A BEAKED HERBIVOROUS ARCHOSAUR WITH DINOSAUR AFFINITIES FROM THE EARLY LATE TRIASSIC OF POLAND

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ABSTRACT—An accumulation of skeletons of the pre-dinosaur *Silesaurus opolensis*, gen. et sp. nov. is described from the Keuper (Late Triassic) claystone of Krasiejów in southern Poland. The strata are correlated with the late Carnian Lehrberg Beds and contain a diverse assemblage of tetrapods, including the phytosaur *Paleorhinus*, which in other regions of the world co-occurs with the oldest dinosaurs. A narrow pelvis with long pubes and the extensive development of laminae in the cervical vertebrae place *S. opolensis* close to the origin of the clade Dinosauria above *Pseudolagosuchus*, which agrees with its geological age. Among the advanced characters is the beak on the dentaries, and the relatively low tooth count. The teeth have low crowns and wear facets, which are suggestive of herbivory. The elongate, but weak, front limbs are probably a derived feature.

INTRODUCTION

As is usual in paleontology, with an increase in knowledge of the fossil record of early archosaurian reptiles, more and more lineages emerge or extend their ranges back in time. It is now clear that dinosaurs already reached a significant diversity before the end of the Triassic (e.g., Sereno, 1997; Buffetaut et al., 2000). Numerous findings prove this, but in most cases the fossils are fragmentary and poorly dated. Age correlation of faunas from different regions is based on rather few shared tetrapod genera, although a reference standard for the succession of assemblages is being developed (e.g., Heckert and Lucas, 1999). A direct biostratigraphic correlation with the marine standard is possible only in the Late Triassic of the Germanic Basin, even if the accessible precision in that region is far from what is needed. The recently discovered fossil locality at Krasiejów in southern Poland is located within this basin (Dzik et al., 2000; Dzik, 2001). The co-occurrence of the phytosaur *Paleorhinus* and the temnospondyl amphibian *Metoposaurus* makes possible correlation with the oldest dinosaur-bearing strata elsewhere (Heckert and Lucas, 1999). Recent excavations in the exposure have yielded rich and well preserved fossil material of a new archosaurian species, including several articulated skeletons that permit a virtually complete restoration of the skeleton. Fragmentary bones of this species have already been reported as a herrerasaurid-like archosaur from this locality (Dzik, 2001).

If the correlation of the oldest dinosaur faunas proposed by Heckert and Lucas (1999) is correct, then the Krasiejów species would be coeval with the other oldest known dinosaurs. According to these authors, the Ischigualasto and upper Santa Maria Formations that yielded the oldest South American dinosaurs correspond in age to the lower Chinle Group of the southwestern U.S.A. Only fragmentary dinosaur remnants from the Salitral Formation of New Mexico and the Popo Agie Formation of Wyoming (see also Heckert et al., 2000) precede them temporally. These co-occur with the phytosaur *Paleorhinus*, which makes them coeval with similarly controversial fragmentary dinosaur remains from the Maleri Formation of India. All these strata are of late Carnian age.

There are claims that dinosaurs already occurred in the early Carnian. The age was proposed for the fragmentary remains of prosauropods from the Isalo II site of Madagascar (Flynn et al., 1999). This contrasts with a rather advanced dental morphology of one of the Madagascar prosauropods, which has well developed nutrient foramina in its maxilla. It is closely related to *Azendohsaurus* from the Argana Formation of Morocco (Gauffre, 1993). The Argana Formation also has *Paleorhinus*, along with other phytosaurs more advanced than those from Krasiejów (see Dutuit, 1977), and it is likely to be somewhat younger. A co-occurrence of dinosaurs with dicynodonts and rhynchosaurs, similar to those of Madagascar, is also known for the upper part of the Santa Maria Formation of Brazil (Langer et al., 1999; Galton, 2000a:418). The Krasiejów findings are thus important, not only because of the anatomical evidence they offer, but also because of their geological age.

Repository abbreviation—ZPAL, Institute of Paleobiology of the Polish Academy of Sciences in Warsaw, Poland.

GEOLOGICAL SETTING

The Krasiejów fossil site is located in a clay pit belonging to the nearby cement plant Strzelce Opolskie near Opole in southern Poland. The red-colored middle Keuper marly claystone crops out there. Boreholes show that the excavated strata are located about 80 m above the Schilfsandstein marker horizon. In southern Germany, the Carnian-Ladinian boundary has been identified immediately above the Bleiglanzbank marker horizon, well below the Schilfsandstein, on the basis of the hypothesized phyletic evolution of a Tethyan bivalve lineage (Urlichs and Tichy, 2000). Based on their position in the lithostratigraphic column, the Krasiejów strata seem to be roughly coeval with the Lehrberg beds in Germany, which probably terminate the Carnian sedimentary cycle initiated by the Schilfsandstein (Aigner and Bachmann, 1998).

Virtually all the vertebrate fossil material from Krasiejów has been collected from two beds. The lower fossiliferous horizon (Fig. 1A) extends over the whole quarry with a rather uniform thickness of about 1 m (Dzik et al., 2000). It has yielded abundant cranial and postcranial material of metoposaurs and phytosaurs. Aetosaurs, capitosauroid temnospondyls, and the new archosaur, which is the subject of the present study, are also present but rare. Ganoid and dipnoan fishes also occur. Invertebrates are represented mostly by abundant unionid bivalves and rare conchostracans. Among microfossils, characean oogonia are dominant, being extremely common in the clay. All this suggests a lacustrine sedimentation episode, preceded and succeeded by a deltaic sedimentary regime (Dzik et al., 2000).

The temnospondyl *Metoposaurus* found at Krasiejów (Dzik et al., 2000) is probably conspecific with, or at least closely

related to, *M. diagnosticus*, that occurs in Germany in the Schilfsandstein and in overlying strata above it. The phytosaurs belong to a species of *Paleorhinus* (Dzik, 2001), geologically the oldest and anatomically the least derived of phytosaurs (Buffetaut, 1993; Long and Murry, 1995). The oldest German phytosaur, *Paleorhinus broili*, comes from the Blasensandstein of Franconia (Kuhn, 1933, 1936), a time equivalent of the Kieselsandstein in Baden-Württemberg, which overlies the Lehrberg beds. The co-occurrence of *Metoposaurus* and *Paleorhinus* is consistent with a lithologically based correlation with the Lehrberg Beds of Germany and indicates that chronologically the Krasiejów fauna belongs to the lower, late Carnian part of the *Paleorhinus* biochron in the North American standard of Hunt and Lucas (1991; Lucas, 1998).

A calcareous grainstone bed of varying thickness terminates the sedimentation of claystone with abundant fossil bone occurrences. However, an incomplete, partially articulated skeleton of the rauisuchian *Teratosaurus* and an isolated humerus of a bipedal archosaur have been found 0.8 m above the grainstone bed.

The upper fossiliferous horizon was identified about 7 m above the lower one during excavations in 2000. It is restricted spatially to an area about 30 m wide in the NE corner of the clay pit and it was excavated to its northern limit. It is unclear whether the fossil occurrences extend northward or not. The horizon is a horizontal claystone bed overlying an obliquely stratified mudstone sequence with locally developed calcareous grainstone beds and lenses. Above the clay, which contains rare bivalve shells and innumerable charophyte oogonia, an unstratified clay-like rock resembling synsedimentary breccia is exposed, covered by a Quaternary sand. Partially disarticulated skeletons occur at the base of the clay sequence, at the boundary between the obliquely stratified gray calcareous quartz mudstone and the variegated claystone.

Unlike the lower fossiliferous Krasiejów horizon, the fossil assemblage of the upper horizon is dominated by terrestrial reptiles and capitosauroid amphibians that were less well adapted to aquatic life than the underlying metoposaurids. This terrestrial faunal association, as well as the lithology and scarcity of aquatic invertebrates and algae to the rock, suggests that this is a flood deposit. In the relatively small area of excavation, several disarticulated skeletons of a large-sized species of the aetosaur *Stagonolepis* have been found, along with skulls and pelvic girdle bones of the amphibian *Cyclotosaurus*, teeth and bones of the rauisuchian *Teratosaurus* (T. Sulej, pers. comm.), and the skeletons which are the subject of this study. Phytosaur remains are rare and fragmentary (probably *Paleorhinus*), and metoposaurids seem to be absent.

All the articulated specimens described in this paper, and most of the referred isolated bones, were found close to the western margin of the fossiliferous field, but several isolated bones were scattered in other parts of the lower fossiliferous horizon (Fig. 1B). The largest accumulation of skeletons is virtually monospecific; only a single serrated tooth, probably of *Teratosaurus*, has been found in association with them. Somewhat east of the field, an accumulation of large *Cyclotosaurus* specimens was found in the grey quartz mudstone. In the central part of the field, bones of the aetosaur *Stagonolepis* dominate, preserved in a red claystone. Articulated portions of the skeletons of the new archosaur are invariably oriented E–W. In the most complete of them (ZPAL Ab III/361; Figs. 1C, 2), the tail was disarticulated at the base and displaced parallel to the neck, both these parts of the vertebral column lying eastward of the pelvis. Apparently the pelvis, being the heaviest part of the body, dragged behind the rest of the skeleton, which was displaced eastwards by the current. This is consistent with the inclination of laminae in the rock. The fossiliferous stratum wedges out just west of the dinosaur skeletons, and was prob-

ably the margin of a depression in which the bone-bearing sediment was deposited. Presumably the capitosaur bones, the new archosaur skeletons, and the aetosaur bones represent successive waves of sediment accumulating from west to east, so they did not necessarily live together at the same time.

All the vertebrate species found in the upper fossiliferous horizon also occur in the lower horizon. This, and the relatively close proximity of both horizons, as compared with the thickness of the whole Late Triassic succession, suggest that the two horizons represent different environments of virtually the same geological age.

METHODS

The excavations of both fossiliferous horizons in the Krasiejów clay pit were done in the same manner. A rectangular network of 1-m-wide trenches were dug 3 m apart to allow drainage of rain water (Fig. 1B). The trenches were deep enough to reach the base of the fossiliferous bed. In the case of the lower horizon, this was a thin grainstone intercalation with a yellow lamina separating the grey fossiliferous claystone from the underlying red mudstone (see Dzik et al., 2000). A grey calcareous quartz mudstone marks the base of the upper horizon. Bones had already been removed at this stage. Whenever an articulated skeleton was reached, the trench was expanded laterally. If no articulated material was found, the elevations separating trenches were removed later on.

The claystone and mudstone exposed at Krasiejów are soft and easily disintegrate in water. This makes the fossils prone to destruction by weathering. The upper horizon was just below the soil, so grass roots penetrated fissures in some of the bones. Specimens found loose are invariably fragmentary, even if preserved in limestone concretions or within the grainstone beds. Therefore, special efforts had to be undertaken to protect the fossils during excavation. Specimens preserved in claystone without a limestone crust were impregnated with dilute cyanoacrylic glue while being exposed from above. Isolated bones were then usually removed intact from the rock. More fragile specimens and articulated skeletons were covered from above with plaster. The first thin layer was made of plaster with talc added. As usual in such cases, several layers of cotton fabric immersed in plaster followed, with a wooden frame if necessary to make the construction sufficiently rigid. The block was then undercut and removed. In the laboratory, the rock matrix was removed until only the bones and plaster were left.

The locally thicker limestone crust was removed mechanically and the final cleaning of the bone was done with dilute formic acid. Fragile parts of the bones were impregnated with cyanoacrylic glue. If necessary, particular bones can be easily removed from the soft first plaster layer.

MATERIAL

More than four hundred bones have been collected, some found in close proximity to one another or even in articulation. Four partially articulated skeletons were removed intact from the rock.

