Journal of Vertebrate Paleontology 30(4):1127–1141, July 2010
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ARTICLE

THE AXIAL SKELETON OF *SILESAURUS OPOLENSIS*

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ABSTRACT—A recent find of an articulated skeleton of *Silesaurus opolensis* at its early Late Triassic type locality Krasiejów (Poland), with skull, neck, pectoral girdle, and thorax, supplemented by additional preparation of previously collected articulated specimens, enables complete restoration of the vertebral column and associated skeletal parts. Cervical ribs of *Silesaurus*, well preserved in their original disposition, are parallel to the neck and extend backward for a few vertebral lengths. There is a sudden change in their morphology behind the seventh vertebra, although otherwise the transition from the cervical to the dorsal vertebrae is very gradual. Parapophyses slowly migrate upward along the anterior margin of the centrum and leave the centrum at the sixth or seventh dorsal vertebra. Narrowing of the dorsal extremities of the neural spines of the fourth and neighboring vertebrae suggests the ability of this region of the vertebral column to bent upward. There is thus a disparity between the structural and functional neck-thorax transition. The presence of three sacrals firmly connected by their ribs with the ilia and the long tail of *Silesaurus*, providing a counterbalance to the weight of the body in front of the pelvis, suggests the ability for fast bipedal running. However, unusually long but gracile forelimbs of *Silesaurus* suggest that it represents a transition towards secondarily quadrupedal locomotion, characterizing most of the later herbivorous dinosaurs.

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INTRODUCTION

The Late Triassic was a time of rapid evolution and diversification of archosaurs that resulted in the diversification of numerous lineages of dinosaurs and dinosaur-like forms (Parker et al., 2005; Nesbitt, 2007; Irmis et al., 2007b; Brusatte et al., 2008). The main difficulty with deciphering the actual course of the evolutionary transformations and pattern of relationships is the scarcity of data. Especially for the early Late Triassic, knowledge of the skeletal anatomy of possible early dinosaurs and their close relatives is very limited. There are few reports on articulated skeletons, isolated in time and separated by great geographic distances. Among the best known species is *Silesaurus opolensis* Dzik, 2003, from late Carnian strata exposed at Krasiejów in southern Poland, represented by several articulated skeletons and numerous isolated bones (Dzik, 2001, 2003; Dzik and Sulej, 2007). Closely related forms have been reported from several other regions of the world (Ezcurra, 2006; Ferigolo and Langer, 2007; Irmis et al., 2007b; Nesbitt et al., 2007).

In this paper we present a description of the axial skeleton of *S. opolensis*, more complete and reliable than those previously published, based on all the available materials, including a new articulated specimen collected recently at its type locality Krasiejów. We also compare the restored skeletal morphology with those of possibly related early dinosaurs and rauisuchians.

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

MATERIAL

Most of the new information presented here is derived from the recently collected and prepared specimen ZPAL AbIII/1930 (Dzik and Sulej, 2007), which preserves a partial skull articulated with the anterior part of the postcranial skeleton (Figs. 1, 2). The specimen was found in the lower lacustrine fossiliferous horizon, from which previously a few isolated bones of *Silesaurus opolensis* had been collected, including the first known specimen of this species (Dzik, 2001). The axial skeleton of specimen ZPAL AbIII/1930 shows well-preserved and articulated presacral vertebrae (including the atlas) of proximal part of the column with their ribs and gastralia, mostly in original disposition, although in places some sets of bones are displaced. Proximal elements of the pectoral girdle are also preserved. The tail is represented by a few articulated caudal vertebrae found in proximity.

All other specimens of *S. opolensis* were collected from the upper fluvial fossiliferous horizon at Krasiejów (Dzik, 2003; Dzik and Sulej, 2007). Except for the proatlas and a few distal caudals, elements of the entire vertebral column are represented in the studied material. Despite some difference in size, all specimens show complete co-ossification of the neural arches with the centra. The morphological sequence and number of the vertebrae, in particular subdivisions of the column not represented in specimen ZPAL AbIII/1930, is inferred from previously described, partially articulated specimens ZPAL AbIII/361, 362, and 363 (Dzik, 2003).

The holotype of *S. opolensis* (ZPAL AbIII/361) includes all presacral vertebrae except for the atlas. The sacrum is associated. Only 15 caudals of the proximal part of the tail are present, including a few crushed chevrons. The ribs are more or less displaced from their original articulation. The vertebral column is broken in a few places, with its bones dispersed over some area, but it is possible to determine the morphological sequence of the vertebrae within the column.

The vertebral column of the skeleton ZPAL AbIII/364 includes 16 presacral vertebrae of the proximal part of the column (including atlas) with most of their ribs. These bones are preserved mostly in articulation.

In specimen ZPAL AbIII/362, the vertebral column is represented by the well-preserved sacrum and fragmentary cervical, dorsal, and caudal series.

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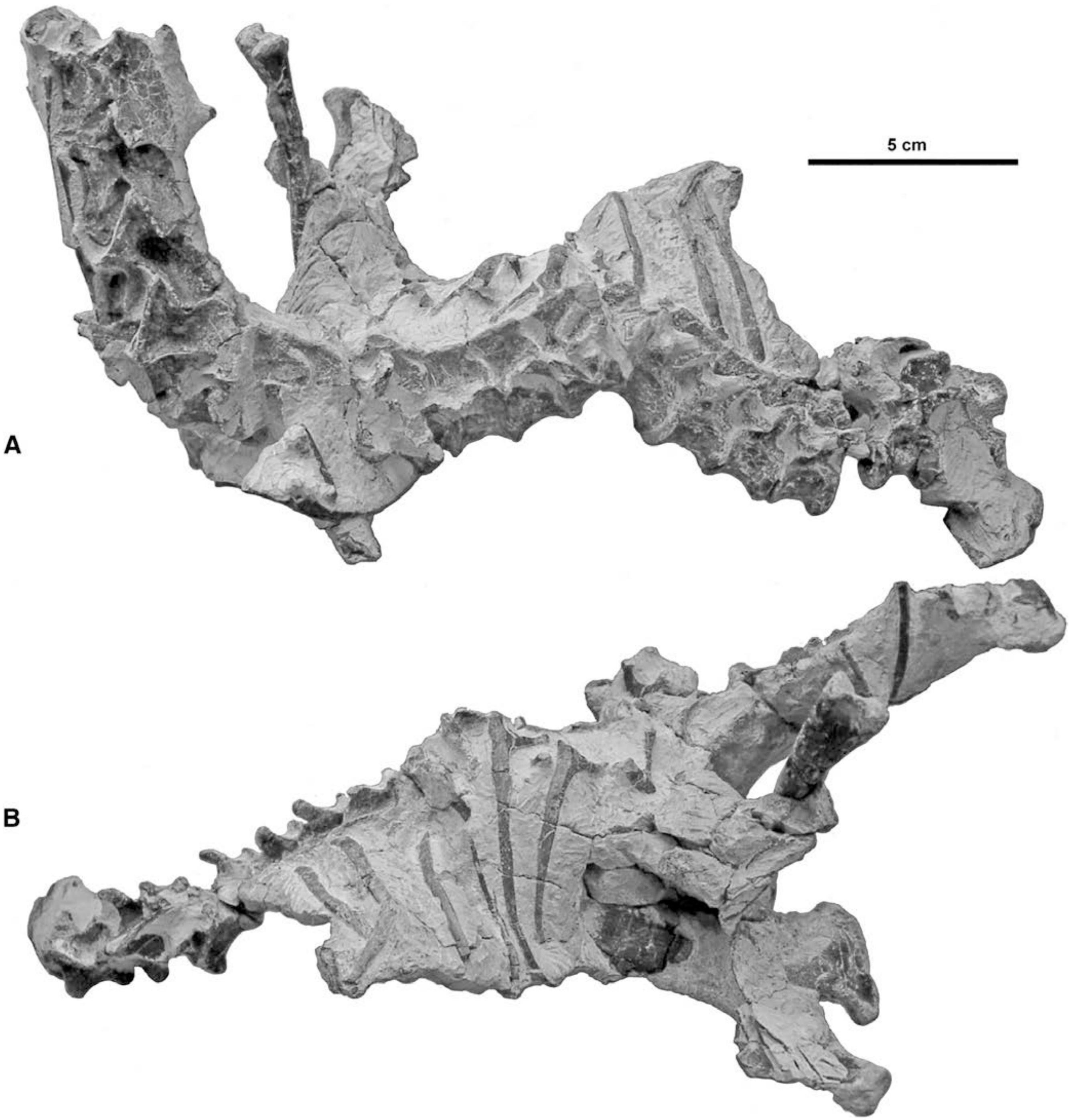

FIGURE 1. Articulated partial skeleton ZPAL AbIII/1930 of *Silesaurus opolensis* Dzik, 2003 from the early Late Triassic lacustrine horizon in Krasiejów near Opole, Poland. **A**, left lateral side; **B**, right dorsolateral side.

Specimen ZPAL AbIII/363 includes only the sacrum. Numerous isolated vertebrae were collected in addition to the articulated specimens within the same lenticular rock unit, probably representing a single depositional episode (Dzik and Sulej, 2007).

