

POSTCRANIAL ANATOMY OF *ANGISTORHINUS*, A LATE TRIASSIC PHYTOSAUR FROM WEST TEXAS

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Abstract—We describe here an incomplete postcranial skeleton associated with a complete skull and jaws of the phytosaur *Angistorhinus grandis* Mehl from the Otischalkian (late Carnian) Colorado City Formation of the Chinle Group in Howard County, Texas. The skeleton consists of two cervical vertebrae and parts of others, complete sacrum and pelvis, 12 ribs, 30 gastralia, an incomplete fibula, fragments of other long bones, and 32 scutes. Particularly interesting features include: (1) the thin neural spines of the sacral vertebrae; (2) the ilia of *Angistorhinus* do not appear to differ significantly from that of *Rutiodon* (= "*Machaeropsopus*"), casting doubt on the taxonomic use of differences in phytosaur ilia; and (3) *Angistorhinus* apparently possesses dermal armor that is unique among phytosaurs in having few pits, most of them small, on the dorsal surface of the primary scutes.

Keywords: phytosaur, postcrania, skeleton, *Angistorhinus*, Otischalkian, Colorado City Member

INTRODUCTION

Phytosaurs are the most common tetrapod fossils from Upper Triassic strata of the Chinle Group. They have a longstanding use in Upper Triassic tetrapod biostratigraphy, though their alpha taxonomy remains in a state of relative confusion (Ballew, 1989; Hunt, 1994; Long and Murry, 1995). This taxonomy is based primarily on cranial characters, and relatively little attention has been paid to phytosaur postcranial anatomy. This is partly because associated crania and postcrania are not well known for many phytosaur taxa. Here, we describe the postcrania associated with a skull of *Angistorhinus* for the first time, and thus provide one of the first published descriptions of diagnostic characters of phytosaur postcrania, particularly vertebrae and dermal armor.

PROVENANCE

The skull and postcrania of *Angistorhinus* described here are from the Colorado City Formation of the Chinle Group at a locality near Otis Chalk in Howard County, Texas (Fig. 1). This is locality 9 of Lucas et al. (1993, fig. 2). At this locality, the skull, lower jaw and partial postcranial skeleton of *Angistorhinus* were found disarticulated, but in close association, in a 15-cm-thick bed of sandy mudstone. Some of the bones, however, also extended into part of the overlying 50-cm-thick bed of fine-grained sandstone. Still, there is no duplication of elements and the relative size of the elements is consistent with a single individual.

The *Angistorhinus* specimen described here is part of the "type assemblage" of the Otischalkian land-vertebrate faunachron (Lucas and Hunt, 1993; Lucas, 1998). Thus, it is of Otischalkian (Carnian) age. The fossil is in the private collection of Robert Kahle.

TAXONOMY

Mehl (1913) established the genus *Angistorhinus* by naming a skull from the Popo Agie Formation in Wyoming *Angistorhinus grandis*. He later named a second skull from the same locality *Angistorhinus gracilis* (Mehl, 1915) and a third, from another Popo Agie locality in Wyoming, *Angistorhinus maximumus* (Mehl, 1928). The holotype skull of *Angistorhinus alticephalus* Stovall & Wharton is from Otischalkian strata near Otis Chalk (Stovall and Wharton, 1936), as is the holotype and referred specimens of *Brachysuchus megalodon* Case (Case, 1929). Long and Murry (1995), following