The skeleton ZPAL Ab III/361 (Fig. 2) includes a crushed skull with its bones dispersed over a large area; the right quadrate was located among the dorsal vertebrae. The vertebral column is broken in a few places, but all presacral vertebrae seem to be represented. Of the pectoral girdle, only the right scapulocoracoid is present, associated with radii and ulnae (150 mm) of both limbs still in articulation. The right humerus (136 mm long) is preserved. The left humerus, measuring 138 mm, is displaced together with the right ischium, and both are preserved on another plaster slab in proximity to specimen ZPAL Ab III/362 (Fig. 3). Other bones of the pelvis are only slightly displaced. The left pubis, 160 mm long, is in articulation with
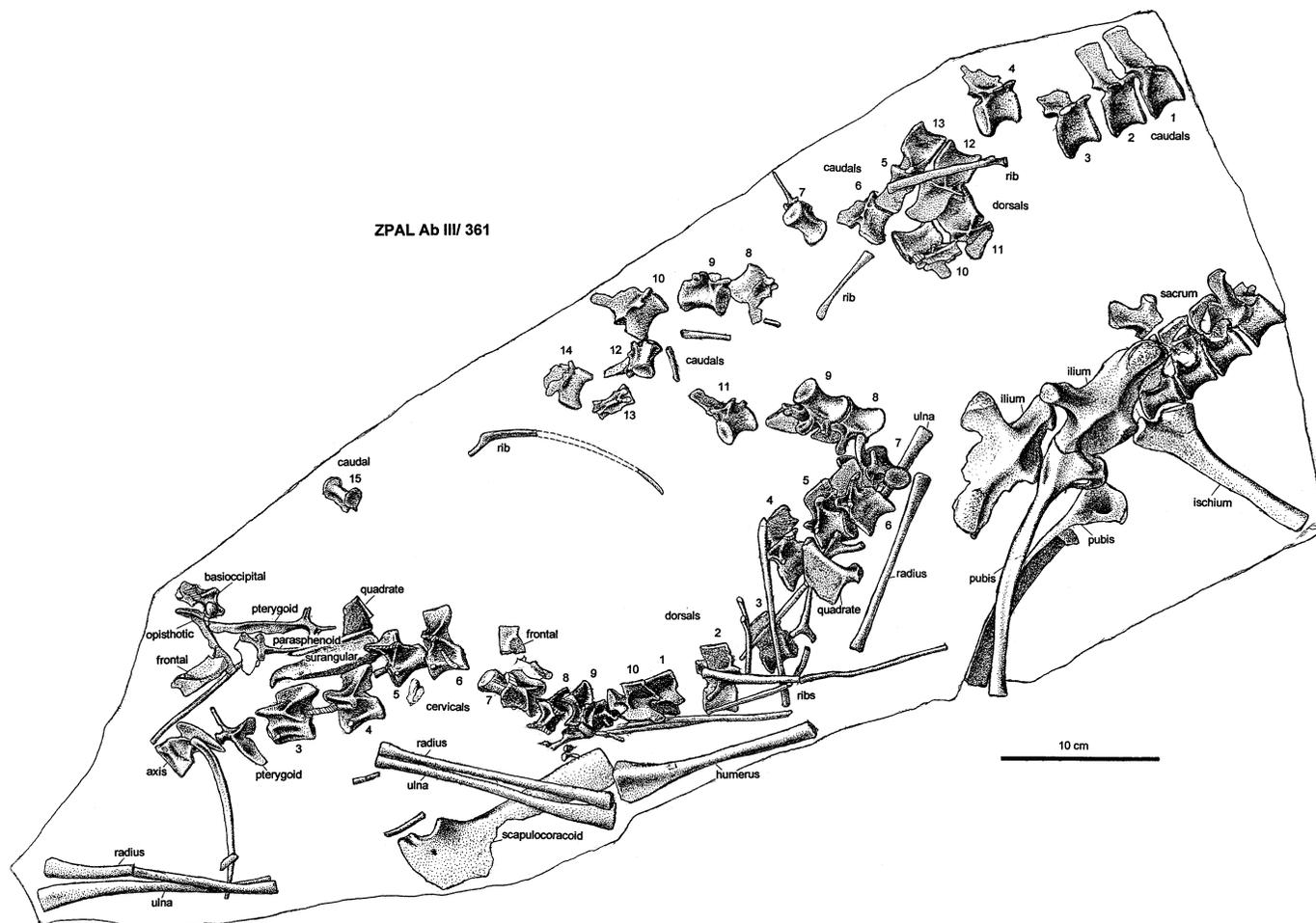
FIGURE 2. Diagrammatic drawing of *Silesaurus opolensis* bones in holotype slab ZPAL Ab III/361 in basal view, squares 21a, 22a. 27a, and 28a of the upper horizon in Krasiejów near Opole, Poland. Note that the radius and ulna in the center of the slab belong to specimen from slab ZPAL Ab III/362 (see Fig. 3).

the ilium. The associated ischium is 120 mm long. Both hind limbs are represented by disarticulated bones found outside the monolith (Fig. 1C). The processes of sacral rib 2 are well preserved. Only the proximal part of the tail is present; the rest was apparently broken off at its base and displaced. As no other vertebra was found outside the monolith in proximity to the pelvis (see Fig. 1C), it seems that all the proximal caudals are represented. The bones that are not covered with a limestone crust are crushed. Only a few ribs are reasonably well preserved, and all are more or less displaced from their original places of articulation.

The skeleton ZPAL Ab III/362 (Fig. 3) was found in proximity to the one described above, parallel to it but facing in the opposite direction (Fig. 1C). This specimen is smaller than ZPAL Ab III/361 but mature, as shown by the completely co-

ossified vertebral arches and centra. It is mostly disarticulated, and the braincase is the only part of the skull which can be identified (Fig. 3). The pectoral girdle is represented by the right scapulacoracoid (121 mm) and the left scapula, two humeri 116 mm long (note that the third one preserved on the same slab, of larger size, belongs probably to ZPAL Ab III/361) and a radius and ulna (119 mm long) displaced intermixed with bones of ZPAL Ab III/361 (near ilium). Only a few vertebrae and ribs are preserved. The pelvic girdle shows the sacral vertebrae still in articulation with the ilia, and associated with the pubes and ischia, which are displaced and deformed. Both humeri are preserved. The right one is almost in articulation with the radius and ulna, which are preserved in association. A group of vertebrae preserved outside the monolith (Fig. 1C, lower left corner) may or may not belong to the skeleton ZPAL Ab III/361.

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FIGURE 1. Fossil locality of *Silesaurus opolensis* from the early Late Triassic of Krasiejów near Opole, southern Poland. **A**, diagrammatic presentation of the NE corner of the Krasiejów clay pit and the location of excavation trenches in 2000 (see also Dzik et al., 2000 and Dzik, 2001). **B**, numbering of squares in the upper fossiliferous horizon, with position of trenches illustrated in **A** (the fossiliferous rock has been subsequently completely removed). **C**, the largest accumulation of *Silesaurus* bones and spatial relationship between two monoliths taken from this place (plaster slabs seen from the base, note reversal with respect to **B**).
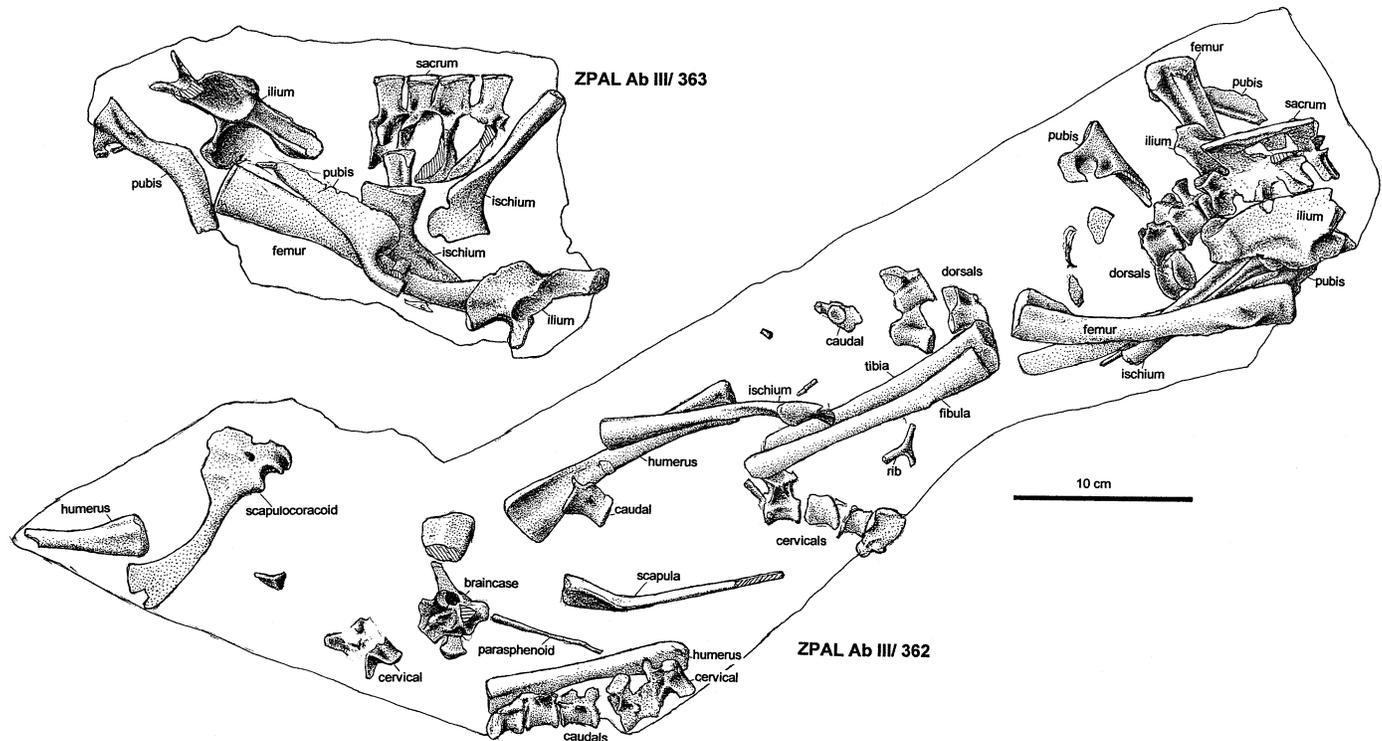
FIGURE 3. Diagrammatic drawing of *Silesaurus opolensis* bones in slab ZPAL Ab III/362, squares 27a–21a and ZPAL Ab III/363, square 32a of the upper fossiliferous horizon in Krasiejów near Opole, Poland.

The fragmentary skeleton ZPAL Ab III/363 (Fig. 3) is represented only by the pelvis and a femur with all the bones in close proximity. Some other bones from the same individual may be represented in the isolated material, but this cannot be decided with reasonable confidence. Alternatively, those may be a part of skeleton ZPAL Ab III/364 (Fig. 4), which is found close to it. That specimen has the braincase, neck, and dorsal vertebrae with their ribs (heavily crushed so only some of them survived preparation) preserved mostly in articulation. The incomplete right scapulocoracoid, incomplete humeri and radius with ulna in association represent the pectoral girdle and forelimb. Hind limbs are represented only by an incomplete femur and epipodials in articulation (tibia 154 mm long).

Numerous isolated bones were collected near these specimens and some of them, found in close proximity to each other and similar in size, can be identified as belonging to the same individual with some confidence. This is usually indicated by their numbering. How many individuals are represented is difficult to determine; it is definitely more than seven, perhaps up to twenty. Several bone elements (e.g., femora and ilia) are represented by 14 paired examples in the collection, which limits the minimum number of individuals represented to seven. They vary in size, but virtually all bones belong to mature animals. Perhaps this was a single herd killed catastrophically, as was the case also with some other Late Triassic and Early Jurassic dinosaurs (Welles, 1984:90; Colbert, 1989, 1990).

Apart from the assemblage occurring in the upper fossiliferous horizon, several more bones of this animal have been found. The humerus ZPAL Ab III/563/7 occurred together with the incomplete skeleton of *Teratosaurus* 80 cm above the lower horizon. The second sacral vertebra ZPAL AbIII/284 (Dzik, 2001:fig. 2 as a possible herrerasaurid), an isolated ischium and a few vertebrae come from the lower horizon.

SYSTEMATIC PALEONTOLOGY

DINOSAURIFORMES Novas, 1992
Family uncertain
Genus *SILESAURUS* nov.

Type Species—*S. opolensis*, gen. et sp. nov.
Diagnosis—As for the type species.

SILESAURUS OPOLENSIS, gen. et sp. nov.

Type Specimen—Incomplete skeleton ZPAL Ab III/361 (Fig. 2).

Locality—Clay-pit in Krasiejów near Opole, southern Poland.

Horizon—Upper fossiliferous horizon about 1 m below the top of the Late Triassic succession exposed in Krasiejów; *Paleorhinus* Chron (Heckert and Lukas, 1999), late Carnian.