DESCRIPTION OF THE VERTEBRAL COLUMN

There seems to be some individual variation in the gradation from the cervical to the dorsal vertebrae, as the morphology of particular vertebrae differs slightly between particular articulated specimens (Dzik, 2003). A sudden change in morphology of the ribs in specimen ZPAL AbIII/1930 shows that the junction between the neck and trunk is located between the seventh and eighth presacral vertebrae, although migration of the parapophyses from the centrum to the neural arch continues to the middle of the dorsal series. The vertebral formula in *Silesaurus opolensis*, with 23 presacral vertebrae, of which 16 are dorsals, probably represents a primitive condition for dinosauriforms, as suggested by the same vertebral formula in *Coelophysis* and other theropod dinosaurs, especially coelurosaurs. Four fused sacrals are

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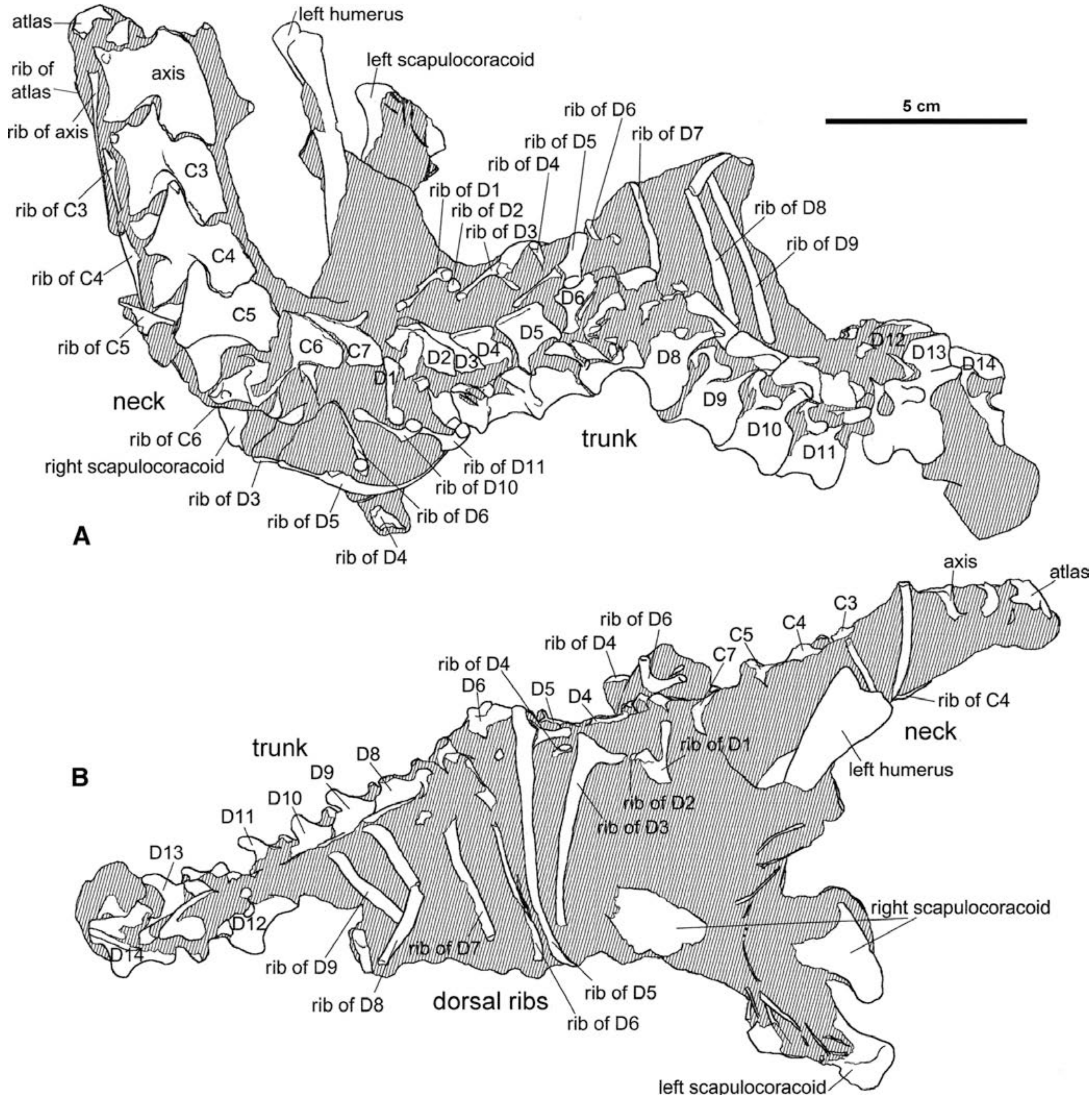

FIGURE 2. Identification of *Silesaurus opolensis* bones in specimen ZPAL AbIII/1930 (see Fig. 1). **A**, left lateral side; **B**, right dorsolateral side.

represented by several specimens (Dzik, 2003); their modified restoration was published recently (Dzik and Sulej, 2007). The number of caudal vertebrae seems to vary from about 35 to perhaps 40.

No evidence of pneumaticity was found on the vertebrae of *Silesaurus*.

Cervical Vertebrae and Ribs

The atlas is partially preserved in ZPAL AbIII/364 and 1930 (Fig. 4A, B). As typical of reptiles, the atlas is composed of three elements—the intercentrum and paired neural arches, occupying a restricted space between the occiput and second cervical vertebra. The intercentrum is a rectangular, thin strip of bone. The atlantal intercentrum is U-shaped in anterior view. The articular surface for the occipital condyle faces anterodorsally. The occipital condyle articulates posteriorly against this trough-shaped surface, which permitted wide movement of the skull in many planes. The articular surface for the odontoid faces posterodorsally. The articular surface for the axial intercentrum is also U-shaped and faces posteroventrally.

Description of the axis is based on specimens ZPAL AbIII/361, 364, and 1930 (Fig. 4C). The axis shows considerable elongation, and each next vertebra in the cervical series shows gradational

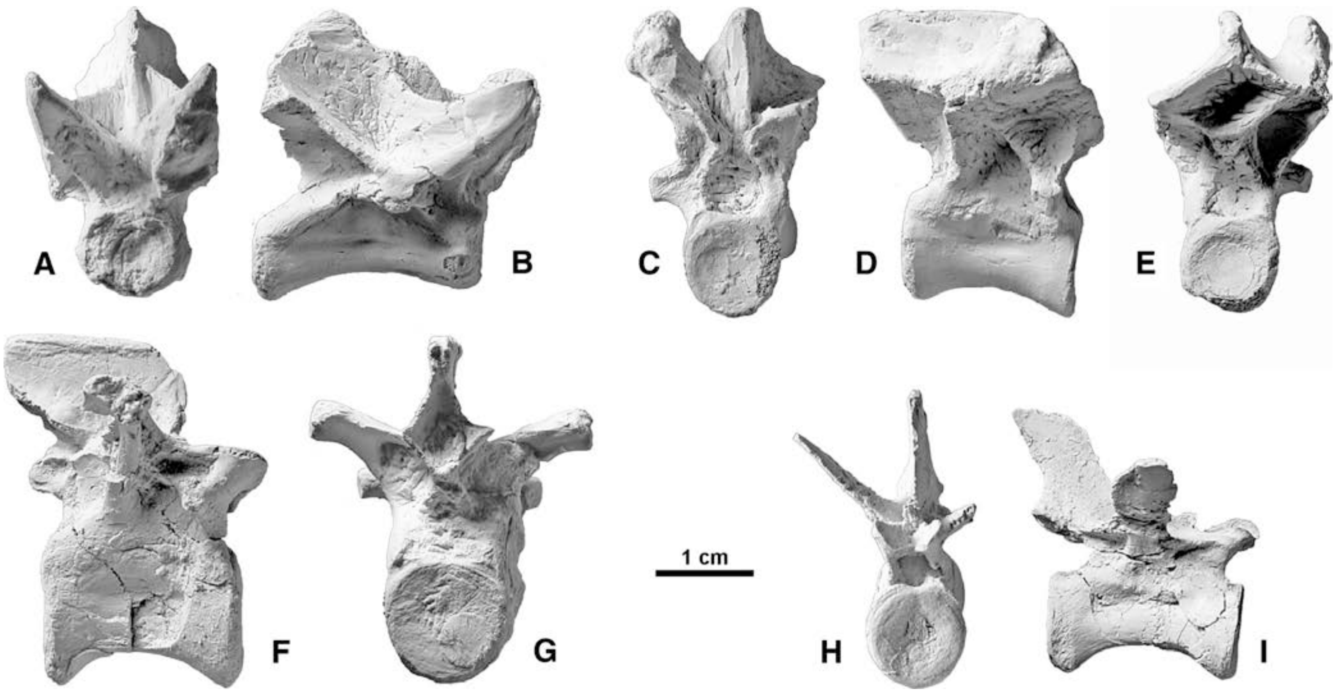

FIGURE 3. Individual vertebrae of *Silesaurus opolensis*. **A**, **B**, 4th cervical ZPAL AbIII/411/7 in anterior and right lateral views. **C–E**, 7th dorsal ZPAL AbIII/433/1 in anterior, right lateral, and posterior views, respectively. **F**, 14th dorsal ZPAL AbIII/1991 in right lateral view. **G**. 13th dorsal ZPAL AbIII/362/11 in posterior view. **H**, **I**, caudal ZPAL AbIII/923 in anterior and right lateral view.

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decrease in length. The axial centrum is almost twice as long as deep. The axial intercentrum is fused with the anterior end of the axis. The anterior surface of the centrum is very broad and deeply concave (cup-shaped), to receive atlantal intercentrum. A strong ventral keel is present. The parapophysis is positioned low on the anterior rim of the centrum. The axis lacks diapophyses, which are represented by low prominences on the third cervical vertebra and are fully developed only in the presacral vertebrae following it. The neural arch of the axis is completely coossified with the centrum. Small, elliptical prezygapophyses are projected anterolaterally. The articular surface of prezygapophysis is gently convex along its long axis. The neural spine is projected anteriorly between the prezygapophyses. At its posterodorsal extremity, the neural spine divides into two ventrolaterally oriented laminae, which terminate ventrally as structures resembling incipient epipophyses that are located posterior to the well-developed postzygapophyses (they do not have recognizable serial homologues behind). In posterior view, a deep postspinal fossa, which is delimited by the spinopostzygapophyseal lamina, is developed between the neural spine and the postzygapophyses. A thin lamina connects the medial edges of the postzygapophyses and floors the postspinal fossa at the base of the neural arch. When looking at the fossa, one gets an impression that its posterior outline is rhomboidal but the interior is actually pentagonal. In the following vertebrae, the postspinal fossa gradually decreases in size, until it almost disappears in the posterior dorsals.

The postaxial cervical vertebrae are best preserved in the articulated specimens ZPAL AbIII/361 and 1930 (Fig. 4D–H). The neck of *Silesaurus* consists of somewhat elongated vertebrae (except for the atlas). These vertebrae are amphicoelous, the centra being slightly more concave at their anterior face. The postaxial cervical centra are parallelogram-shaped in lateral view, with slight skewing and elevation of the anterior centrum face. The centra are compressed from sides. In contrast to the posterior cervical and all dorsal and sacral vertebrae, articulation surfaces of centra of the anterior cervical vertebrae are circular in outline. As on the axis, a strong ventral keel is present on third cervical centrum but it is reduced in depth in more posterior cervicals. Oval parapophyses occupy the low anterior rim of the centrum in all cervical vertebrae. They keep their ventral position up to the last cervical vertebra. The diapophyses, which are developed as low prominences just above the neurocentral suture in the third cervical vertebra, project from the succeeding cervical vertebrae as ventrolaterally directed flanges. In fourth cervical vertebra, the diapophyses are anteroposteriorly shortened and oriented anterolaterally.

Four laminae extend from the diapophyses to the prezygapophyses (prezygodiapophyseal lamina) and postzygapophyses (postzygodiapophyseal lamina) and to the anteroventral (anterior centrodiapophyseal lamina) and posteroventral corners (posterior centrodiapophyseal lamina) of each neural arch behind third cervical vertebra. The laminae merge centrally into a low cross-shaped structure. A fifth lamina (middle centrodiapophyseal lamina) may be present below the diapophysis between the anterior and posterior centrodiapophyseal lamina. As a result, the infradiapophyseal fossa is divided into anterior and posterior parts. The transverse processes appear broadly triangular in dorsal view because the lamina between the diapophyses and prezygapophyses that forms the external surface of the anterior portion of the neural arch is especially strong.

