberg Schichten are of Otischalkian age (Lucas, 1999). Therefore, tetrapod biostratigraphy confirms previous correlations based on other data. The Krasiejów tetrapod assemblage thus further demonstrates the value of Triassic tetrapods in biostratigraphic correlation, based on the global Triassic tetrapod biochronology developed in the 1990s.

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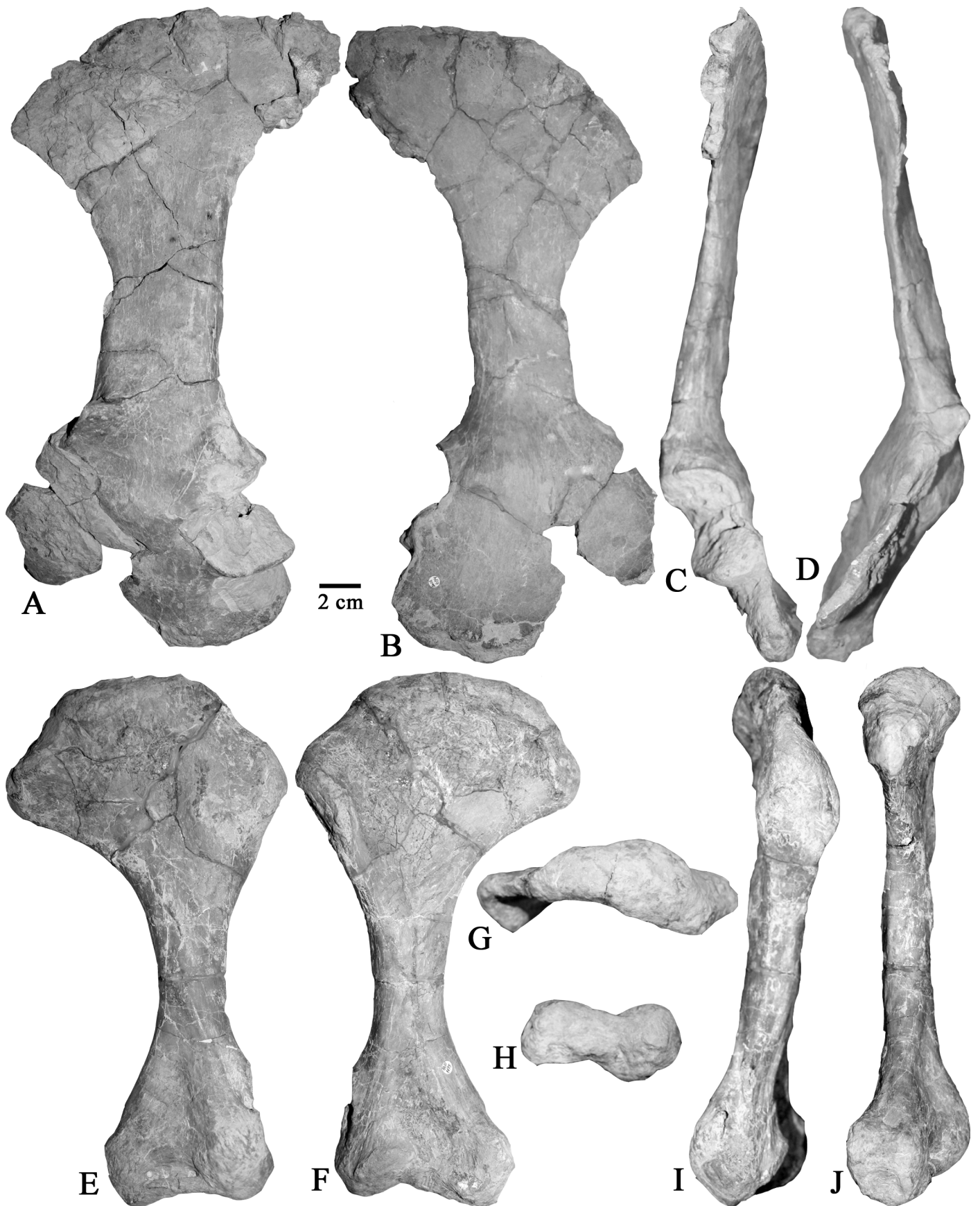


FIGURE 5. A-D, *Stagonolepis robertsoni*, PAN ZPAL AbIII 694, incomplete left scapulocoracoid in A, lateral, B, medial, C, posterior, and D, anterior views. E-J, *Stagonolepis robertsoni*, PAN ZPAL AbIII 1175, left humerus in E, anterior, F, posterior, G, proximal, H, distal, I, medial and J, lateral views.