Diagnosis—Beak on the dentaries; small number of teeth (11–12 in both dentary and maxilla); 25 presacral vertebrae with 9–11 cervicals, and last two dorsals fused with the two sacrals that have deep sacral ribs; elongate, gracile front limbs, and digit I of pes reduced to vestigial metatarsal that probably lacked phalanges. This is a combination of characters unique among members of the lineage leading to dinosaurs, which share with the new species a similar tarsal structure (*Lagerpeton*) and an elongated pubis (*Pseudolagosuchus*).

Comments—The extremely thin, almost horizontal iliac blade in its central, saddle-like part and the separate anterior iliac process make the new taxon different from all early dinosaurs, but these may represent the retention of primitive characters, as suggested by the similarity to the incompletely known supposed rauisuchian *Bromsgroveia* (Galton, 1977, 1985; Galton and Walker, 1996; Benton and Gower, 1997), from which
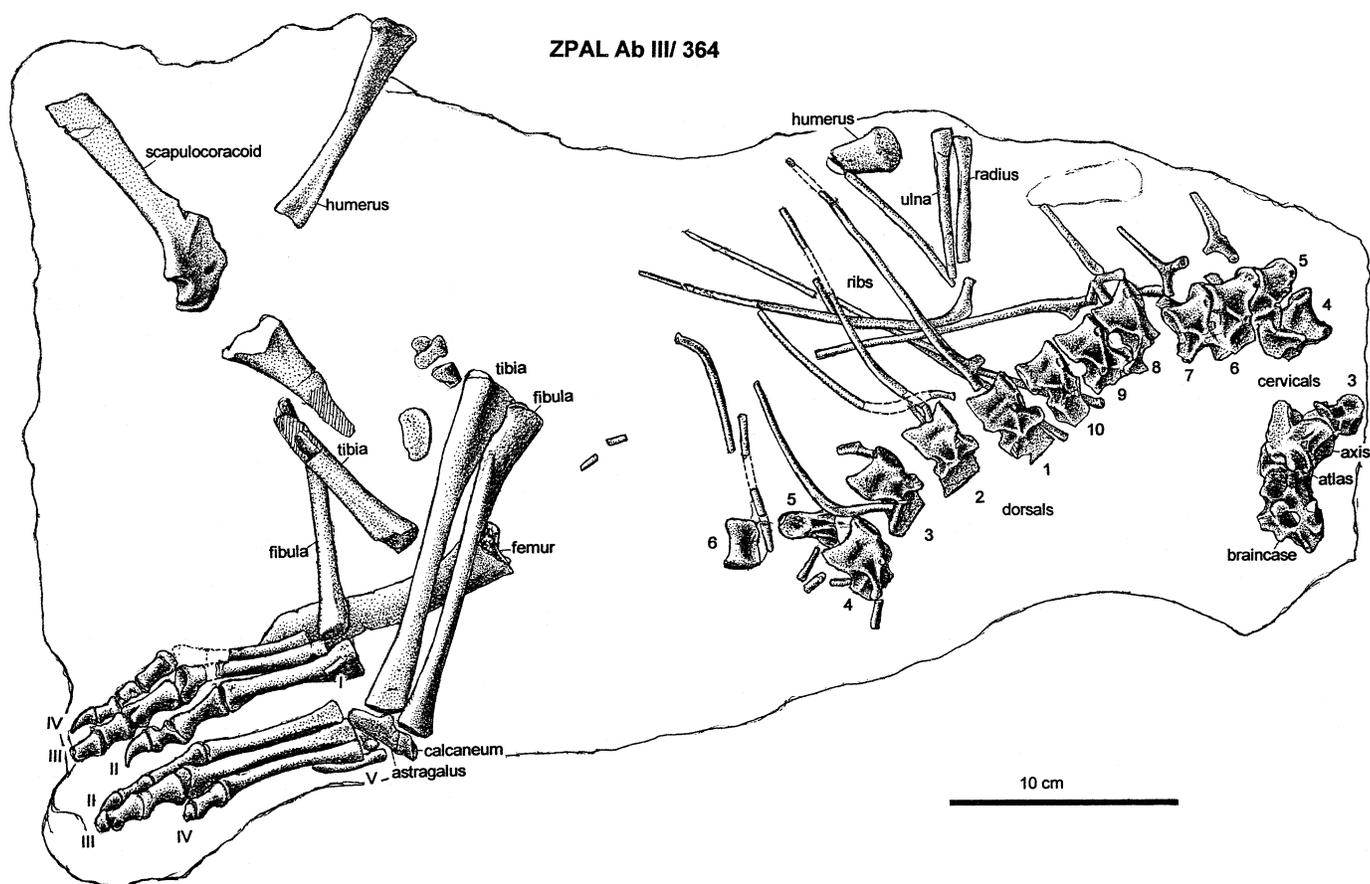
ZPAL Ab III/ 364

FIGURE 4. Diagrammatic drawing of *Silesaurus opolensis* bones in slab ZPAL Ab III/364, square 32a of the upper horizon in Krasiejów near Opole, Poland.

Silesaurus differs in the short posterior iliac process and the more derived form of the vertebrae.

DESCRIPTION

Skull

The skull of *Silesaurus opolensis* is known only from disarticulated bones. The most complete set of them is available from the holotype ZPAL Ab III/361. Of special interest are the jaw bones, which seem to be most characteristic for this animal (Fig. 5).

Two premaxillae have been found. Although they differ in details, both show four alveoli (teeth are missing), a symphyseal facet that covers virtually the entire medial surface, and the lack of any medial wall separating the external nares. Instead, there is a rather strong posterodorsally oriented ramus at the posterior end, which apparently sutured obliquely with the nasal. A well preserved maxilla from specimen ZPAL Ab III/361 shows 11 tooth positions, but several of the alveoli are empty. Some irregularities in the tooth crown shapes are also apparent (Fig. 5A–C). The dorsal ramus is not preserved, but a ridge probably bordered the antorbital fossa ventrally. The suture with the jugal is almost horizontal.

Both nasals were associated with skeleton ZPAL Ab III/361 but only the left one is reasonably complete. This is a very thin and fragile bone. It shows a slight lateral constriction of the snout in its anterior part, a well preserved suture for the premaxilla, and an indistinct and curved depression that possibly delimits the suture with the prefrontal (Fig. 6D). Its ventral surface shows a delicate ridge delimiting the nasal cavity.

The skull roof is poorly represented. Two frontals are preserved in specimen ZPAL Ab III/361, but both are rather fragmentary. The most informative isolated specimen is ZPAL Ab III/14. The ventral surfaces of all these specimens have a well delimited concave orbital margin and a distinct oblique ridge on the anterior part. The dorsal surface has a raised orbital margin. Sutures for the prefrontal and postorbital are clearly visible (Fig. 6D).

The incomplete left jugal is associated with a surangular and quadrate in the limestone-impregnated piece ZPAL Ab III/361/40. The jugal is a flat and posteriorly wide bone with a gentle lateral concavity.

Of the palate, the only known pterygoids are preserved in ZPAL Ab III/361. Although slightly incomplete, with deformation making some details of the restored spatial relationships uncertain, together they show almost the entire structure of the bone (Fig. 6B, C).

The most complete of the four quadrates are the pair from specimen ZPAL Ab III/361. They show a wide trapezoidal pterygoid wing and a prominent vertical ridge connecting the dorsal end (head) of the bone with the condyles that are strongly widened laterally. The total skull length is estimated at about 170 mm.

Braincase

The general proportions of the neurocranium are well shown in ZPAL Ab III/362, which is embedded in a limestone concretion. The braincase ZPAL Ab III/361 is split into three parts with the parasphenoid separated from the rest of the braincase. This exposes the suture between the parasphenoid and the ba-
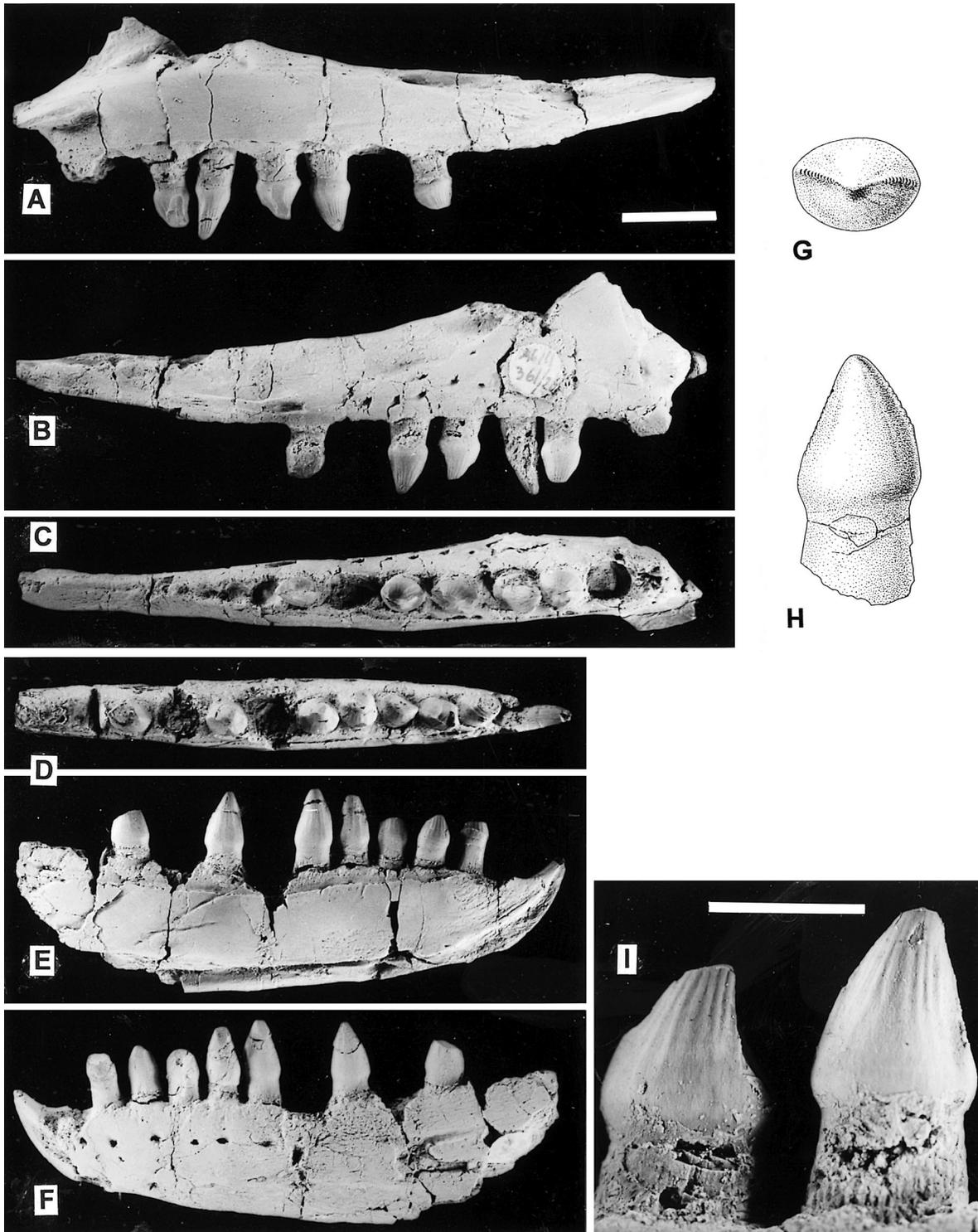
FIGURE 5. Jaw bones of *Silesaurus opolensis* from the early Late Triassic upper horizon in Krasiejów near Opole, Poland. **A–C**, **I**, maxilla ZPAL Ab III/361/26, square 21a (see Fig. 1C) in lingual, labial and occlusal views, and two teeth enlarged. **D–F**, dentary ZPAL Ab III/437/1, square 110 (see Fig. 1b) in occlusal, lingual, and labial views. **G–H**, 9th tooth from dentary ZPAL Ab III/361/27 in occlusal and lingual views. **A–F** × 1.5; **G–I** × 5.

sisphenoid, which is hard to trace in the other two braincases. An isolated opisthotic plus supraoccipital ZPAL Ab III/361/36 provides another opportunity to trace sutures. The braincase wall ZPAL Ab III/361/35 was imbedded in claystone that made

it easy to expose the interior of the endocranial cavity. The cavity was also prepared chemically in ZPAL Ab III/364.