The prezygapophyses project beyond the anterior face of the centrum in the third and succeeding cervical vertebrae. A distinct ridge extends posteriorly behind the parapophyses over most of the length of the centrum in proximal cervicals (except for the atlas). The semioval articular surfaces are flat and face dorsomedially. A narrow spinozygapophyseal fossa demarcated by spinoprezygapophyseal laminae is present at the base of the neural spine between the prezygapophyses. In contrast to the axis, the postzygapophyses of the postaxial cervical vertebrae do not

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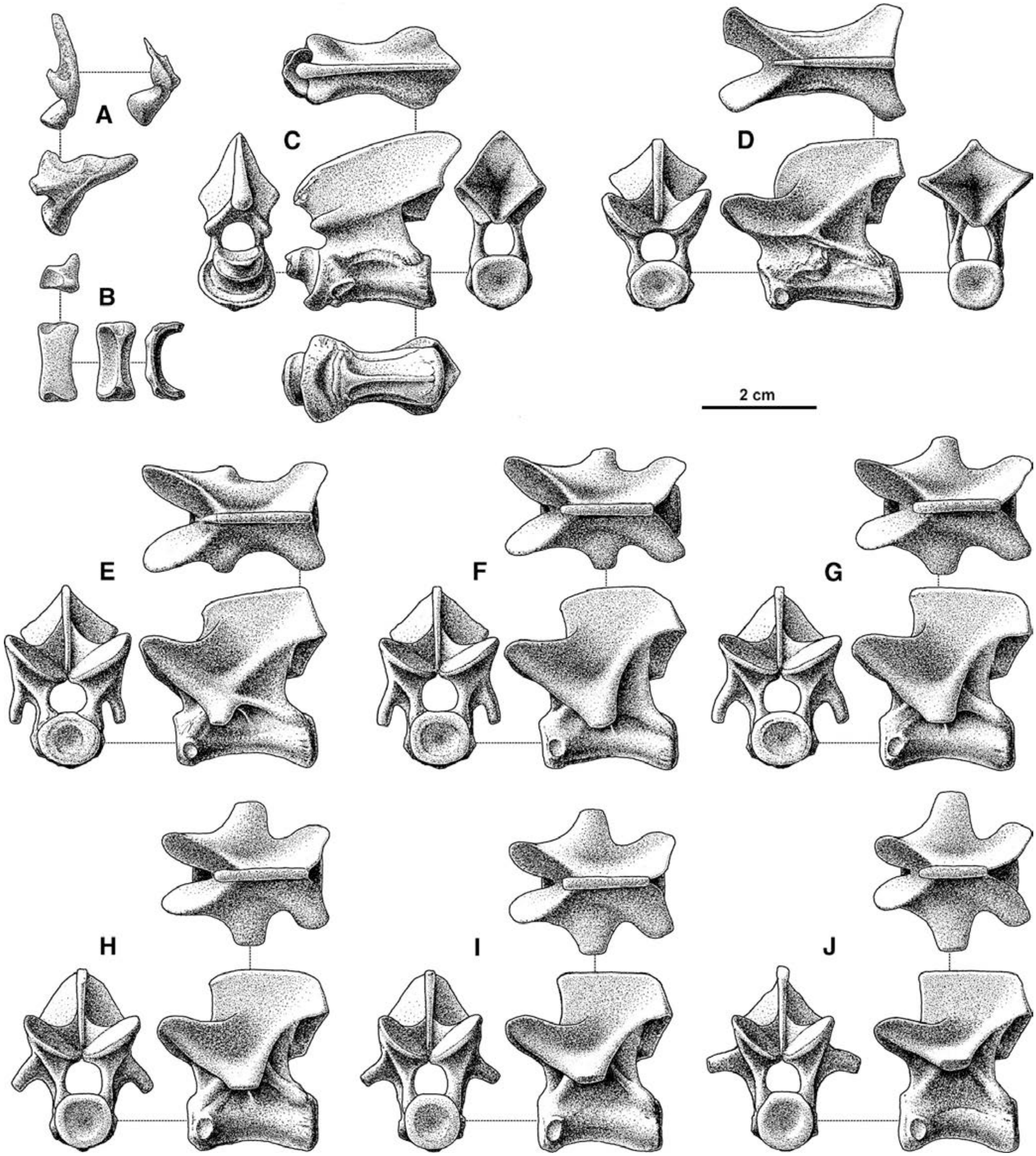

FIGURE 4. Restoration of presacral vertebrae of *Silesaurus opolensis*; dorsal, anterior, and left lateral views (except for A, B, C, where also posterior view is given); based mostly on ZPAL AbIII/1930 and 361. **A**, **B**, neural arch and intercentrum of atlas; **C**, axis; **D**, 3rd cervical; **E**, 4th cervical; **F**, 5th cervical; **G**, 6th cervical; **H**, 7th cervical; **I**, 1st dorsal; **J**, 2nd dorsal.

project behind the posterior centrum face, and the neural spines become there less pointed posteriorly.

Each neural arch of the atlas has a prominent neural spine. The plate-shaped neural spine of the third cervical vertebra is subquadrate in lateral view and inclined posterodorsally. In subsequent cervical vertebrae, posterodorsal corners of the neural spines are blunt. As in the axis, a deep posterior chonos is present at the base of the neural spine between the postzygapophyses.

The cervical ribs (Fig. 5A–G, N) are well preserved in specimen ZPAL AbIII/1930 and relatively well recognizable in the

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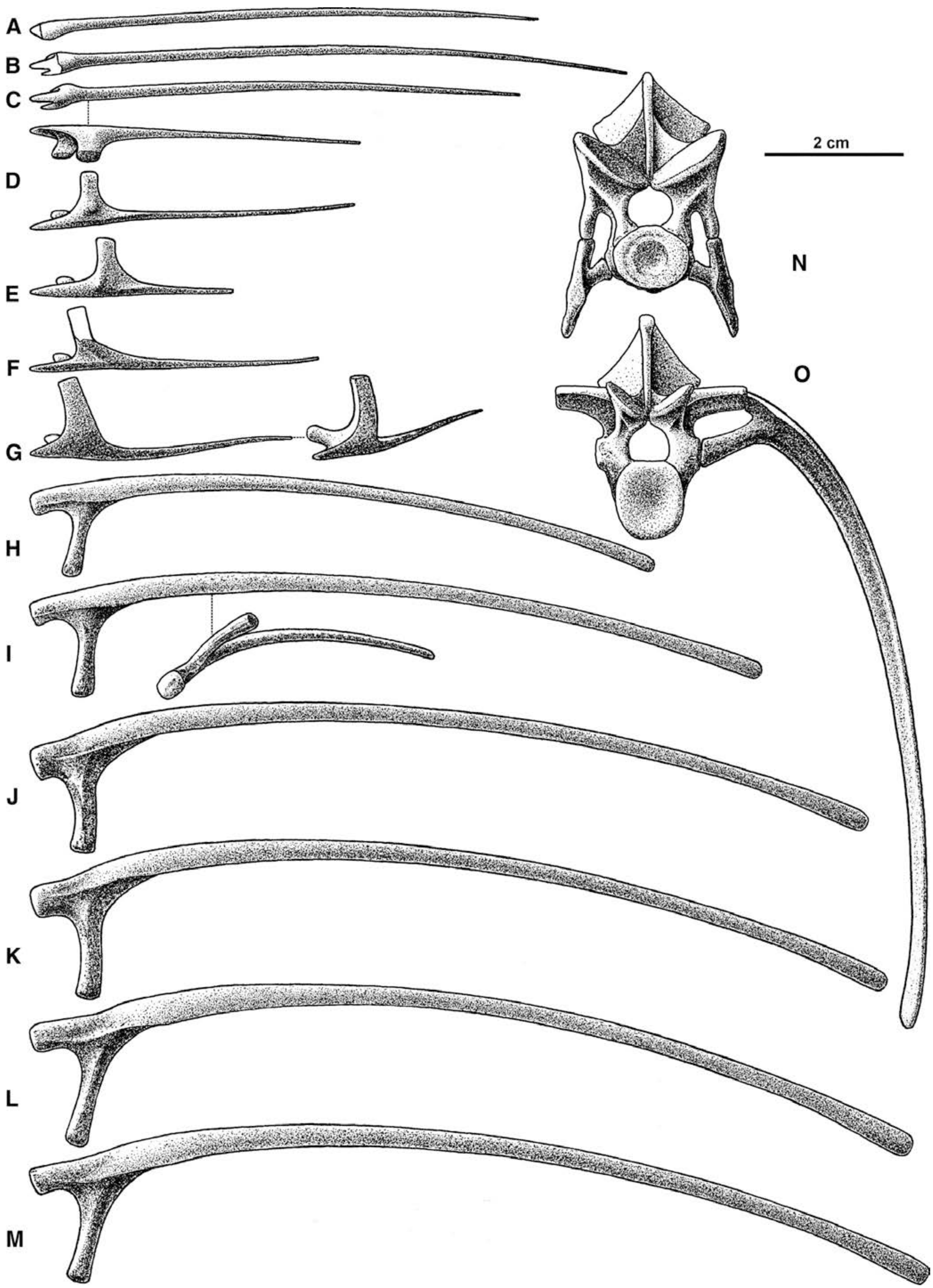

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specimens ZPAL AbIII/361 and 362. Each cervical vertebra, including atlas, bears a rib on either side. Each cervical rib is slender and delicate. The most robust are anteriorly located ribs that extend for more than three lengths of the supporting vertebra. The posterior ribs are much shorter and narrower and cover distance of only two vertebral lengths. The atlantal, axial, and third cervical ribs lack a tuberculum. Other cervical ribs are prominent and double-headed. The capitulum articulates with a parapophysis on the centrum and the tuberculum with a diapophysis located on the deep lateral lamina of the neural arch. Each cervical rib, except for the atlantal rib, has a prominent anterior process in front of its articulation, this process extending anteriorly to terminate acutely. Anteriorly, the cervical ribs are very long, each one extending back along the length of its vertebra and along more than three succeeding vertebrae. Backward their length and thickness decreases but tuberculum becomes more prominent. External surface of the rib, together with its anterior process, is flat.

Dorsal Vertebrae

The series of dorsal vertebrae in ZPAL AbIII/362 and 1930 (Figs. 4I–J, 6A–H, 7A–F) well show details of their structure. The anterior dorsal vertebrae are similar to posterior cervical vertebrae, except that they are shorter than the last cervical vertebra (as well as the posterior dorsal vertebrae). Posteriorly, the dorsal vertebrae increase in their length and even more in height.