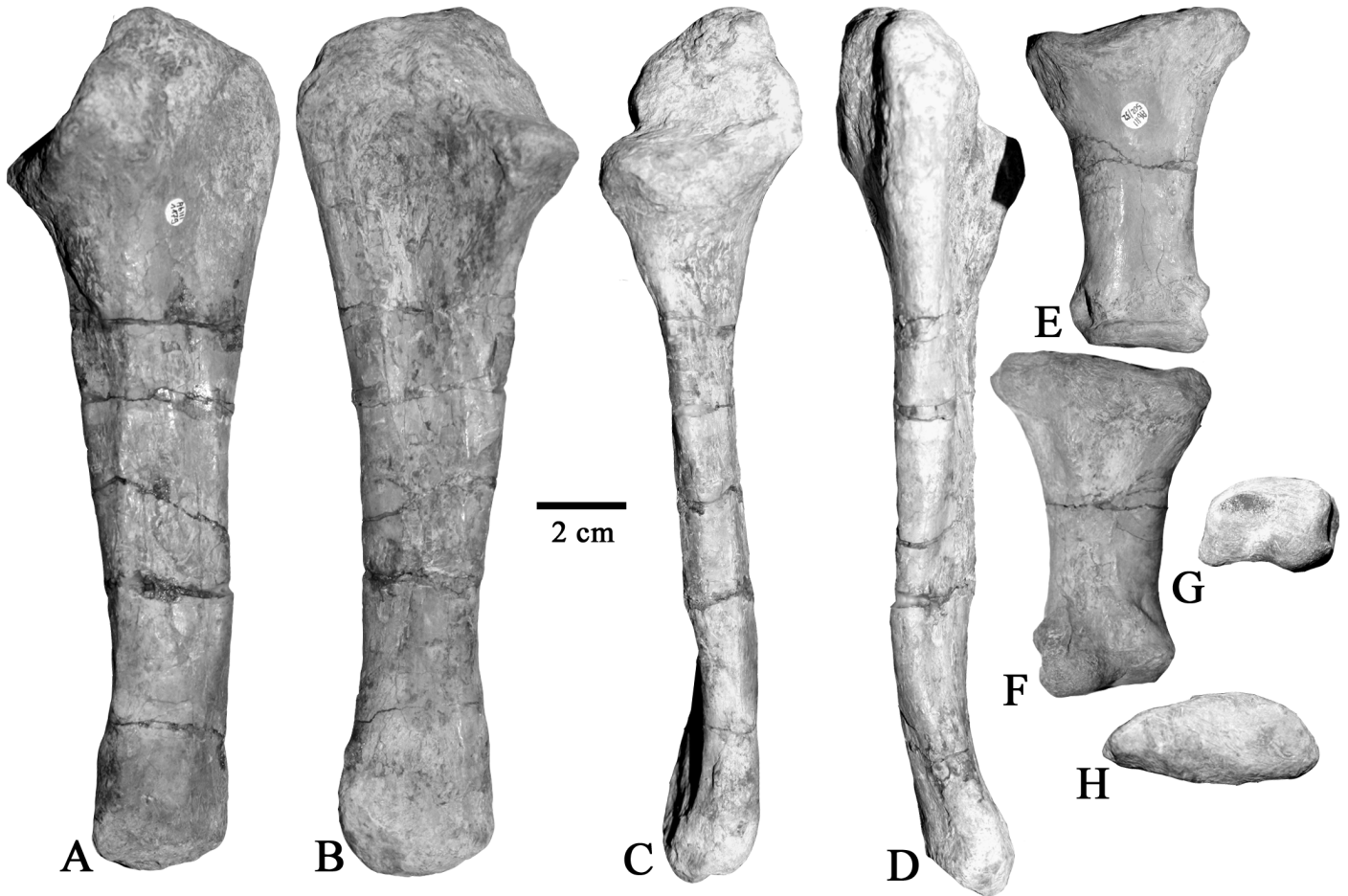


FIGURE 6. **A-D**, *Stagonolepis robertsoni*, PAN ZPAL AbIII 1179, left ulna in **A**, anterior, **B**, posterior, **C**, medial, and **D**, lateral views. **E-H**, *Stagonolepis robertsoni*, PAN ZPAL AbIII 502/52, right? metapodial in **E**, dorsal, **F**, ventral, **G**, distal, and **H**, proximal views.