These specimens enable a restoration of the braincase structure to be made with some confidence (Fig. 7). A deep fissure
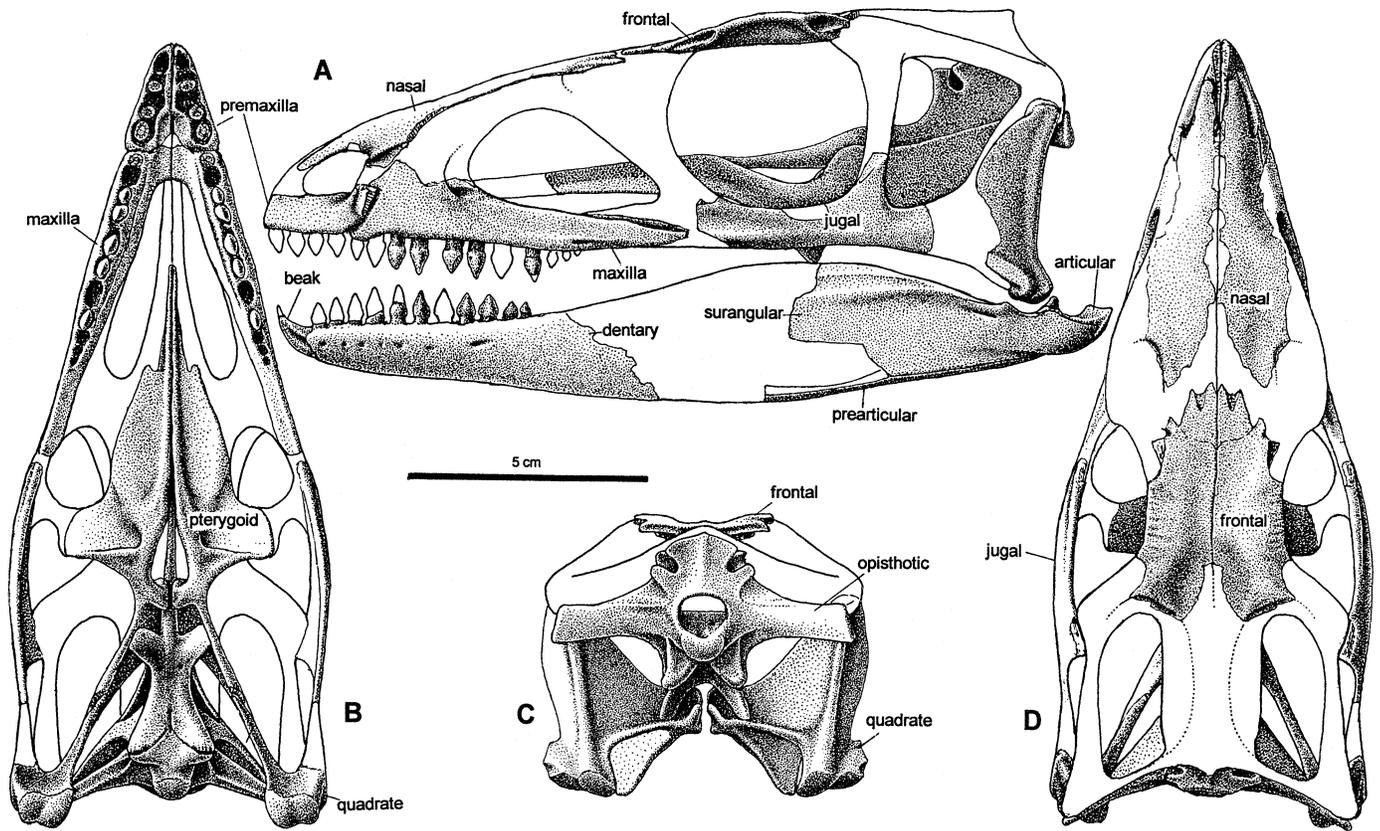
FIGURE 6. Tentative restoration of skull of *Silesaurus opolensis* from the early Late Triassic upper horizon in Krasiejów near Opole, Poland, based on isolated bones of specimens ZPAL Ab III/361 and ZPAL Ab III/437 (see Figs. 2 and 5). **A**, left lateral view, note the form of the tip of dentary that probably bore a horny beak; **B**, palatal view; **C**, posterior view; **D**, dorsal view.

medially separates the posterior part of the basisphenoid and the anterior part of basioccipital. Perhaps the most unusual feature of the braincase of *Silesaurus* is the relatively large incision in the supraoccipital, possibly for the dorsal head vein.

Mandible

The dentary ZPAL Ab III/361/27 shows 12 tooth alveoli, with 11 teeth preserved in situ. This is the most complete dentary in the collection. Its broken anterior end shows an incision at the external side of its base, which probably represents a vascular canal, and a shallow fissure medially below the symphyseal area. The meaning of these structures is explained by specimen ZPAL Ab III/437/1, found isolated in square 110 (Fig. 5D–F), where the canal and incision delimit a sharply curved, edentulous anterior part of the dentary. Its surface is depressed with respect to the rest of the mandible, separated from it by a kind of ramp with an anteriorly oriented openings of vascular canals. One of these continues anteriorly as a lateral furrow. The remaining surface of the rostrum is indistinctly striated. There is a clear symphysis, so the keratinous beak was supported exclusively by the dentaries. No trace of a terminal median bone like the the predentary of ornithischian dinosaurs is present. In both specimens, vascular openings are present in the anterior part of the dentary (behind the beak), on its external surface below and between the teeth (Fig. 5F), and in a narrow furrow immediately below the tooth row on the inner surface of the bone (Fig. 5E). All this suggests that the tip of the dentaries was originally armed with a horny cover that formed a sharp beak. Two other dentaries (ZPAL Ab III/407/4 and 426)

are too fragmentary to add anything important to this description.

The teeth of the dentaries (and maxillae) are firmly imbedded in their alveoli, with almost no space left around their roots. The dental formula is 4, 11–12, 11–12. Tooth 7 is missing in the dentary ZPAL Ab III/437/1 and its replacement is beginning to emerge from the alveolus. All the other teeth seem to be fully erupted, with their tips arranged in a parabolic contour. The low tooth crown is conical, covered with very thin, transparent enamel, which penetrates deeper into the dentine to form longitudinal grooves and ridges. Shallow folds on the crown surface may radiate from the tip, but this is highly variable (Fig. 4G–I). The teeth are oval in cross-section, with weakly denticulated ridges on their anterior and posterior edges. The serrations are variable, occasionally very weak or almost missing. The sides of the tooth apices are usually worn, and this extends to the lingual surface of some maxillary teeth. The wear surfaces are irregular, but mostly flat and smooth.

The middle part of the lower jaw is not represented in the material studied. Specimen ZPAL Ab III/361 has a surangular with articular in situ and a slightly displaced prearticular. The dorsal margin of the surangular, as shown also by ZPAL Ab III/451, is convex. Below it an angulation separates a flat lateral surface from the horizontal dorsal surface that twists anteriorly and joins with the lateral surface to form a gentle concavity (Fig. 6A).

Vertebral Column

The morphological sequence and number of vertebrae in particular subdivisions of the column can be established from the
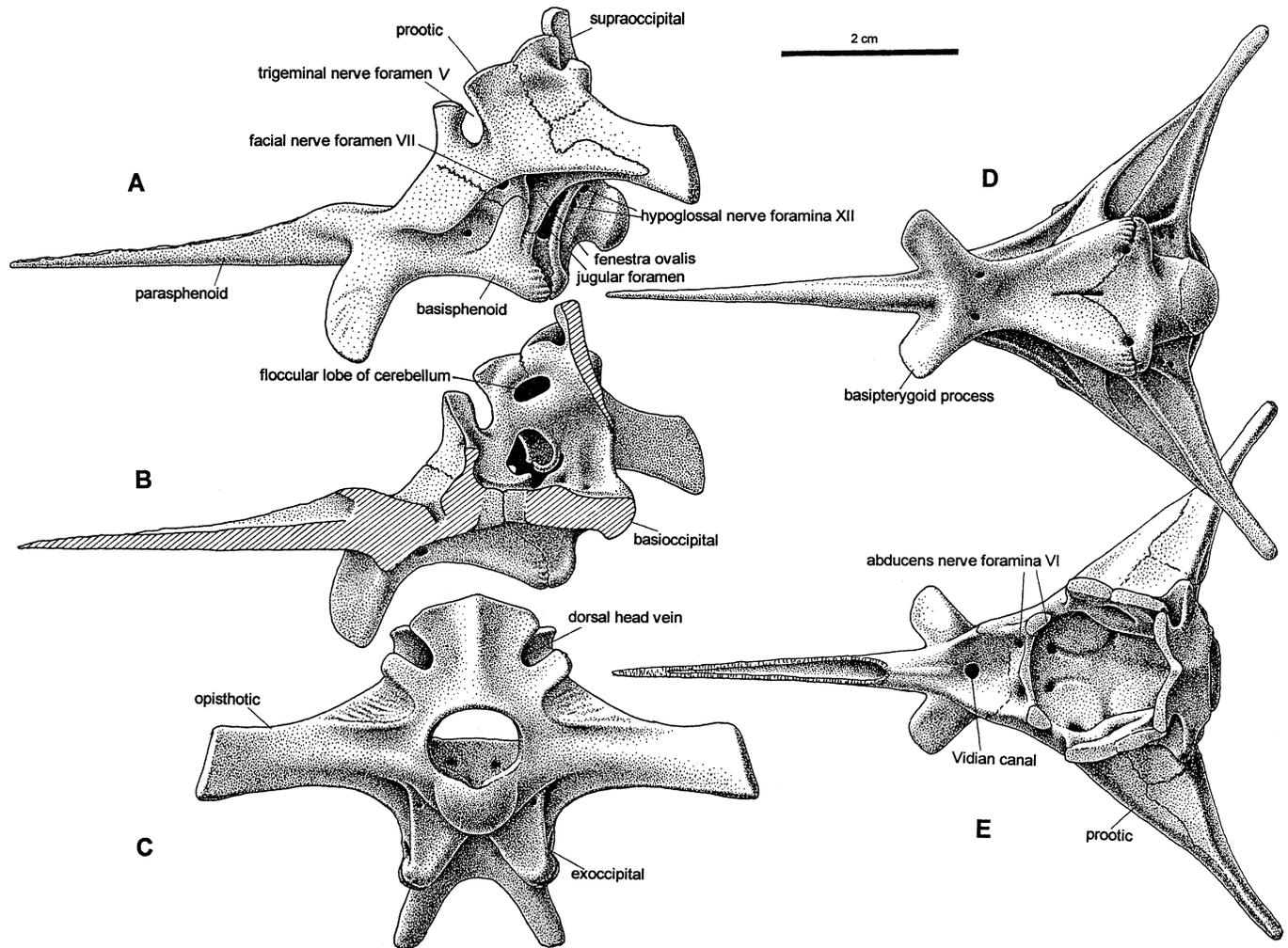
FIGURE 7.   Restoration of neurocranium of *Silesaurus opolensis* from the early Late Triassic upper horizon in Krasiejów near Opole, Poland; based on specimens ZPAL Ab III/364, 362 and 361. **A**, left lateral view; **B**, medial view with reconstructed median section; **C**, posterior view; **D**, ventral view; **E**, dorsal view.

articulated specimens ZPAL Ab III/361, 362, and 364. Ten cervicals are represented in virtually the original arrangement on two of the slabs (Figs. 2 and 4); 13 disassociated dorsals being preserved on one of them (Fig. 2). The presence of four fused sacrals is documented by several specimens. In the cervicals prominent laminae delimit conical cavities (chonoses of Welles, 1984) but there is no clear evidence of pneumatization.

The atlas is partially preserved only in ZPAL Ab III/364, where the atlantal centrum is attached to the centrum of the axis. A concave crescent-shaped surface is developed below. The atlantal intercentrum (destroyed during additional preparation of the braincase) and the left half of the atlantal neural arch are slightly displaced. The intercentrum was a rectangular, thin strip of bone, so perhaps it was ossified only along its ventral surface. The neural arch is also simple, with weakly differentiated pedicles (Fig. 8A). The lateral and ventral surfaces of the centrum are concave.

The axis is well preserved in both ZPAL Ab III/361 (longitudinal axis of spinal process 37 mm long) and 364 (spinal process 29 mm long). The anterior surface of the centrum is gently concave to host the atlantal centrum (odontoid). A small parapophysis is developed on the ventral part of the centrum, at least in ZPAL Ab III/364, but no diapophysis is visible in

the specimens studied. Prezygapophyses are represented by small indistinct protuberances and postzygapophyses are fully developed. They are buttressed anteriorly and ventrally by low ridges and dorsally by prominent laminae connecting their tips with the posterior tip of the spinal process. They lack epipophyses that are characteristic of dinosaurs. As a result, a large conical opening (postspinal chonos; Welles, 1984) is developed behind the spine. Its posterior contours are rhomboidal but the interior is pentagonal (Fig. 8A).