The dorsal centra have wide, slightly concave, intercentral articulation surfaces, larger than in the cervical vertebrae. Each is strongly constricted at the mid-length of the centrum, which gives an hourglass shape, so characteristic of many early archosaurs. A shallow elliptical depression is present on the lateral face of the centrum, the upper rim of which exhibits a semicircular prominence. It does not seem to be a pneumatic feature. In contrast to cervical vertebrae, the amphicoelous articular surfaces of the dorsal vertebrae are at right angle to the median axis of the centrum in both lateral and ventral views. In the cervical region, the articular surfaces are inclined dorsoventrally to the vertebral axis. This reflects the difference in the attitudes between the S-shaped neck posture and slightly arched disposition of the thoracic region.

The parapophyses are prominent at the base of the neural arch of first two dorsal vertebrae. From the third dorsal vertebrae backward, the parapophyses gradually shift dorsally and posteriorly, from their position at the level of the neurocentral suture to the level of the prezygapophysis. At the same time, the parapophyses become more elongated laterally. Near the eleventh dorsal vertebra, the parapophyses raise to reach nearly the same position with the diapophyses on the fourteenth dorsal. The parapophyses of dorsal vertebrae are oriented obliquely posteriorly except for the last dorsals. The parapophyses of the third to sixth dorsals are anteroposteriorly compressed, in contrast to a circular articulation surface for the capitulum of the following dorsal vertebrae. The transverse processes are strong due to their remarkable anteroposterior width. They extend basally towards the pre- and postzygapophyses as the prezygodiapophyseal and postzygodiapophyseal laminae and are essentially horizontal.

The neural arches of the dorsal vertebrae are strong and carry long, neural spines elongated anteroposteriorly. Pronounced lateral ridges (laminae?) developed at the co-ossification of the neural arches with the centra. The neural spines change in shape along the dorsal series. In the first two dorsal vertebrae the neural spines are plate-shaped, similar to those in posterior cervicals. The next three neural spines of dorsal vertebrae have anteroposteriorly narrowed dorsal ends, being inclined somewhat forward. Evidently, this reflects the upward curvature of the neck. Each of the remaining dorsal vertebrae has an anteroposteriorly widened, subquadrate spine. The last five of them show the neural spine slightly curved. The neural spines of the anterior and middle part of the dorsal series are almost equal in height, but they become gradually higher posteriorly, with the dorsal extremity enlarged and strongly thickened. The diapophyses of dorsal vertebrae are supported by anterior and posterior laminae. The laminae have their common origin at the base of the transverse process to the parapophyses (paradiapophyseal lamina) and the posteroventral junction of the neural arch with the centrum (posterior centrodiapophyseal lamina), respectively, from where they run obliquely downward. This system of laminae demarcates three deep cavities below the transverse process: infraprezygapophyseal fossa, infradiapophyseal fossa, and infrapostzygapophyseal fossa. Consequently, the last dorsal vertebra has well-developed buttresses below the parapophyses. The transverse processes in the presacral series increase gradually in length as far as to the eleventh dorsal vertebra. They decrease in length again from that point backward. Like the parapophyses, the diapophyses are oriented obliquely posteriorly except for the last dorsal vertebra, and in a few last dorsals the diapophyses are oriented obliquely dorsally. The diapophyses in the dorsal series form the articular surface of the tuberculum of the rib. In the more posterior region of the dorsal series, it consists of two elements, a short parapophysis for the capitulum and a diapophysis for the tuberculum of its rib.

The prezygapophyses extend beyond the anterior border of the centrum, they are inclined at a wide angle and face dorsomedially. The articular surfaces of prezygapophyses are anteroposteriorly elongated but decrease in length among the last dorsals. The postzygapophyses are short and inclined laterally. Accessory intervertebral articulations are present along the dorsal series. The hypantrum forms a vertical medial articular surface of the prezygapophyses, and the hyposphene constitutes a distinct vertical articular surface below the postzygapophyses.

Dorsal Ribs and Gastralia

Ribs (Figs. 5, 9) are best preserved in specimen ZPAL AbIII/1930 and relatively well recognizable in specimens ZPAL AbIII/361 and 362. The dorsal ribs are double-headed throughout the series. The first ten to eleven dorsal ribs are especially strong and long. Their slightly thickened distal ends suggest that in life they continued ventrally into cartilage. The remaining ribs narrow gradually towards their ends and become progressively shorter; the fourteenth dorsal being the last and shortest. The capitulum of the anterior dorsal ribs articulates with a prominent articulation surfaces of the parapophyses. With the change in the position of parapophyses and diapophyses along the series, the capitulum becomes shorter and the capitular and tubercular facets are more and more closely spaced. The capitulum of the posterior ribs connects with a single transverse process of their vertebrae. The tuberculum of the anterior dorsal ribs articulates in each case with a diapophysis. The tuberculum forms a prominent process on first four ribs, but in the following dorsal vertebrae it is a small facet, dorsolateral to the long capitular process. The rib shafts are usually long and relatively slender and curve gently inward.

Gastralia consist of four rows of slender subparallel rods. Rods of the two admedial rows are alternately fused at the ventral midline at an approximately right angle in groups of up to six.

← FIGURE 5. Restoration of ribs of *Silesaurus opolensis*; left lateral viev (except for D, G, I, where also dorsal view is given, and N, O shown in anterior view); based mostly on ZPAL AbIII/1930 and 361. **A**, 1st cervical; **B**, 2nd cervical; **C**, 3rd cervical; **D**, **N**, 4th cervical; **E**, 5th cervical; **F**, 6th cervical; **G**, 7th cervical; **H**, 1st dorsal; **I**, 2nd dorsal; **J**, **O**, 3rd dorsal; **K**, 4th dorsal; **L**, 5th dorsal; **M**, 6th dorsal.

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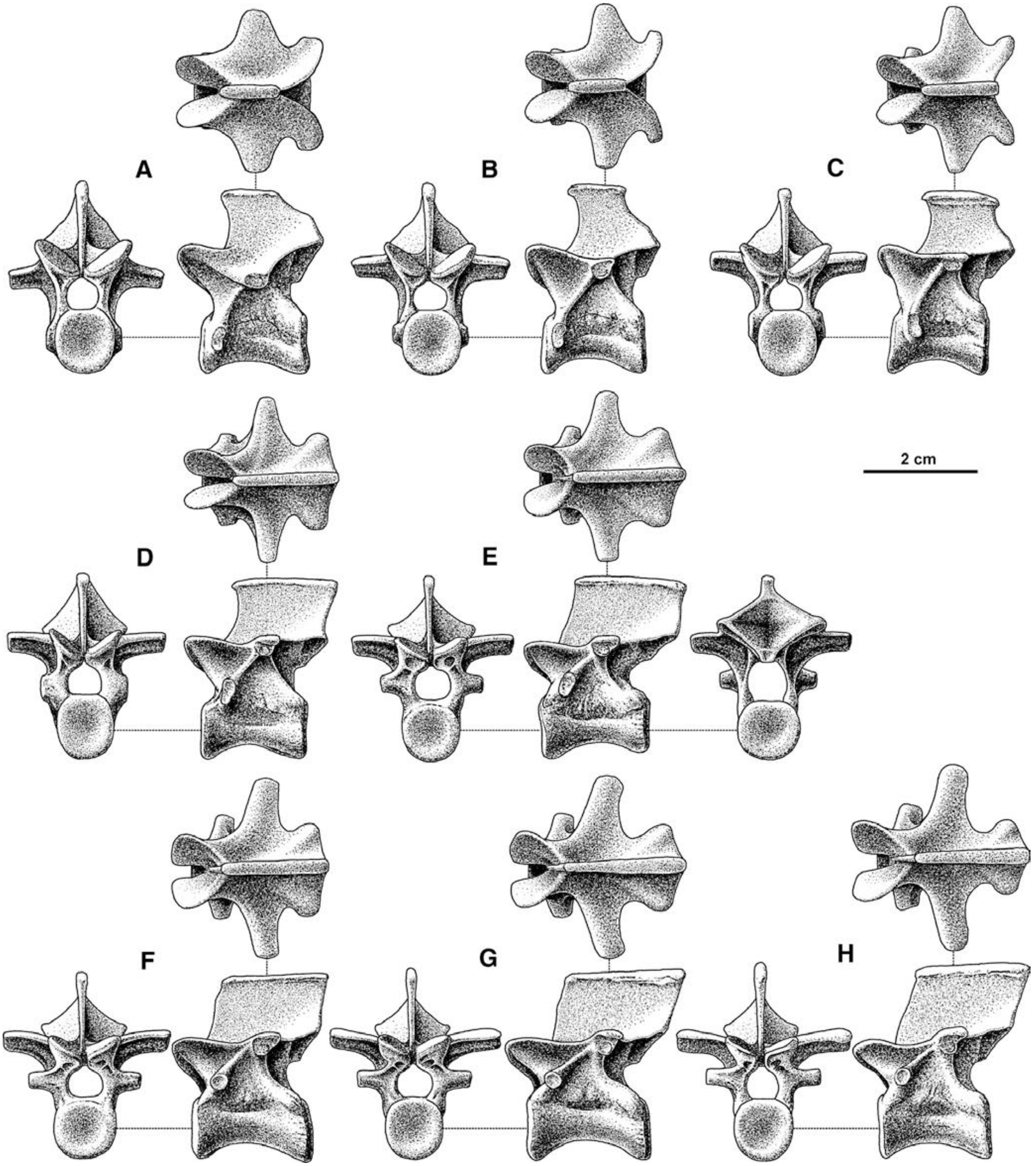

FIGURE 6. Restoration of presacral vertebrae of *Silesaurus opolensis*; dorsal, anterior and left lateral views (except for E, where also posterior view is given); based mostly on ZPAL AbIII/1930 and 361. **A**, 3rd dorsal; **B**, 4th dorsal; **C**, 5th dorsal; **D**, 6th dorsal; **E**, 7th dorsal; **F**, 8th dorsal; **G**, 9th dorsal; **H**, 10th dorsal.

Gastralia of the lateral rows are more slender in appearance, with acute tips. Their total width seems to equal that of the proximal ends of pubes. The original arrangement of gastralia seems to be strictly horizontal.