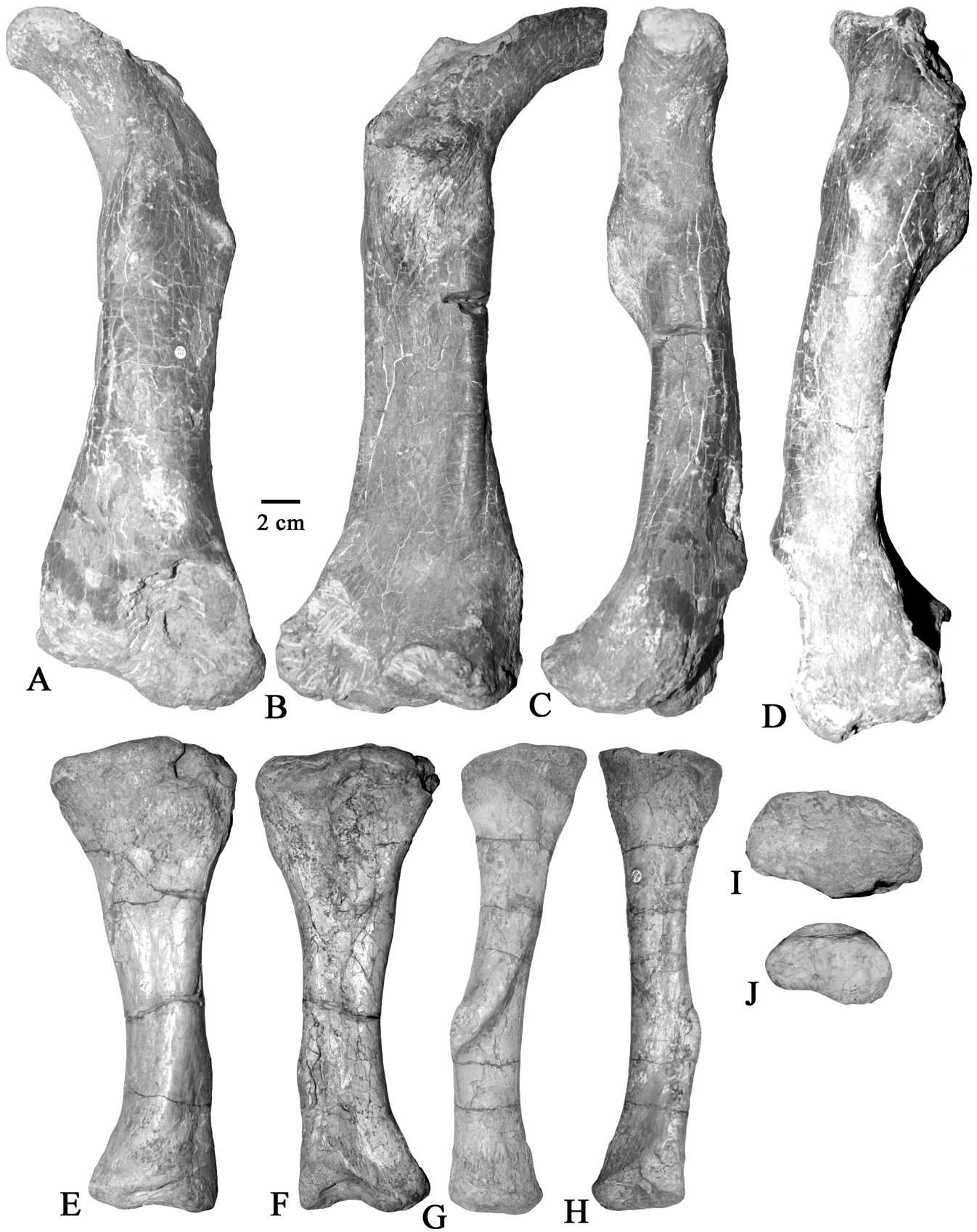


FIGURE 7. A-D, *Stagonolepis robertsoni*, PAN ZPAL AbIII 115, incomplete left femur in A, anterior view; B, posterior view; C, medial view; and D, lateral view. E-J, *Stagonolepis robertsoni*, PAN ZPAL AbIII 1178, left tibia in E, medial view; F, lateral view; G, anterior view; H, posterior view; I, proximal view; and J, distal view.