The succeeding vertebrae also bear such conical posterior openings, but the sizes of the openings decrease gradually, almost completely disappearing in the posterior dorsals. Like the axis, cervical 3 shows a distinct, ventrally located parapophysis but no diapophysis. Laminae buttressing the well developed zygapophyses merge centrally into a low X-shaped structure. A distinct diapophysis develops at the point where these ridges merge in cervical 4. The diapophysis is oriented obliquely ventrally but the angle of inclination is difficult to determine accurately as all available specimens are more or less deformed. From this point on the neural spines become less pointed posteriorly. Among loose cervicals, ZPAL Ab III/411/7 is especially informative. Parapophyses keep their ventral position up to cervical 10, which is well preserved in specimens ZPAL Ab
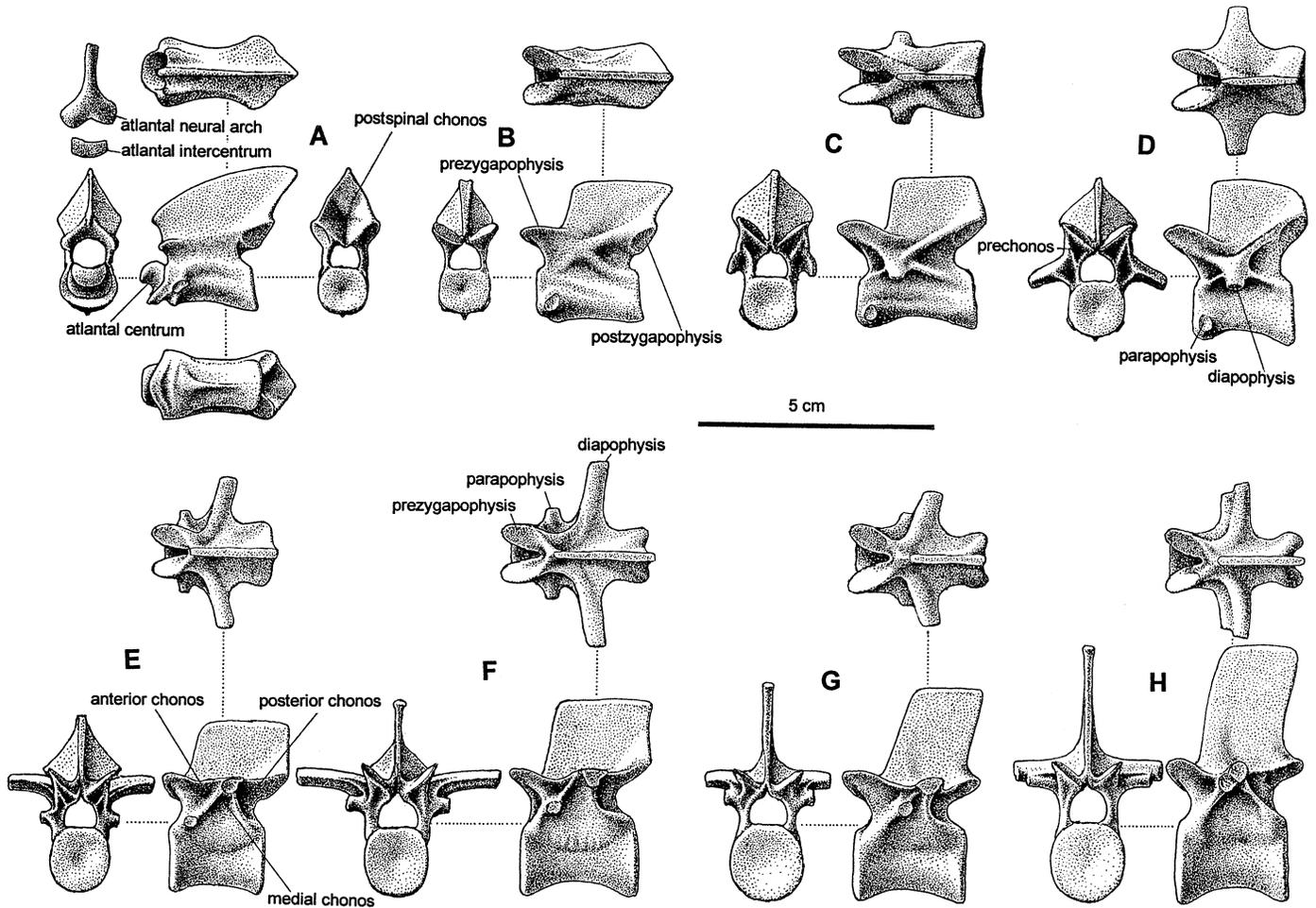
FIGURE 8. Restoration of presacral vertebrae of *Silesaurus opolensis* from the early Late Triassic upper horizon in Krasiejów near Opole, Poland; based mostly on ZPAL Ab III/361 and 364. **A**, atlas, and axis in dorsal, anterior, left lateral, posterior, and ventral views; displaced atlantal intercentrum and atlantal neural arch shown separately. **B**, 3rd cervical in dorsal, anterior, and left lateral views. **C**, 4th cervical in dorsal, anterior, and left lateral views. **D**, 6th cervical in dorsal, anterior, and left lateral views. **E**, 1st dorsal in dorsal, anterior, and left lateral views; details based on ZPAL Ab III/433/1. **F**, 6th dorsal in dorsal, anterior, and left lateral views. **G**, 10th dorsal in dorsal, anterior, and left lateral views. **H**, 13th dorsal in dorsal, anterior, and left lateral views.

III/364 and 361. They are slightly raised, however, with respect to cervical 9, and even in vertebra 11 (ZPAL Ab III/364) the parapophyses are located relatively low—at the boundary between the centrum and neural arch. There seems to be some individual variation in the prominence of the transition from the cervical to the dorsal region of the vertebral column.

In the following dorsal vertebrae, the parapophyses gradually rise from their initial position at the dorsal margin of the centrum to the level of the prezygapophysis. At the same time, the diapophyses become elongate as far as dorsal 5; then their length shortens again. The series of dorsals ZPAL Ab III/362/7–10 clearly shows details of their structure. Approximately at dorsal 10, the parapophysis merges with the diapophysis and this condition is retained in the next four vertebrae.

The ribs are slender and strongly crushed, which made their preparation difficult. The cervical ribs are relatively well represented in specimen ZPAL Ab III/361 and 362 (Figs. 2, 4). The longest preserved specimens, probably belonging to vertebrae 10–12 (thus either cervical or thoracic) were more than 150 mm long. The shortest rib, belonging to vertebra 20–23, was about 67 mm long, with a relatively wide proximal end.

The sacrum consists of four fused vertebrae that are well

preserved and undeformed in specimen ZPAL Ab III/404/3 (Fig. 10, combined central length 91 mm). The anterior one, dorsosacral 2, does not differ from the neighboring presacrals except that it is firmly co-ossified with the rest of the sacrum. Dorsosacral 1 has its apophyses modified into a wing-like structure that projects anterolaterally. Similar structures occur in the two sacrals proper, but they are transversely oriented. In sacral 2 an additional wing-like process extends posterodorsally, as shown by ZPAL Ab III/361. In both sacrals, the modified apophysis is connected to the base of the sacral rib by a vertical blade. In sacral 1, this blade is relatively low, in sacral 2 it connects the tip of the rib almost directly with the wing-like process. The ribs are attached between the centra. The posterior surface of the centrum of sacral 2 is obliquely oriented, but this varies among specimens.

Only the basal half of the tail can be safely restored but its actual length remains conjectural. Caudal vertebrae found in partial articulation in ZPAL Ab III/361 (Fig. 11A–C), isolated specimens ZPAL Ab III/361/3–5 found outside the slab, and also ZPAL Ab III/448/3–6 and 362/28–29, show an almost complete gradation of morphologies for the proximal region.
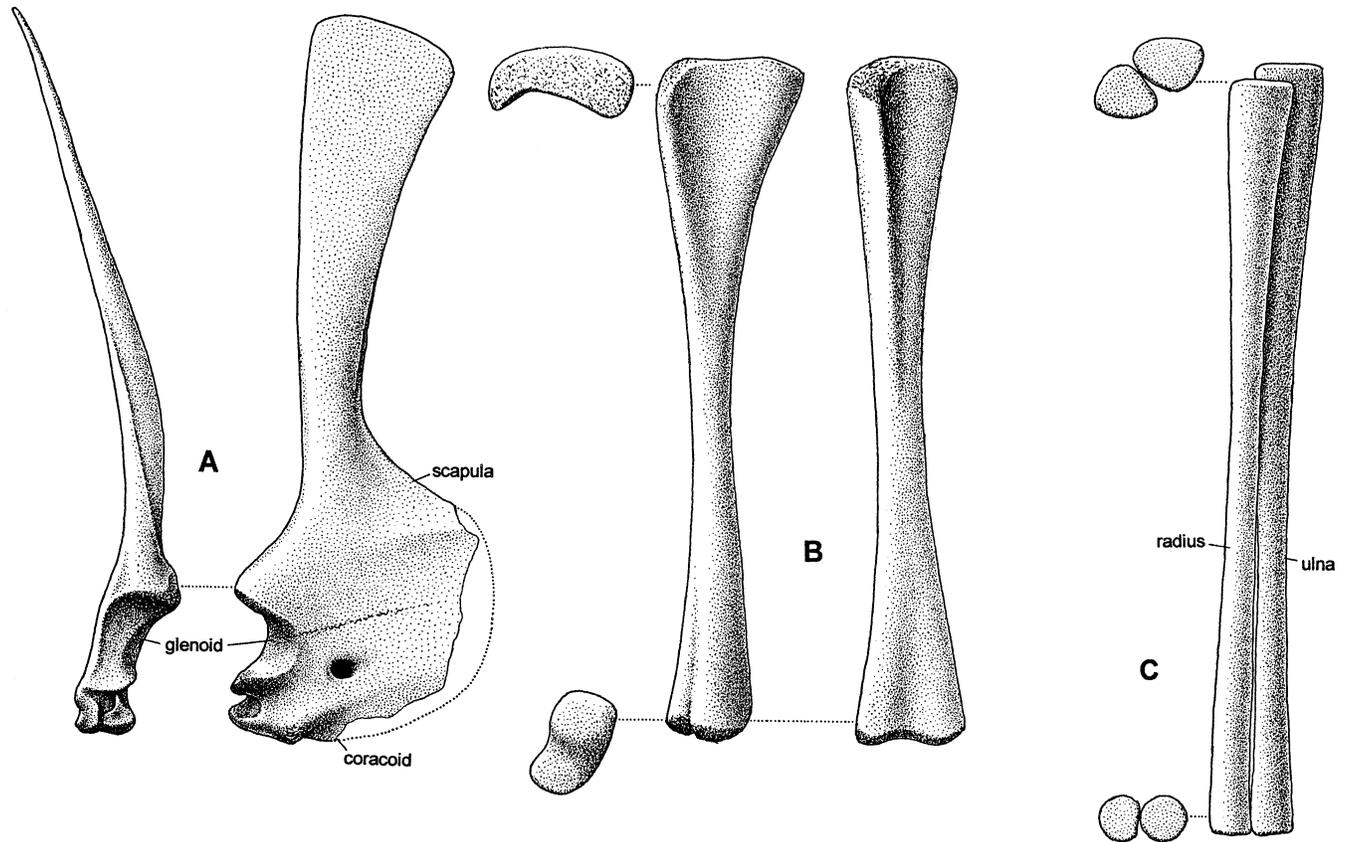
FIGURE 9.   Restoration of pectoral girdle and limb elements of *Silesaurus opolensis* from the early Late Triassic upper horizon in Krasiejów near Opole, Poland. **A**, left scapulocoracoid in anterior and lateral views, based mainly on ZPAL Ab III/361 and 363. **B**, right humerus in proximal, anterior, distal, and medial views, based mostly on ZPAL Ab III/452. **C**, radius and ulna in articulation, proximal, anterior, and distal views, based on ZPAL Ab III/453.