Sacral Vertebrae and Ribs

The sacral vertebrae are preserved in partially articulated skeletons of *Silesaurus* and as isolated specimens. The sacrum of *Silesaurus* is composed of four fused vertebrae. Three posterior

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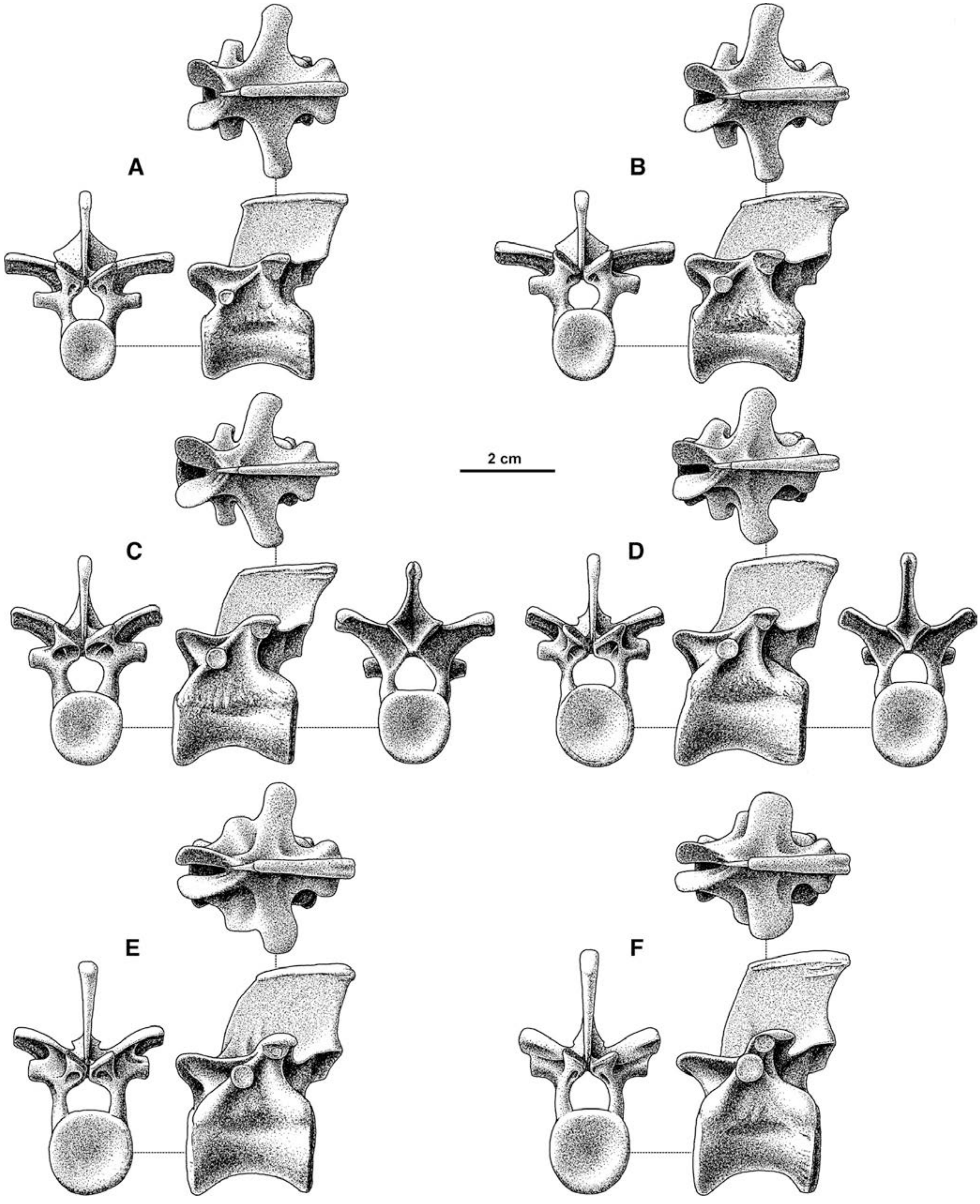

FIGURE 7. Restoration of presacral vertebrae of *Silesaurus opolensis*; dorsal, anterior and left lateral views (except for C, D, where also posterior view is given); based mostly on ZPAL AbIII/1930 and 361. **A**, 11th dorsal; **B**, 12th dorsal; **C**, 13th dorsal; **D**, 14th dorsal; **E**, 15th dorsal; **F**, 16th dorsal.

elements of the complex are broadly united to the ilia through robust ribs. The ribs are attached outwardly between the centra by two distinct structures, semioval in lateral aspects, broadly co-ossified with one another. The structure is homologous to the para- and diapophyses on the centrum and to corresponding capitula and tubercula in the ribs. The first sacral vertebra is placed behind the tip of the anterior iliac spine. This bone is morphologically similar to the preceding presacrals, except that it is firmly co-ossified with the rest of the sacrum and its neural spine is higher and more stout, with the dorsal extremity greatly thickened. The transverse processes and sacral ribs diverge from each other. The transverse processes of first sacral vertebra are anteroposteriorly narrow and buttressed ventrally by delicate thin laminae. The processes project anterolaterally to contact the ilia close to the iliac spine. This vertebra lacks a rib and thus may be considered a dorsosacral rather than a true sacral.

The second sacral vertebra has its broad transverse processes modified into wing-like structures that project anterolaterally. Similar structures are present in next sacral vertebrae but they are broad and oriented transversely. In the last sacral vertebra, an additional wing-like process extends posterodorsally; its centrum and neural arch are similar to those in proximal caudal vertebrae. All specimens show an extensive fusion of transverse processes and corresponding sacral ribs. The second sacral vertebra bears fan-like ribs broadly attached to the ilia, forming an anterior vertical blade.

The anterior blade of the sacral ribs extends backward ventrally forming a floor that connects the ribs of consecutive vertebra. The transverse processes and ribs of the third and fourth sacrals form an almost continuous floor. In the third sacral, a vertical blade is present; in the last sacral, it connects directly to the wing-like process.

The neural spines of the sacral vertebrae are high, stout, with the dorsal extremities greatly thickened and fused with each other dorsally. In all specimens, the posterior surface of the centrum of the last sacral vertebra is oblique, facing upwards.

Caudal Vertebrae

The holotype preserves 14 caudal vertebrae. The caudal vertebrae are preserved in partial articulation in specimens ZPAL AbIII/361 and 1930, and are represented by many isolated specimens. The proposed restoration of the tail is based on articulated sections fit together and on size gradation among isolated vertebrae (Figs. 8B, C, 9). The inferred number of caudal vertebrae is 33. The total number was probably closer to 35 or even 40, but remains conjectural.

The length of caudal vertebrae seems to be approximately uniform along the tail, slightly increasing only in the distal part of the tail. The vertebrae are amphicoelous, spool-shaped, and compressed transversely, as are all other vertebrae in *Silesaurus*. The articular surfaces of all caudal vertebrae are circular. An elliptical depression on the lateral surface of the centrum is present as far as to eighteenth caudal vertebra.

The neural spines of the anterior caudal vertebrae are oblique, very high, with the dorsal extremity thickened in the first three caudals, and are widened anteroposteriorly. In the succeeding vertebrae, the slender, oblique neural spines progressively decrease in height distally along the series. They are reduced to low crests in caudals 26 to 31. The anterior process of the neural spines extends upward, reaching its maximum size in eight caudal vertebrae. Neural spines are absent on the last caudal vertebrae.

The transverse processes are broad, wing-like, and horizontally oriented in most caudal vertebrae, reaching maximum length in second caudal vertebra. Distal to this vertebra, the transverse processes gradually decrease in length and on caudal vertebra 22 they are positioned on the centrum. From caudal vertebra 11, the transverse processes project anterolaterally, in contrast to the preceding caudals, where they project posterolaterally. The transverse processes are reduced to rounded promontories on caudal vertebra 24 and are absent on more posterior caudals. They remain only as longitudinal ridges on lateral faces of their centra. The pre- and postzygodiapophyseal laminae are weakly developed in anterior and middle caudals, similarly as the ridge-like anterior and posterior centrodiapophyseal laminae.

The prezygapophyses lie well above the centrum, placed close to the midline; in the anterior four caudals far from the centrum and transverse processes. Short prezygapophyses extend upward just beyond the centrum faces as far as in caudal vertebra 27. The zygapophyseal articulations are steeply inclined. In the following vertebrae the prezygapophyses significantly increase in their length, reaching maximum length at about caudal vertebra 27. Distal to this vertebra, their length slightly shortens again. Short postzygapophyses are adjusted to the articular surface of prezygapophyses, fitting the changes in their length. Ventral facets on adjoining centra jointly support a single chevron.

Chevrons are incompletely preserved only in the holotype. The first chevron is borne between the second and third caudal vertebrae. Chevrons of the second to fourth caudal vertebrae increase in length, but distal to that point, the chevrons progressively decrease in length and disappear at about caudal 26 or 27.

COMPARISON WITH POSSIBLY RELATED FORMS

There is some controversy regarding evolutionary meaning of buttressing apophyses of cervical vertebrae with prominent laminae, which is a feature of the vertebral column in *Silesaurus*. Wilson (1999) suggested that the distribution of vertebral laminae is generally restricted to saurischian dinosaurs because in the Ladinian *Marasuchu*s no laminae occur in cervicals and only in the ninth presacral vertebra two rudimentary laminae are present below the diapophysis (Sereno and Arcucci, 1994). However, well-defined laminae below diapophyses of dorsal vertebrae were present already in the poposaurids *Postosuchus* and *Sillosuchu*s (Chatterjee, 1985; Alcober and Parrish, 1997). The laminae may have developed earlier than in the Dinosauria and seem to be present (although often not described and variably developed) in many Triassic archosaurs (Gower, 2001; Nesbitt, 2005; Parker, 2008).

It is thus puzzling that vertebral laminae are absent on the vertebrae of ornithischian dinosaurs (Ostrom and McIntosh, 1966; Santa Luca, 1980; Norman, 1980; Brítt 1993). There is a rudimentary lamina below the transverse process of the dorsal vertebrae of some ornithischians, but this lamina does not reach the ventral margin of the neural arch (Norman, 1980; Galton and Powell, 1980). Probably the poor development of laminae in these dinosaurs is a secondary feature.

A deep postspinal fossa delimited by spinopostzygapophyseal laminae that extend between the postzygapophyses (Welles, 1984) in the cervical vertebrae in *Silesaurus* occurs also in *Staurikosaurus*, *Herrerasaurus*, and prosauropods (Zhang, 1988; Bonaparte, 1999; Yates, 2003a; Langer and Benton, 2006). A similar excavation is present in theropods (Madsen, 1976; Colbert, 1989; Madsen and Welles, 2000; Langer and Benton, 2006; Martínez et al., 2008) and some non-dinosaurian archosaurs, for example *Polonosuchus* (Sulej, 2007). No comparable cavity occurs in the basal ornithischians (Ostrom and McIntosh, 1966; Galton, 1974), most non-dinosaurian archosaurs (Ewer, 1965; Bonaparte, 1972, 1999; Chatterjee, 1978; Fraser et al., 2002; Ferigolo and Langer, 2007), or *Marasuchus* (Bonaparte, 1975; Sereno and Arcucci, 1994). This seems thus to be a primitive trait of *Silesaurus*, lost by the ornithischians together with laminae.