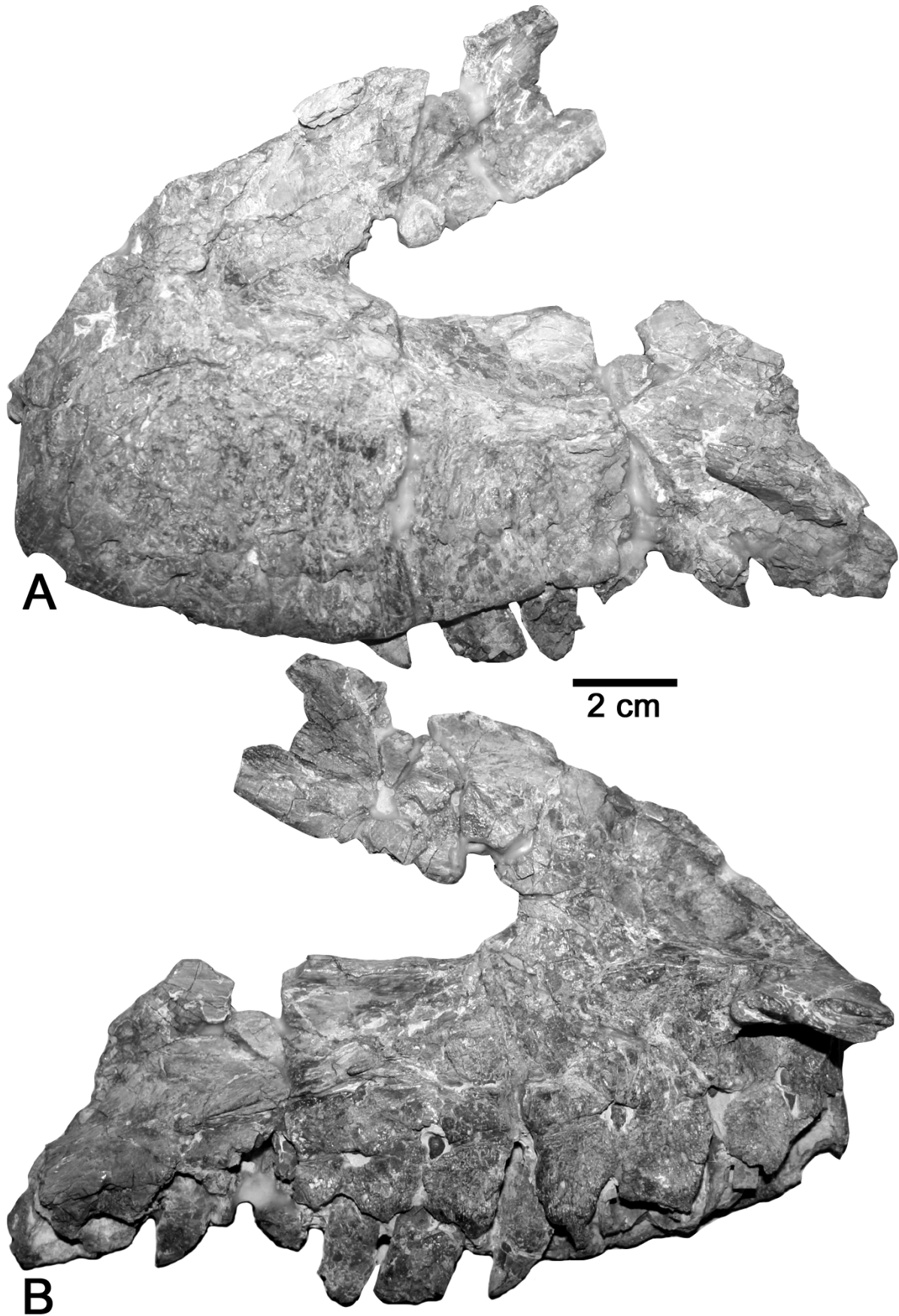


FIGURE 8. A-B, *Teratosaurus suevicus*, PAN ZPAL Ab III 563, part of holotype of *Teratosaurus* “*silesiacus*,” left maxilla in A, lateral and B, medial views.