Pectoral Girdle and Forelimb

Three scapulocoracoids and seven isolated scapulae are known. In the scapulocoracoids, the scapula and coracoid are firmly connected, and the suture is difficult to trace. The best preserved scapulocoracoid, ZPAL Ab III/404/8 (131 mm long), shows a narrow, spatulate blade and a wide anterior projection with an indistinct angulation in its upper part (Fig. 9A). The projection is very thin and its margin is broken in all specimens, but the bone becomes massive around the glenoid, being most completely preserved in ZPAL Ab III/361. The horizontal groove between the buttresses of the glenoid and subglenoid fossae is rather deeply incised. The lateral opening of the coracoid foramen is oriented somewhat anteriorly.

Fourteen humeri have been found, but most are fragmentary. The most complete are specimens ZPAL Ab III/452, 120 mm long, and 411/11, 138 mm long. All specimens are almost straight and surprisingly simple in their structure (Fig. 9B). The proximal surface of the bone is rather featureless and it was probably capped by a prominent cartilaginous part. The deltopectoral crest is weakly developed and gradually disappears distally, with no angulation. The distal end is sinuous in profile, showing a clear ectepicondyle and entepicondyle. In larger specimens they are more distinctly separated, with furrows running up to the middle of the bone.

Seven radii and 10 ulnae are available, four in original articulation. Among articulated specimens, ZPAL Ab III/453 is the most informative. These bones have even less features than the humerus (Fig. 9C), so they are hard to identify when found

isolated. The distal head of the radius is slightly depressed at its contact with the ulna.

There are two isolated possible carpals (specimens ZPAL Ab III/439/8 and 440/1) and no bones are known from the manus.

Pelvic Girdle and Hindlimb

The best preserved isolated ilium, ZPAL Ab III/404/2 (90 mm long), shows an extremely thin, almost horizontal iliac blade in its central, saddle-like part. This is also clearly visible in the deformed specimen ZPAL Ab III/362. Specimens ZPAL Ab III/361, 362 (Figs. 2 and 3), 404/2-3, 5, and 404/1 show how the ilium articulated with the sacrum. The blade seems to have been originally in contact with the wing-like modified apophyses of the sacrals (Fig. 7E). The strongest and most prominent part of the ilium is its posterior process, which bears two longitudinal scars for muscle attachment separated by a prominent, ventrally oriented ridge (Figs. 11, 12). The apical surfaces of both processes are roughened. The anterior process is relatively short and curved. It is not directly connected to the semicircular supra-acetabular crest at the dorsal margin of the acetabulum (Fig. 12E), so this prominent structure is not actually buttressed by the process.

The pubis is still in articulation with the ilium in ZPAL Ab III/361, but the adjacent part of the extremely thin medial blade is incomplete, as it is in all isolated specimens. The best preserved of these is ZPAL Ab III/404/5, which is 168 mm long. The actual extent of the blade can be estimated on the basis of the partially articulated specimen ZPAL Ab III/363, and results
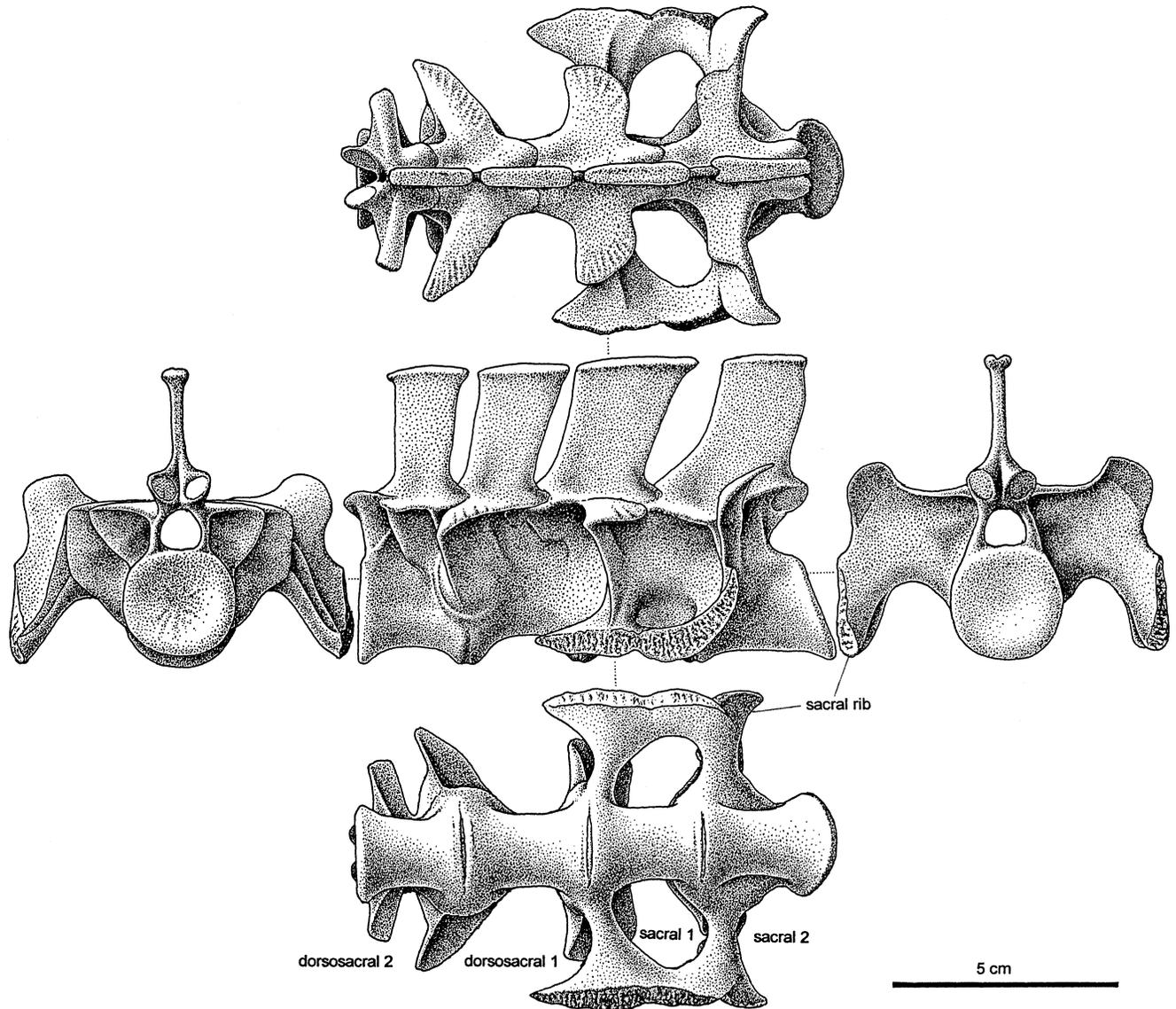
FIGURE 10. Restoration of sacrum of *Silesaurus opolensis* from the early Late Triassic upper horizon in Krasiejów near Opole, Poland; dorsal, anterior, left lateral, posterior and ventral views; based mainly on ZPAL Ab III/404/3.

are consistent with those inferred from the restored geometry of the pelvis (Figs. 11 and 12D). The anterior process of the pubis is comma-like in cross-section and most of its strength is provided by the thickened lateral margins (Fig. 12).

The ischia are displaced even in the most complete specimen ZPAL Ab III/361 (Fig. 3). The shapes of the acetabular walls of the ischium, pubis, and ilium are such that they were most probably in close contact (Fig. 12). If there was a perforation at all, then this would at most have been only a narrow horizontal fissure.

Fourteen femora are represented in the collection, several of them virtually complete. The best preserved specimens ZPAL Ab III/361/25 (200 mm long), 361/23, and 460/1 show similar proportions and curvature. Both proximal and distal femoral heads are rather simple morphologically. The proximal head is poorly defined and it is not offset from the shaft by a distinct neck. The greater trochanter is not delimited, but there is an indistinct ridge surrounding the caput (Fig. 13A).

The anterior trochanter is usually prominent, with a longi-tudinal blade and a transverse tuber (Fig. 13). However, in ZPAL Ab III/457 it is represented only by two separate longi-tudinal ridges. The fourth trochanter is more prone to defor-mation and less variable.

An articulated tibia and fibula are represented by the good specimen ZPAL Ab III/361/8, and they are supplemented by isolated tibiae ZPAL Ab III/361/22 (150 mm long), 460/3, 461, and the fibula ZPAL Ab III/361/24. Both epipodials have a rather simple structure. The proximal end of the tibia is trian-gular in contour, the fibular flange and spiral ridge are low (Fig. 13B, C), and the distal end shows a prominent astragalar over-hang.