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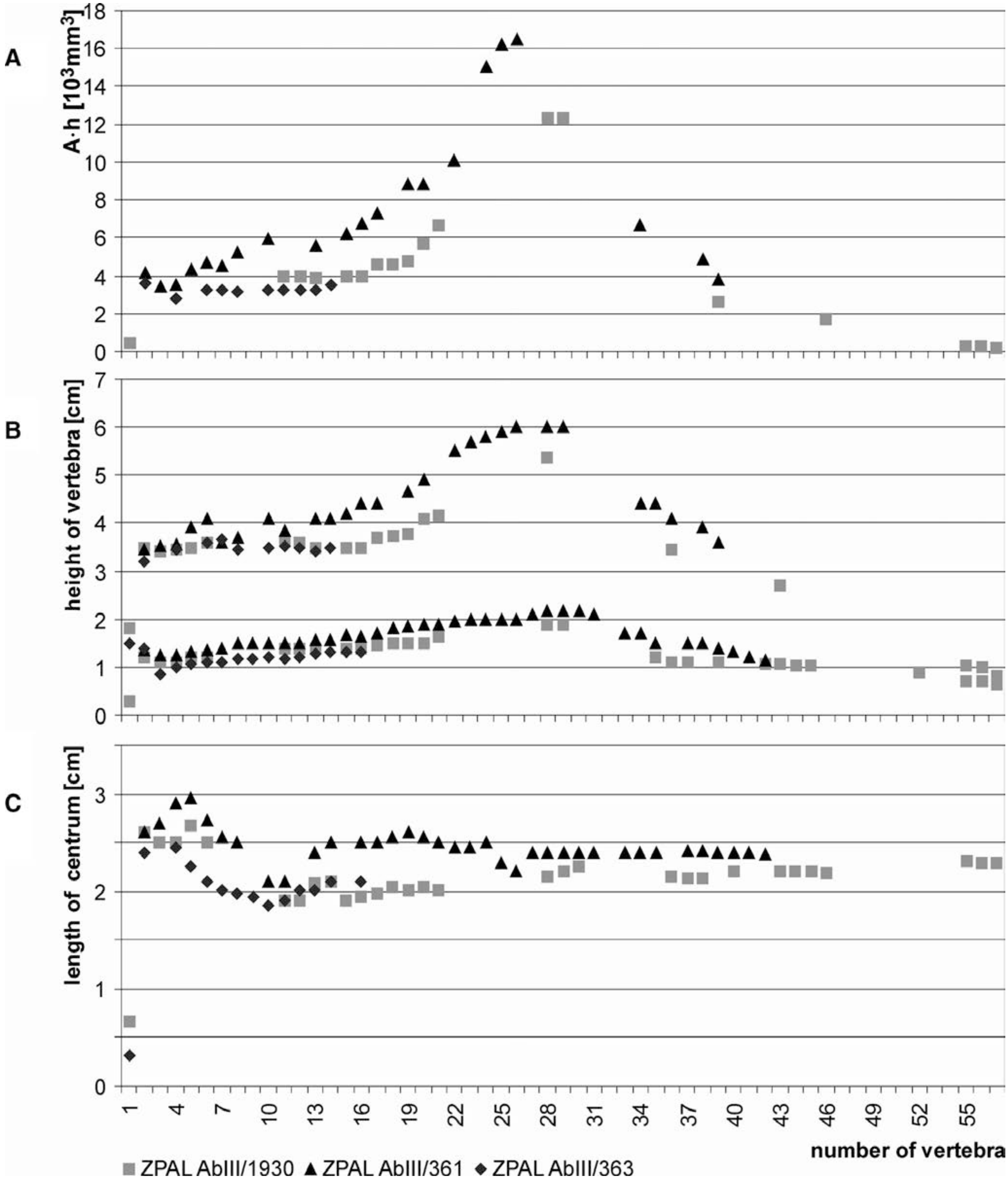

FIGURE 8. Measurements of vertebrae of *Silesaurus opolensis* from the early Late Triassic at Krasiejów near Opole, Poland; based on ZPAL AbIII/1930, 363, and 361. **A**, Changes in functionally important ratio between the area of the frontal surface of the centrum (A) and height of the vertebra measured from the middle of centrum to the tip of the spinal process (h). **B**, Changes in height of the centrum (lower series) and the complete height (upper series) along the vertebral column. Extent of the regions of vertebral column missing in some specimens was inferred from gradients in corresponding regions preserved in other articulated specimens. **C**, Changes in vertebral centrum length along the vertebral column of *Silesaurus opolensis*; based on ZPAL AbIII/1930, 363, and 361.

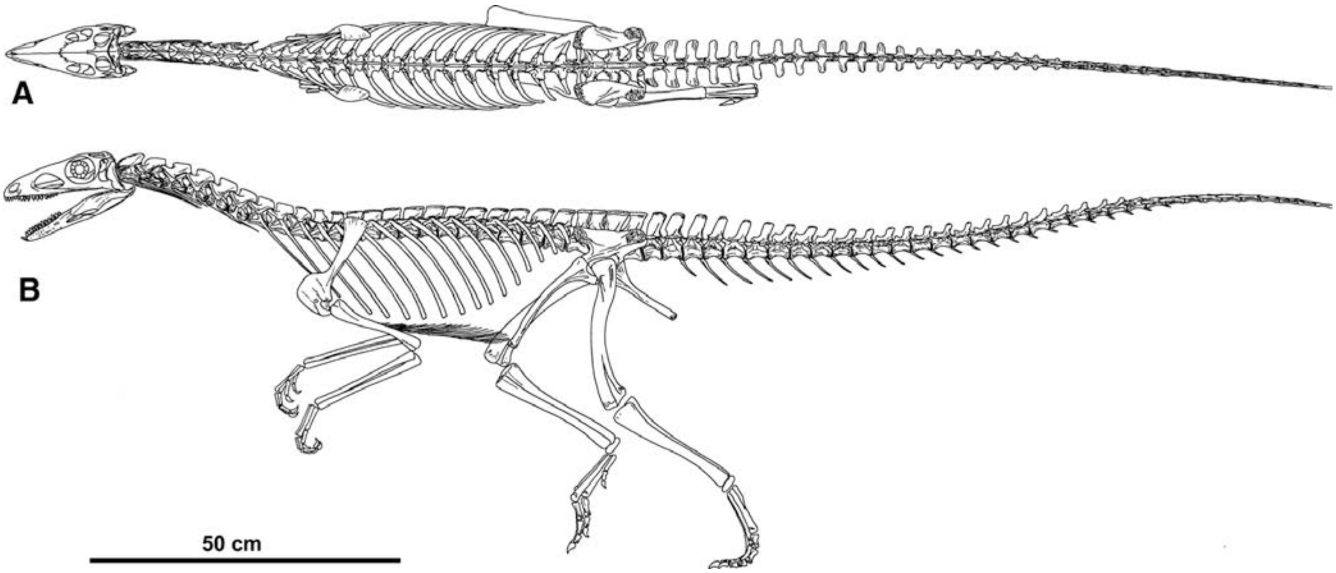

FIGURE 9. Restoration of the skeleton of *Silesaurus opolensis* from the early Late Triassic of Poland in facultative bipedal running pose; based mostly on ZPAL AbIII/1930 and 361.

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The neck of *Silesaurus* was slightly sigmoidal, with curvature presumably similar to that restored in *Coelophysis*, as suggested by a similar disposition of the cervical ribs (Colbert, 1989). The slightly parallelogram-shaped cervical centra are present as far posteriorly as the ninth presacral. This character seems to be weakly expressed in *Herrerasaurus* (Sereno and Novas, 1994) and *Marasuchus* (Sereno and Arcucci, 1994). Unfortunately, the neck anatomy is unknown in *Lagerpeton* (Arcucci, 1986; Sereno and Arcucci, 1994). It must remain unsettled whether the relatively straight neck of *Silesaurus* is a primitive trait or it is rather connected with secondary quadrupedality.

Long sub-parallel cervical ribs, similar to those of *Silesaurus*, are present in *Eoraptor* (Sereno et al., 1993). Cervical ribs of the Late Triassic dinosaurs are generally poorly known because few fossil specimens are preserved well enough to show their morphology and distribution. Probably they are best known is the Norian or Rhaetian *Coelophysis bauri* from the Chinle Formation of New Mexico (Colbert, 1989). The cervicals of *Coelophysis* are longer anteriorly and diminish in length posteriorly. Unlike *Silesaurus*, where the acute anterior process suddenly disappears behind the seventh vertebra, they gradually change toward the dorsals and the change is parallel to the shortening of the vertebral centra of the ninth and tenth cervicals, as interpreted by Colbert (1989:83). That is, the vertebrae change first, the ribs later, opposite to the condition in *Silesaurus*. Quite elongated cervical ribs are present also in prosauropods (Galton, 1976; He et al., 1988; Zhang, 1988; Langer and Benton, 2006; Galton, 2007) and basal theropods (Ostrom, 1978; Colbert, 1989; Rowe, 1989; Bonaparte et al., 1990; Harris, 1998; Martínez et al., 2008). In contrast, the cervical ribs of ornithischians (Galton, 1974; Santa Luca, 1980; Norman, 1986; Forster, 1990; Irmis et al., 2007a) are much shorter and protrude ventrally from the neck. Again, this may reflect change in flexibility of the neck in the evolution towards quadrupedality of ornithischians.

A sacrum comprising two vertebrae is the plesiomorphic condition for dinosaurs and other archosaurs (Walker, 1961; Ewer, 1965; Chatterjee, 1978; Bonaparte, 1984), including *Lagerpeton* and *Marasuchus*. In the evolution of the Dinosauria, the number of sacral vertebrae increased. In most dinosaurs, the sacrum is composed of three or more sacral vertebrae, as seen in basal ornithischians (Galton, 1974; Santa Luca, 1980; Langer and Benton, 2006; Nesbitt et al., 2007) and basal theropods (Raath, 1969; Welles, 1984; Colbert, 1989; Cuny and Galton, 1993; Langer and Benton, 2006). The sacrum of *Silesaurus* consists of four extensively fused vertebrae broadly attached to the ilia by three robust sacral ribs. Rather surprisingly, a similar condition is present in the Anisian *Bromsgroveia* (Galton, 1977; Galton and Walker, 1996; Benton and Gower, 1997); other poposaurid rauisuchians, such as *Effigia*, *Poposaurus*, and *Shuvosaurus*, also have four sacrals (Nesbitt, 2007; Weinbaum and Hungerbühler, 2007; Long and Murry, 1995).