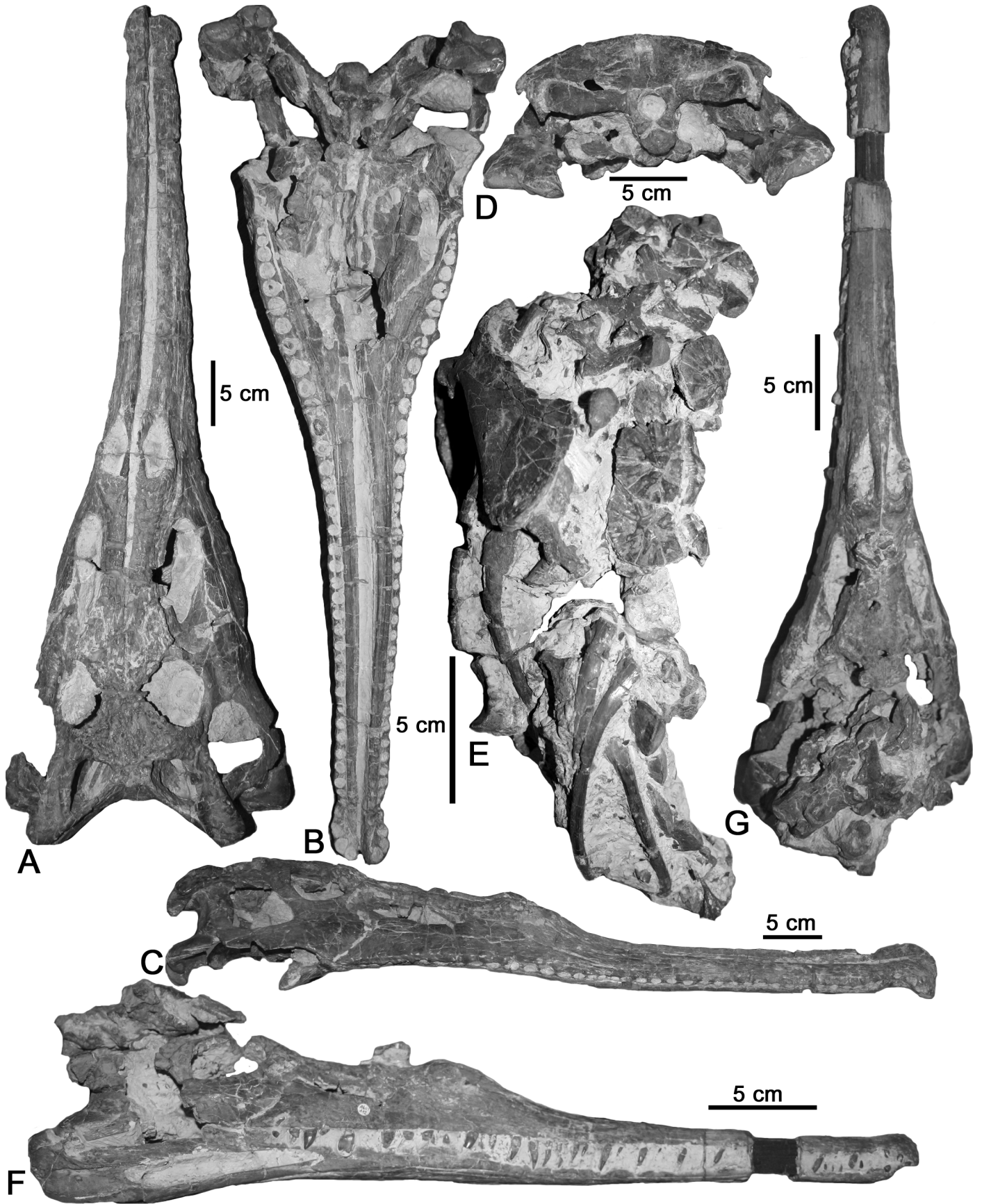


FIGURE 9. A-D, *Parasuchus bransoni*, PAN ZPAL Ab III 200, nearly complete skull in A, dorsal, B, ventral, C, right lateral and D, occipital views. E-G, *Parasuchus* sp., PAN ZPAL Ab III 112, nearly complete skull in F, right lateral and G, dorsal views. E, incomplete, associated torso of ZPAL Ab III 112, consisting of dorsal osteoderms and ribs, in matrix block.

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