An isolated astragalus, preserved with the calcaneum, is rep-resented by specimen ZPAL Ab III/361/20 (35 mm wide; Fig. 13D). Their counter-pair is still in articulation with the tibia and fibula, similar to the articulated specimen ZPAL Ab III/364 (Fig. 4) in which both pes are articulated and almost complete except for a few digital phalanges. In all these specimens the astragalus and calcaneum are tightly articulated, but the oblique
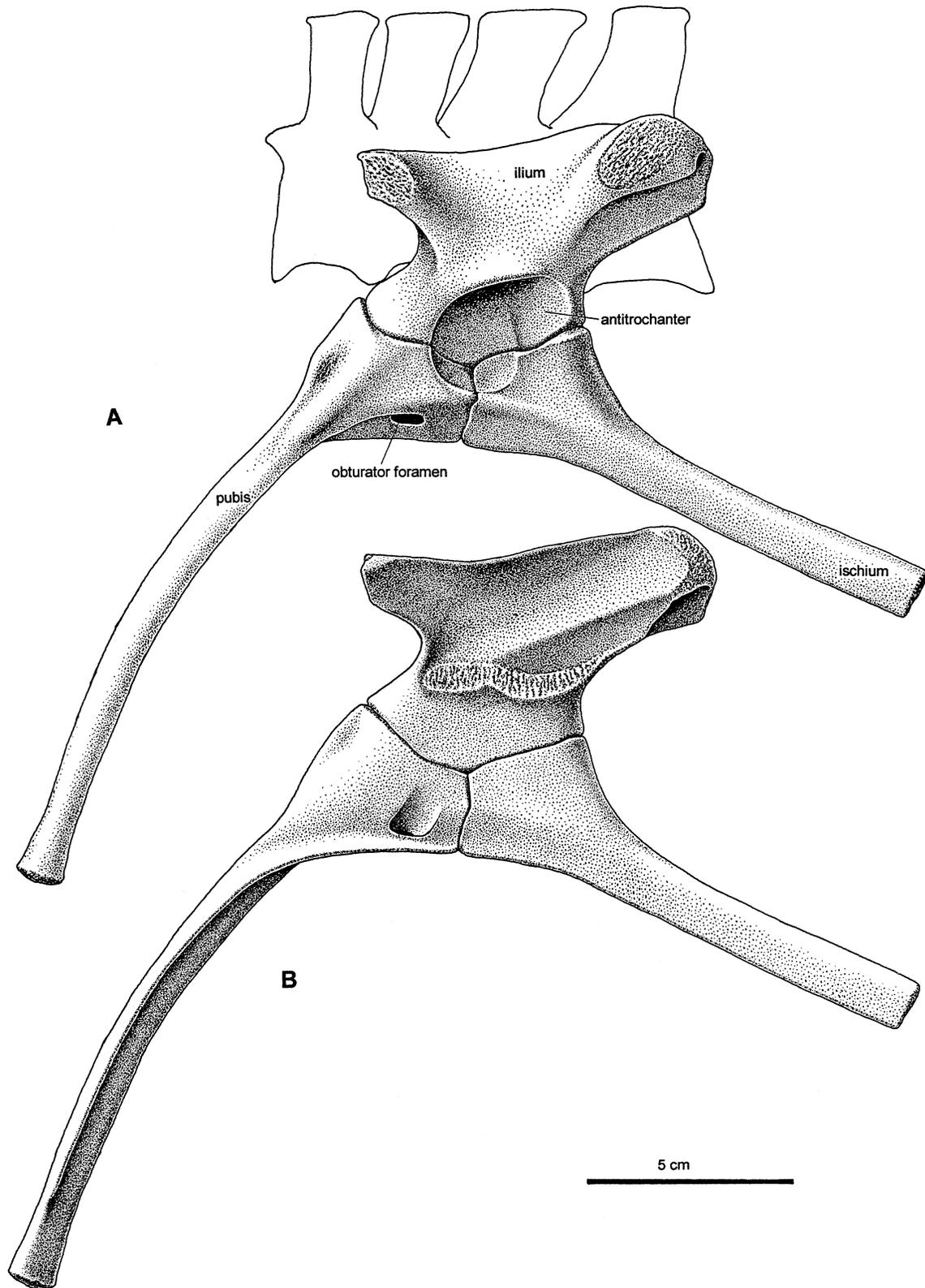
FIGURE 11.   Restoration of pelvis of *Silesaurus opolensis* from the early Late Triassic upper horizon in Krasiejów near Opole, Poland; left lateral and medial views; based mainly on ZPAL Ab III/361.
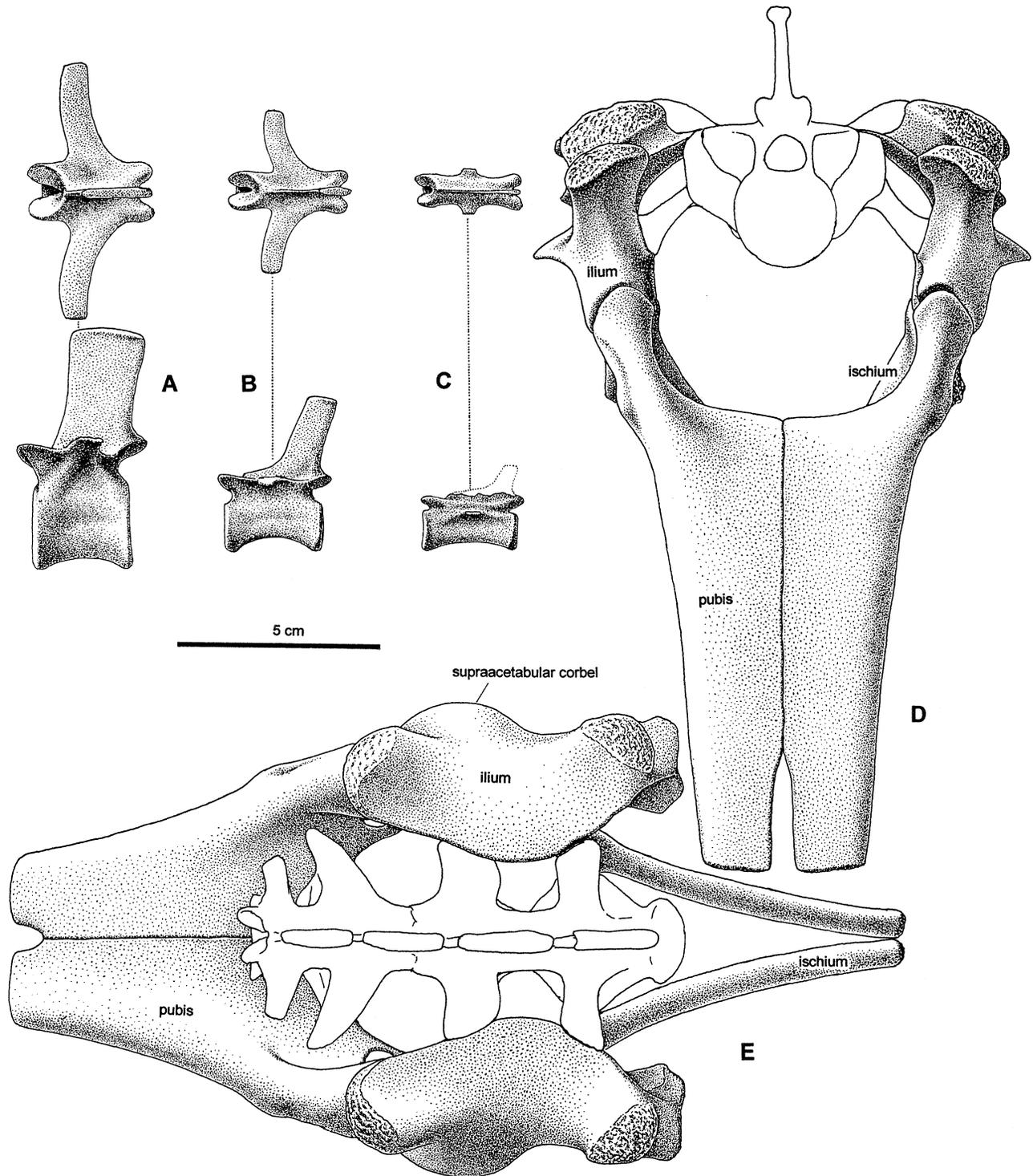
FIGURE 12. Restoration of caudal vertebrae and pelvis of *Silesaurus opolensis* from the early Late Triassic upper horizon in Krasiejów near Opole, Poland. **A**, 2nd caudal in dorsal and left lateral views. **B**, 10th caudal in dorsal and left lateral views. **C**, distal caudal in dorsal and left lateral views; all based mainly on ZPAL Ab III/361. **D**, pelvis in anterior view; **E**, pelvis in dorsal view; both based mainly on ZPAL Ab III/363 (Fig. 3).

straight suture between them is clearly visible. The calcaneum is small and covers about half of the area of articulation with the fibula, which is gently concave. The facet for tibia on the astragalus is saddle-shaped, forming an incipient dorsal basin, corresponding in shape to the distal end of the tibia (Fig. 13B).

The ascending process of the astragalus that separates articulation facets is rather low, as is the whole bone.

The metatarsals occur in articulation in ZPAL Ab III/364 (Figs. 4 and 13E), and isolated specimens ZPAL Ab III/361/2, 14–16, 19, 460/4–6, and 439/2 show that there is much vari-
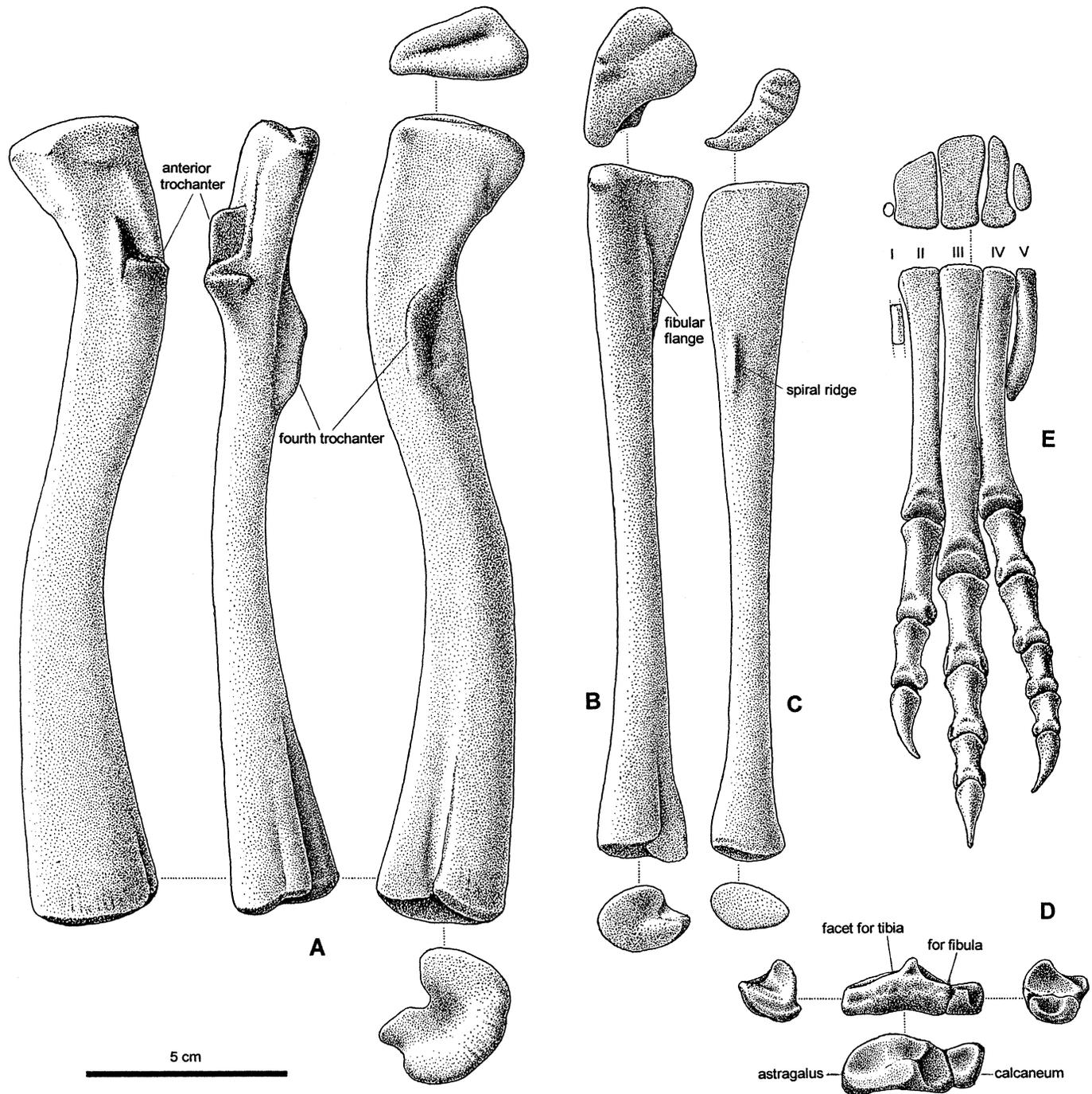
FIGURE 13.   Restoration of hind limb elements of *Silesaurus opolensis* from the early Late Triassic upper horizon in Krasiejów near Opole, Poland. **A**, left femur in anterior, lateral, posterior, with proximal and distal views, based mainly on ZPAL Ab III/361/23. **B**, left tibia in proximal, anterior, and distal views. **C**, left fibula in proximal, anterior, and distal views, both based mainly on ZPAL Ab III/361/8. **D**, right astragalus and calcaneum in medial, posterior, lateral, and dorsal views, based mainly on ZPAL Ab III/361/20. **E**, restoration of right pes in anterior view with proximal view of ends of metatarsals.

ability in the shapes of their proximal ends. The proximal end of metatarsal II is always trapezoidal, but the other metatarsals apparently had only to fit together into an oval contour, and their individual shapes are subject to much variation. The specimens are usually twisted by deformation but the central part of the metatarsals also seems to show similar variability. The only possible remnant of digit I is a narrow bone attached to the right metatarsal II. It resembles a piece of a broken rib but

no other rib was found in close proximity. Digit V is represented only by the metatarsal, which is a small curved bone (Fig. 13E) preserved in situ.

The isolated metatarsal II ZPAL Ab III/361/19 is 77 mm long, ZPAL Ab III/361/16, 74 mm; metatarsal III ZPAL Ab III/361/14, 86 mm; metatarsal IV ZPAL Ab III/361/2, 72 mm; in articulated specimen ZPAL Ab III/364 metatarsal III is 77 mm long.

The pedal phalanges are incompletely preserved in ZPAL Ab III/364 (Fig. 4). Digit II is complete in both feet; it bears two phalanges and a prominent ungual. Three phalanges are preserved in digit III of the right pes, but the ungual is missing. In digit III of the left pes, the ungual is misplaced to contact the second phalanx; the third phalanx is apparently missing. In the right pes, the first phalanx is missing in digit IV, but the rest is complete. However, phalanx 1 is represented in digit IV of the left pes, although the other phalanges are missing. Knowledge of the morphology of particular phalanges is supplemented by the isolated specimens ZPAL Ab III/361/13 and 32.

COMPARISON

Silesaurus seems to be close to the point of origin of dinosaurs both in respect to its structure and geological age. It shows most of the characters listed by Novas (1996; also Sereno, 1991b; Juul, 1994; Bennett, 1996; Novas, 1996; and Benton, 1999) as diagnostic apomorphies for members of the lineage leading to dinosaurs. The following characters (numbering follows Novas, 1996) place *Silesaurus* above *Marasuchus* in the Dinosauriformes: femur with a trochanteric fossa on the head (character 7), an anterior trochanter (8), and a trochanteric shelf (9); a tibia with a cnemial crest (10) and a quadrangular distal end (11) with a lateral longitudinal groove (12). Paradoxically, the first character of Novas' (1996) list for Dinosauriformes is lacking in *Silesaurus*, as its neck was not strongly sigmoidal (6), but this character seems to be weakly expressed even in *Herrerasaurus* (as restored by Sereno and Novas, 1994; excluded from Dinosauria by Fraser et al., 2002).

The length of the narrow pubis, approaching that of the femur (character 13 of Novas, 1996), in association with the pyramid-shaped ascending process on the astragalus (14) and metatarsal IV being sigmoidal in anterior view (15), make *Silesaurus* at least as advanced as *Pseudolagosuchus*.