In *Silesaurus,* three posterior elements of the fused complex of four vertebrae in the sacral region are broadly attached to the ilia by three robust sacral ribs. The ribs are attached outwardly between the centra. The first sacral vertebra is morphologically similar to the preceding presacrals. This similarity suggests that the last dorsal vertebra was incorporated into the sacrum. The last sacral vertebra shows an analogous condition: its centrum and neural arch are similar to those of the anterior caudal vertebrae. Perhaps the first caudal vertebra was incorporated into the sacrum.

The new morphological evidence presented in this paper does not provide anything that could affect the numerous cladistic analyses, in which data for *Silesaurus* were included (e.g., Langer and Benton, 1991; Irmis et al., 2007b; Martinez and Alcober, 2009).

FUNCTIONAL INTERPRETATION

The cervical vertebrae of *Silesaurus* bear prominent vertebral laminae, similar to those in long-necked dinosaurs (sauropodomorphs), although the neck of *Silesaurus* is relatively short. Comparable laminae are also present in short-necked theropods. Such laminae are usually interpreted as structural elements for resisting stress generated by movement of elongate neck or as osseous septa of pneumatic chambers (McIntosh, 1989; Wilson, 1999). The laminae are clearly aligned along principal axes of stress on the neural arches generated by muscle contraction (Herring, 1993; Carter et al., 1998). Ossification seems to be restricted to the laminae primarily as a measure to reduce weight of the skeleton. Schwarz at al. (2007) suggested that the laminae served to increase the attachment area of axial muscles. Some

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authors suggested that the prominent vertebral fossae housed an air sac system (e.g., O'Connor and Claessens, 2005; O'Connor, 2006) and in pneumatized vertebrae the laminae had a double function, separating the diverticula and providing surfaces for attachment for axial muscles. The air-sac system has been reconstructed for the common ancestor of pterosaurs and dinosaurs (e.g., Wedel, 2007; Butler et al., 2009). However, there is no evidence of pneumatization in *Silesaurus* (Dzik, 2003; Butler et al., 2009). The posterior chonos formed by laminae probably served for insertion of interarticular vertebral ligaments (Baumel and Raikow, 1993).

The enlarged dorsal extremities of the neural spines of the dorsal, sacral, and anterior caudal vertebrae in *Silesaurus* suggest that they afforded considerable surfaces for muscle attachments. The morphology of neural spines of dorsals 3 to 5 of *Silesaurus* suggests a raised, S-shaped neck posture. Sereno (1991) and other authors consider parallelogram-shaped cervical centra an adaptation for a flexed neck. Among the dinosaur vertebral columns measured by Christian and Preuschoft (1996) for proportions of vertebrae that are believed to be of functional importance in locomotion (Fig. 8A), the one most similar to *Silesaurus* is that of *Iguanodon* (Christian and Preuschoft, 1996:fig. 6), which had both bipedal and quadrupedal gait. Somewhat unexpectedly, that of the sauropod *Dicraeosoaurus* is also similar, although the tail of *Dicraeosaurus* was apparently shorter than that of *Silesaurus*.

Silesaurus had long, sub-parallel cervical ribs. Presumably, these ribs were flexible and their movement along the neck was possible to allow its bending, although at the same time they apparently served to strengthen the neck. Similarly, overlapping cervical ribs of sauropods are believed to have been connected with each other by intercostal ligaments that probably supported the neck (Martin et al., 1998; Schwarz et al., 2007). The gradual change in the morphology of the ribs and the position of the parapophyses at the neck-trunk transition corresponds to the change from the narrow neck to the broad thorax. It extends for several vertebrae, and there is no correspondence between the changes in the morphology of the vertebrae and the morphology of the ribs.

Gracile limbs similar to those in *Silesaurus* are typical of fast-running, quadrupedal animals (e.g., Schmidt and Fischer, 2009), but there is a remarkable disparity between its forelimbs and hind limbs. The forelimbs of *Silesaurus* are unusually gracile (despite their remarkable length), whereas the hind limbs are of proportions typical for the Triassic relatives of dinosaurs. This suggests a greater load on the pelvic girdle and the ability of *Silesaurus* to run bipedally on occasion. The relatively high spinal processes of vertebrae suggest well-developed musculature that enabled *Silesaurus* to carry all the body weight on its hind limbs (Christian and Preuschoft, 1996). Its long tail, considerably exceeding the length of the presacral series, probably formed a strong and flexible counterbalance to the weight of the body in front of the pelvis, although by itself it does not need to be connected functionally with facultative bipedality. In fact, the difference in skeletal proportions between quadrupedal and facultatively bipedal reptiles is usually minor (e.g., Snyder, 1954; Aerts et al., 2003).

CONCLUSIONS

New data on the vertebral column of *Silesaurus* provide some insight into the early evolution of this skeletal system within the dinosauromorph lineage. *Silesaurus opolensis* is one of the most completely known and important basal dinosauromorphs from anywhere in the world. The geological age of *Silesaurus* has been determined, based on associated fauna and flora, as late Carnian (Dzik and Sulej, 2007). Late Carnian strata in Italy, biostratigraphically correlated with Krasiejów, have yielded a radioisotopic age of 230.91 ± 0.33 Ma (Furin et al., 2006b). The Ischigualasto Formation, from which most information on probable early dinosaurs come, is radioisotopically dated at 227.8 ± 0.3 Ma (Rogers et al., 1993; but 230.3–231.4 according to Furin et al., 2006b:1011). *Silesaurus* is thus coeval with, possibly even slightly older than, the oldest known predatory and herbivorous dinosaurs, but only the significantly younger *Coelophysis* is represented by skeletons preserved well enough to provide comparable information on the axial skeleton (Colbert, 1989).

This makes it difficult to decide whether the peculiar disparity between the structural and functional neck-thorax transition in *Silesaurus* is a primitive or derived feature. More apparent is the meaning of the rather smooth gradient in functional aspects of the vertebrae, consistent with elongation of the forelimbs and the presence of three sacrals firmly connected by their ribs with the ilium. All these aspects of the skeleton suggest a secondarily quadrupedal stance and gait. The long tail of *Silesaurus*, providing a counterbalance to the weight of the body in front of the pelvis, as well as the disproportionally gracile forelimbs, suggest that *Silesaurus* retained the ability for fast bipedal running, retained from its *Marasuchus*-like dinosauromorph ancestors. Unfortunately, published data on species that might be closely related to *Silesaurus* are extremely scarce. Until additional reliable evidence is available, the exact phylogenetic position of *Silesaurus* must remain unresolved.

ACKNOWLEDGMENTS

Excavations at Krasiejów in 2006, led by Tomasz Sulej (Instytut Paleobiologi PAN, Warszawa), were partially financed by the borough of Ozimek. We are grateful for helpful comments on a draft of this paper by Richard J. Butler (Cambridge) and Stephen L. Brusatte (American Museum of Natural History, New York). Suggestions by anonymous reviewers improved the manuscript and are deeply appreciated.

LITERATURE CITED

Aerts, P., Van Damme, R., D'Aout, K., and Van Hooydonck, B. 2003. Bipedalism in lizards: whole-body modelling reveals a possible spandrel. Philosophical Transactions of the Royal Society of London B 358:525–1533.

Arcucci, A. 1986. Nuevos materiales y reinterpretation de *Lagerprton chanarensis* Romer (Thecodontia, Lagerpetontidae nov.) del Triasico medio de La Rioja, Argentina. Ameghiniana 23:233–242.

Baumel, J. J., and R. J. Raikow. 1993. Arthrologia; pp. 133–187 in J. J. Baumel (ed.) Handbook of Avian Anatomy: Nomina Anatomica Avium. Publications of the Nuttal Ornithological Club, Cambridge, U.K.

Benton, M. J., and D. J. Gower. 1997. Richard Owen's giant Triassic frogs: archosaurs from the Middle Triassic of England. Journal of Vertebrate Paleontology 17:74–88.

Bonaparte, J. F. 1972. Los tetrápodos del sector superior de la Formacion Los Colorados, La Rioja, Argentina (Triássico Superior). Opera Lilloana 22:1–183.

Bonaparte, J. F. 1975. Nuevos materiales de *Lagosuchus talampayensis* Romer (Thecodontia—Pseudosuchia) y su significado en el origin de los Saurischia. Chañarense inferior, Triasico Medio de Argentina. Acta Geologica Lilloana 13:5–90.

Bonaparte, J. F. 1984. Locomotion in rauisuchid thecodonts. Journal of Vertebrate Paleontology 3:210–218.

Bonaparte, J. F. 1999. Evolución de las vértebras presacras en Sauropodomorpha. Ameghiniana 36:115–187.

Bonaparte, J. F., J. Ferigolo, and A. M. Ribeiro. 1999. A new early Late Triassic saurischian dinosaur from Rio Grande do Sul State, Brazil. National Science Museum Monographs 15:89–109.

Bonaparte, J. F., F. E. Novas, and R. A. Coria. 1990. *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnosaur from the Middle Cretaceous of Patagonia. Natural History Museum of Los Angeles County, Contributions in Science 411:1–42.

Brítt, B. B. 1993. Pneumatic postcranial bones in dinosaurs and other archosaurs. Ph.D. dissertation, University of Calgary, Calgary, Alberta, 383 pp.

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Brusatte, S. L., M. J. Benton, M. Ruta, and T. Lioyd. 2008. Superiority, competition, and opportunism in the evolutionary radiation of dinosaurs. Science 302:1485–1488.

Butler, R. J., P. M. Barret, and D. J. Gower. 2009. Postcranial skeletal pneumaticity and air-sacs in the earliest pterosaurs. Biology Letters 5:557–560.

Carter, D. R., B. Mikie, and K. Padian. 1998. Epigenetic mechanical factors in the evolution of long bone epiphyses. Zoological Journal of the Linnean Society 123:163–178.

Chatterjee, S. 1978. A primitive parasauchid (phytosaur) reptile from the Upper Triassic Maleri Formation of India. Paleobiology 21:83–127.

Christian, A., and H. Preuschoft. 1996. Deducing the body posture of extinct large vertebrates from the shape of the vertebral column. Palaeontology 39:801–812.

Colbert, E. H. 1989. The Triassic dinosaur *Coelophysis*. Museum of Northern Arizona Bulletin 57:1–160.

Cooper, M. R. 1981. The prosauropod dinosaur *Massospondylus caritanus* Owen from Zimbabwe: its biology, mode of life and phylogenetic significance. Occasional Papers of the National Museums and Monuments of Rhodesia, series B, Natural Sciences 6:689–840.

Currie, P. J., and X. J. Zhao. 1994a. A new carnosaur (Dinosauria, Treropoda) from the Jurassic of Xinjiang, People's Republic of China. Canadian Journal of Earth Sciences 30:2037–2081.

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

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

Dzik, J., and T. Sulej. 2007. A review of the Early Late Triassic Krasiejów biota from Silesia, Poland. Palaeontologia Polonica 64:1–27.

Ewer, R. F. 1965. The anatomy of the thecodont reptile *Euparkeria capensis* Broom. Philosophical Transactions of the Royal Society of London B 248:379–435.

Ezcurra, M. D. 2006. A review of the systematic position of the dinosauriform archosaur *Eucoelophysis baldwini* Sulivan & Lucas, 1999 from the Upper Triassic of New Mexico, U.S.A. Geodiversitas 28:649–684.

Ferigolo, J., and M. C. Langer, 2007. A late Triassic dinosauriform from south Brazil and the origin of the ornithischian predentary bone. Historical Biology 19:23–33.

Forster, C. T. 1990. The postcranial skeleton of the ornithopod dinosaur *Tenontosaurus tilletti*. Journal of Vertebrate Paleontology 10:273–294.

Fraser, N. C., K. Padian, G. M. Walkden, and A. L. M. Davis. 2002. Basal dinosauriform remains from Britain and the diagnosis of the Dinosauria. Palaeontology 45:79–95.

Furin, S., N. Preto, M. Rigo, G. Roghi, P. Gianolla, J. L. Crowley, and S. A. Bowring. 2006. High-precision U-Pb zircon age from the Triassic of Italy: implications for the Triassic time scale and the Carnian origin of calcareous nannoplankton and dinosaurs. Geology 34:1009–1012.

Galton, P. M. 1974. The ornithischian dinosaur *Hypsilophodon* from the Wealden of the Isle of Wight. Bulletin of the British Museum of Natural History (Geology) 25:1–152.

Galton, P. M. 1976. Prosauropod dinosaur (Reptilia: Saurischia) of North America. Postilla 169:1–98.

Galton, P. M. 1977. On *Staurikosaurus pricei*, an early saurischian dinosaur from the Triassic of Brazil, with notes on the Herrerasauridae and Poposauridae. Paläontologische Zeitschrift 51:234–245.

Galton, P. M., and H. P. Powell. 1980. The ornithischians dinosaur *Camptosaurus prestwichii* from the Upper Jurassic of England. Palaeontology 23:411–443.

Galton, P. M., and A. D. Walker. 1996. *Bromsgroveia* from the Middle Triassic of England, the earliest record of a poposaurid thecodontian reptile (Archosauria: Rauisuchia). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 201:303–325.

Gower, D. J. 2001. Possible postcranial pneumaticity in the last common ancestor of bidrs and crocodilians: evidence from *Erythrosuchus* and other Mesozoic archosaurs. Naturwissenschaften 88:119–121.

Harris, J. D. 1998. A reanalysis of *Acrocanthosaurus atokensis*, its phylogenetic status, and paleobiogeographic implications, based on a new specimen from Texas. Bulletin of the New Mexico Museum of Natural History and Science 13:1–75.

He, X., K. Li, and K. Cai. 1988. The Middle Jurassic Dinosaurian Fauna from Dashanpu, Zigong, Sichuan: Sauropod Dinosaurs (2) Omeisaurus tanfuensis. Sichuan Scientific and Technological Publishing House, Chengdo, 145 pp.

Herring, S. W. 1993. Epigenetic and functional influences on skull growth; pp. 153–206 in J. Hanken and B. K. Hall (eds.). The Skull, Volume 1. University of Chicago Press, Chicago and London.

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

Irmis, R. B., W. G. Parker, S. J. Nesbitt, and J. Liu. 2007a. Early ornitischian dinosaurs: the Triassic record. Historical Biology 19:3–22.

Irmis, R. B., S. J. Nesbitt, K. Padian, N.D. Smith, A.H. Turner, D. Woody, and A. Downs. 2007b. A late Triassic dinosauromorph assemblage from New Mexico and the rise of dinosaurs. Science 317:358–361.

Langer, M. C., and M. J. Benton. 2006. Early dinosaurs: a phylogenetic study. Journal of Systematics Paleontology 4:309–358.

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

Martin, J., V. Martin-Rolland, and E. Frey. 1998. Not cranes or masts, but beams: the biomechanics of sauropod necks. Oryctos 1:113–120.

Martínez, R. N., P. C. Sereno, and O. A. Alcober. 2008. A new basal theropod from the Ischigualasto Formation of San Juan Province, Argentina; p. 153 in Libro de Resúmenes, III Congreso Latinoamericano de Paleontología de Vertebrados, Neuquén, Patagonia, Argentina.

Madsen, J. H. 1976. *Allosaurus fragilis*: a revised osteology. Utah Geological Survey Bulletin 109:3–163.

Madsen, J. H., and S. P. Welles. 2000. Ceratosaurus (*Dinosauria*, Theropoda); A Revised Osteology. Utah Geological Survey Miscellaneous Publication 00–2:1–80.

McIntosh, J. S. 1989. The sauropod dinosaurs: a brief survey; pp. 85–99 in K. Padian and D. J. Chure (eds.), The Age of Dinosaurs. Short Courses in Paleontology Number 2. University of Tennessee, Knoxville, Tennessee.

Nesbitt, S. J. 2005. The osteology of the pseudosuchian *Arizonasaurus babbitti*. Historical Biology 17:19–47.

Nesbitt, S. J., 2007. The anatomy of *Effigia okeeffeae* (Archosauria, Suchia), theropod-like convergance, and the distribution of related taxa. Bulletin of the American Museum of Natural History 302:1–84.

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

Norman, D. B. 1980. On the ornithischian dinosaur *Iguanodon bernissartensis* from the Lower Cretaceous of Bernissart (Belgium). Institute Royale de Sciences Naturelles de Belgique Mémoire 178:1–103.

Norman, D. B. 1986. On the anatomy of *Iguanodon atherfieldiensis* (Ornithischia: Ornithopoda). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique: Sciences de la Terre 56:281–372.

O'Connor, P. 2006. Postcranial pneumaticity: an evaluation of soft-tissue influences on the postcranial skeleton and the reconstruction of pulmonary anatomy in archosaurs. Journal of Morphology 267:1199–1226.

O'Connor, P., and L. Claessens. 2005. Basic avian pulmonary design and flow-through ventilation in non-avian theropod dinosaurs. Nature 436:253–256.

Ostrom, J. H. 1978. The osteology of *Compsognathus longipies* Wagner. Zitteliana 4:73–118.

Ostrom, J. H., and J. S. McIntosh. 1966. Marsh's Dinosaurs. Yale University Press, New Haven, Connecticut, 388 pp.

Parker, W. G. 2008. Description of new material of the aetosaur *Desmatosuchus spuriensis*. PaleoBios 28:1–40.

Parker, W. G., R. B. Irmis, S. J. Nesbitt, J. W. Martz, and L. S. Browne. 2005. The Late Triassic pseudosuchian *Revueltosaurus callendri* and its implications for the diversity of early ornithischian dinosaurs. Proceedings of the Royal Society of London Series B 272:963–969.

Raath, M. A. 1969. A new coelurosaurian dinosaur from the Forest Sandstone of Rhodesia. Arnoldia 4:1–25.

Rogers, R. R., C. Swisher III, P. C. Sereno, A. M. Monetta, C. A. Forster, and R. N. Martínez. 1993. The Ischigualasto tetrapod assemblage (Late Triassic, Argentina) and ^{40}Ar/^{39}Ar dating of dinosaur origins. Science 260:794–797.

Rowe, T. 1989. A new species of the theropod dinosaur *Syntarsus* from the Early Jurassic Kayenta Formation of Arizona. Journal of Vertebrate Paleontology 9:125–136.

Santa Luca, A. P. 1980. The postcranial skeleton of *Heterodontosaurus tucki* (Reptilia, Ornithischia) from the Stormberg of South Africa. Annals of the South African Museum 79:159–211.

Schmidt, M., and M. S. Fischer. 2009. Morphological integration in mammalian limb proportions: dissociation between function and development. Evolution 63:749–766.

Schwarz, D., E. Frey, and C.A. Meyer. 2007. Pneumaticity and soft-tissue reconstructions in the neck of diplodocid and dicraeosaurid sauropods. Acta Palaeontologica Polonica 52:167–188.

Sereno, P. C., and A. B. Arcucci. 1994. Dinosaurian precursors from the Middle Triassic of Argentina: *Marasuchus lilloensis*, gen. nov. Journal of Vertebrate Paleontology 14:53–73.

Sereno, P. C., and F. E. Novas. 1994. The skull and neck of the basal theropod *Herrerasaurus ischiqualastensis*. Journal of Vertebrate Paleontology 13:451–476.

Sereno, P. C., C. A. Forster, R. R. Rogers, and A. M. Monetta. 1993. Primitive dinosaur skeleton from Argentina and the early evolution of Dinosauria. Nature 361:64–66.

Snyder, R. C. 1954. The anatomy and function of the pelvic girdle and hindlimb in lizard locomotion. American Journal of Anatomy 95:1–14.

Sulej, T. 2007. A new rauisuchian reptile (Diapsida: Archosauria) from the Late Triassic of Poland. Journal of Vertebrate Paleontology 25:78–86.

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

Welles, S. P. 1984. *Dilophosaurus wetherilli* (Dinosauria, Theropoda), osteology and comparisons. Palaeontographica Abteilung A 185:85–180.

Wedel, M. 2007. What pneumaticity tells us about 'popsauropods', and vice versa. Special Papers in Paleontology 77:207–222.

Wedel, M. 2009. Evidence for bird-like air-sacs in saurischian dinosaur. Journal of Experimental Zoology 311A:611–628.

Weinbaum, J. C., and A. Hungerbühler. 2007. A revision of *Poposaurus gracilis* (Archosauria, Suchia) based on two new specimens from the Late Triassic of the southwestern U.S.A. Paläontologische Zeitschrift 81:131–145.

Wilson, J. A. 1999. A nomenclature for vertebral laminae in sauropods and other saurischian dinosaurs. Journal of Vertebrate Paleontology 19:639–653.

Yates, A. M. 2003. A new species of the prosauropod dinosaur *Thecodontosaurus* (Saurischia: Sauropodomorpha) and its implications for the systematics of early dinosaurs. Journal of Systematic Palaeontology 1:1–42.

Zhang, Y. 1988. The Middle Jurassic dinosaur fauna from Dashanpu, Zigong, Sichuan. Journal of the Chengdu College of Geology 3:1–87.

Submitted July 17, 2009; accepted January 4, 2010.

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