Much less obvious is the relationship of *Silesaurus* to dinosaurs as its skeletal anatomy is a rather bizarre combination of primitive and advanced characters (Fig. 14). Unfortunately, the skull is inadequately known and data on the manus are missing, which precludes determination of several characters (16–20, 23, 32 of Novas, 1996). The very proximally located deltopectoral crest (character 22) and lack of epiphyses on the cervical vertebra (21) make *Silesaurus* less derived than dinosaurs. However, the presence of a brevis shelf on the ilium (26), an ischium with a slender shaft (27), a femur with reduction of the tuberosity that laterally bounds the ligament of the femoral head (28) and the presence of a prominent lesser trochanter (29), overlap of the ascending process of the astragalus with the tibia (30), and a concave proximal articular surface for the reception of the distal end of the fibula on the calcaneum (31), are synapomorphies of the Dinosauria. A closed acetabulum (25) is also known to occur in the early dinosaurs *Guaibasaurus* and *Saturnalia* (Bonaparte et al., 1999; Langer et al., 1999). The three sacral vertebra (24) are of limited taxonomic use in early dinosaurs because either a dorsal (Sereno et al., 1993:*Eoraptor*) or a caudal vertebra may unite with the two sacrals in the sacrum (Galton, 2000b, 2001:Prosauropoda).

Along with those characters of more or less clear phylogenetic meaning, *Silesaurus* shows some rather unexpected aspects of its anatomy: the saddle-like appearance of the ilium, the morphology of the cervical vertebrae, and adaptations to herbivory. To clarify their phylogenetic meaning, more data on possible close relatives of *Silesaurus* are needed. The fragmentary holotype of *Pseudolagosuchus* offers rather limited clarification (Arcucci, 1987). However, there are some other Middle and Late Triassic archosaurs, such as *Bromsgroveia* and *Spondylosoma* which may help in this.

Pelvis

Probably the most surprising aspect of the skeletal anatomy of the pelvic girdle of *Silesaurus* is the separate anterior iliac process and saddle-like appearance of the iliac blade. Such a structure is not considered primitive for the dinosaur lineage. Instead, Gower (2000) proposed this to be a derived character for rauisuchians. Ilia of this type are known from strata of similar or older age than *Silesaurus*. One of them belongs to *Bromsgroveia walkeri* (Galton, 1977, 1985; Galton and Walker, 1996; Benton and Gower, 1997) from the probably Anisian Bromsgrove Sandstone Formation of Warwick in England (Benton et al., 1994). The other is an isolated ilium from the Dockum Group of Texas, tentatively attributed to the poposaurid *Chindesaurus* by Long and Murry (1995; but see Hunt et al., 1998, and Heckert et al., 2000). In both, the supra-acetabular crest is buttressed by the anterior iliac process, which forms a vertical ridge coming close to the dorsal margin of the acetabulum (see Long and Murry, 1995:fig. 147), very similar to that in *Silesaurus*. Although no evidence on the tarsal anatomy is available, *Bromsgroveia* was tentatively classified among rauisuchians, which implies a crurotarsal ankle and crocodilian relationships (Benton and Clark, 1988). An alternative is that it is a member of the mesotarsal *Silesaurus* lineage.

Whatever its exact age and affinity, *Bromsgroveia* seems to be the geologically oldest archosaur with a buttressed acetabulum (with possible exception of *Anisodontosaurus* from the Moenkopi Formation of Arizona; Welles, 1947). *Silesaurus* is similar in this respect, as well as in the length of the posterior iliac process, to *Bromsgroveia*, but different from later saurischian and ornithischian dinosaurs, in which the body of the ilium is more or less vertically oriented. This poses the question whether the saddle-like ilium of *Silesaurus* is a primitive trait inherited after a common ancestry with *Bromsgroveia* (so it is not a rauisuchian) and modified in subsequent evolution.

Cervical Vertebrae

Rauisuchian affinities were also suggested (but not proven with evidence on the ankle structure) for *Spondylosoma*, the oldest known archosaur in which apophyses are buttressed by vertebral laminae (Wilson, 1999; Galton, 2000a). It comes from the lower part of the Santa Maria Formation of Brazil, correlated with the Ladinian Ischichuca (Los Chañares) Formation of Argentina, the type horizon of *Pseudolagosuchus*. *Silesaurus* is advanced in respect to *Spondylosoma* in the general shape of the cervicals, having an oblique orientation of the posterior face of the centra. This feature is already recognizable, however, in *Marasuchus* from the Ladinian Ischichuca Formation (Sereno and Arcucci, 1994), which is roughly coeval to *Spondylosoma*. The association of a mesotarsal ankle in *Silesaurus*, with cervical vertebrae similar to *Spondylosoma* (and ilium similar to *Bromsgroveia*), poses the question about rauisuchian affinities of the Brazilian animal. It may also be related to *Silesaurus*.

Although buttressed apophyses were possibly inherited by *Silesaurus* from its ancestors, the presence of a deep conical cavity in the neural spine (postspinal chonos of Welles, 1984) seems to be a novelty. Such a cavity is typical of the cerato-saurian cervicals, including those of *Liliensternus* from the Knollenmergel of Germany (Huene, 1934; Welles, 1984; Rowe and Gauthier, 1990).

Thus, the cervical vertebrae of *Silesaurus* also show a mixture of characters considered either primitive (lack of neck sinuosity and epipophyses) or advanced (well developed laminae) within the lineage leading to dinosaurs.

Probable Herbivory

In the shape of their crowns and pattern of serration, the teeth of *Silesaurus* are not similar to those of carnivorous archosaurs.

25 cm
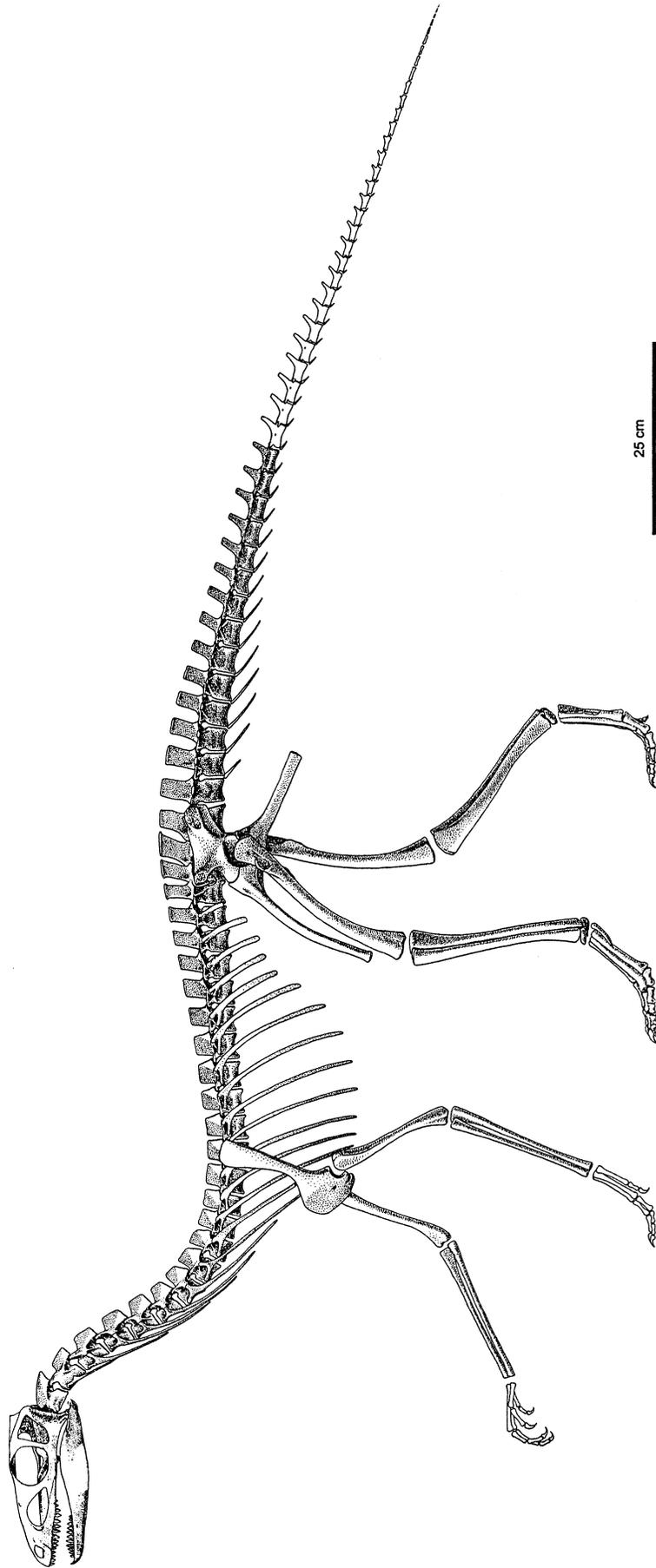
FIGURE 14.   Restoration of complete specimen of *Silesaurus opolensis* from the early Late Triassic upper horizon in Krasiejów near Opole, Poland.

Instead, in their rather low conical shape and worn tips they are suggestive of herbivory. Nevertheless, in their weak serration, with denticles oriented slightly laterally, they are not much more morphologically derived than teeth of the associated aetosaur *Stagonolepis*. As in early herbivorous dinosaurs, the number of teeth is significantly reduced. Thus, *Thecodontosaurus* had 21 teeth in the adult dentary (Benton et al., 2000) and 14 in a juvenile (Kermack, 1984) as compared with 12 in the adult *Silesaurus*. There are only 15 teeth in *Pisanosaurus* but they cover a much larger proportion of the dentary (Bonaparte, 1976) than in *Silesaurus*.

The feature of possibly the most far-reaching phylogenetic consequences is the presence of a horny beak on the lower jaw of the Krasiejów animal. This situation is similar to that in ornithischians, like *Lesothosaurus* (Sereno, 1991a), although without any additional predentary ossification. Unfortunately, in the mandible of the oldest known ornithischian, *Pisanosaurus* from the Ischigualasto Formation, the anterior area of the dentary with the predentary is not preserved, so it is not completely certain that it was present. Crompton and Attridge (1986) and Sereno (1997:451) proposed that prosauropods might also have had a narrow horny beak at the anterior end of the upper and lower jaws. He referred to a raised bony platform on the premaxillae in *Riojasaurus* from the Los Colorados Formation of Argentina, and in *Plateosaurus* from the Knollenmergel of Germany. This is hardly visible in the original illustrations (Galton, 1984; Bonaparte and Pumares, 1995), which means that these structures are not easy to discern. This is not the case with *Silesaurus*, in which the area for the beak is prominent, but restricted to the lower jaw.

These similarities to herbivorous dinosaurs may mean that (1) *Silesaurus* is an early member of the ornithischian lineage, (2) belongs to the lineage leading to both the Ornithischia and Prosauropoda after its emergence from the ancestral carnivorous stock but prior to splitting, or (3) form a lineage that developed herbivory independently of dinosaurs. The fossil record of the early Late Triassic evolution of dinosaurs is too incomplete to make a reasonable choice.

CONCLUSIONS

In the presence of a pyramidal ascending process of the astragalus associated with a depression (dorsal basin), which articulates with a rather broad posterior process of the tibia, *Silesaurus* is close to the basal Dinosauria, being more advanced than the earliest known mesotarsal archosaurs from the Ischichuca fauna of Argentina. The narrow pelvis with long pubes, the structure of the hind limb, prominent laminae in the cervical vertebrae, and the structure of the braincase place *Silesaurus* within the main lineage leading to dinosaurs. It is more advanced than *Pseudolagosuchus*, but lacks some characters used by Novas (1996) to characterize Dinosauria (e.g., epipophyses on cervical vertebrae and perforate acetabular wall). This position in the morphological spectrum seems to be consistent with the geological age of *Silesaurus*, between *Lagerpeton*, *Marasuchus*, and *Pseudolagosuchus* from the Ischichuca fauna of Argentina, and the first undoubted dinosaurs from the Ischigualasto Formation of Argentina or the Lower Stubensandstein of Germany. Thus *Silesaurus* from Krasiejów strengthens the evidence for a pattern of mosaic or stepwise origin of the diagnostic characters of dinosaurs. This is especially striking in the co-occurrence of a closed pelvic acetabulum and horizontal iliac blade with an aetosaur-like dentition and a horny beak reminiscent of that in the ornithischians (although without any additional predentary ossification) in the lower jaw. *Silesaurus* is the earliest herbivore among the mesotarsal archosaurs.

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