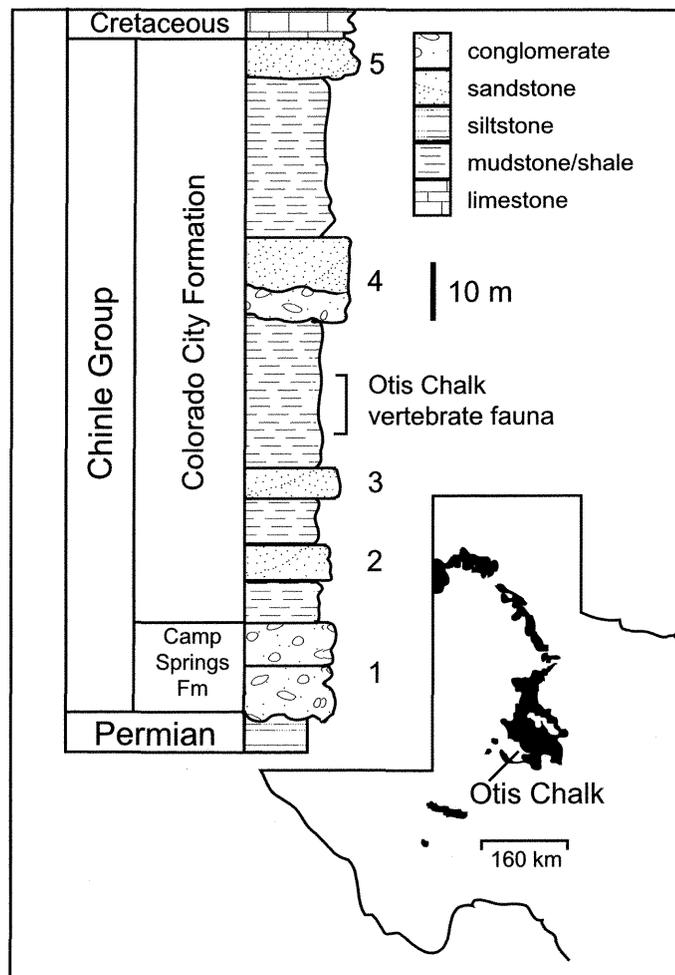


FIGURE 1. Generalized Triassic stratigraphy of the Otis Chalk area and its location in the Chinle Group outcrop belt in West Texas. Numbers refer to Grover's (1984) sandstone bed numbering system.

Gregory (1962), referred *B. megalodon* to *Angistorhinus*, but Ballew (1989, p. 318) and Hunt (1994, p. 139-140) rejected this assignment. Hunt (1994, p. 137-138) regarded *Angistorhinus* as a monospecific

genus (*Angistorhinus grandis* = *A. alticephalus* Stovall and Wharton, 1936 and the other species named by Mehl) and, like Long and Murry (1995, p. 40-41), regarded the Moroccan phytosaur material Dutuit (1977) assigned to *Angistorhinus* to represent a distinct genus. For the purposes of this paper, we follow Hunt's (1994) taxonomy and thus recognize *Angistorhinus* as monospecific. Therefore, we refer the fossils of *Angistorhinus* described here to *A. grandis*.

Recently, Hungerbühler (2001) has claimed that *Angistorhinus* Mehl, 1913 is a junior subjective synonym of *Rutiodon* Emmons, 1856. We doubt this claim because it is largely based on characters of the skull roof that are not preserved in the *Rutiodon* neotype (cf. Colbert, 1947; Hunt and Lucas, 1989). Also, we are unable to replicate Hungerbühler's (2001) claim that the distinctive narial morphology of *Angistorhinus* is present in the *Rutiodon* neotype. Therefore, we continue to recognize *Angistorhinus* as a taxon distinct from *Rutiodon*.

DESCRIPTION

Skull and jaws

Lucas et al. (1993, fig. 6A-B) already illustrated the skull and lower jaws found near Otis Chalk, and we repeat that illustration here (Fig. 2). The skull displays several features that in combination are diagnostic of *Angistorhinus* (Ballew, 1989; Hunt, 1994; Long and Murry, 1995): (1) posteriorly positioned external

nares; (2) supratemporal fenestra at the level of the skull roof; (3) elongate narrow rostrum with no crest; (4) parietals do not protrude posterior to the occipital condyle; (5) short postorbital region of skull; (6) high and arched postorbital-squamosal bar; (7) extensive sulcus on postero-lateral surface of the squamosal; and (8) in lateral view, round posterior squamosal process. We thus are certain this specimen and the associated postcrania can be assigned to *Angistorhinus grandis*. We note here that when photographed, the lower jaw was not properly articulated, so that it appears longer than the snout. However, when properly articulated it is located more posteriorly and thus does not actually protrude beyond the recess between the anteriormost premaxillary teeth.

Postcrania

The postcrania associated with the skull and jaw include two cervical vertebrae and parts of others (Fig. 3), sacrum and pelvis (Fig. 4A-C), 12 ribs and 30 gastralia (Fig. 5), an incomplete fibula (Fig. 4D-E), fragments of other long bones, and 32 scutes (Fig. 6).

Vertebrae

Two nearly complete cervical vertebrae of *Angistorhinus* are preserved (Fig. 3). These cervicals are posterior to the atlas and axis, but their exact position among the remaining cervicals (phytosaur have 7-9 cervical vertebrae: Camp, 1930, p. 63;

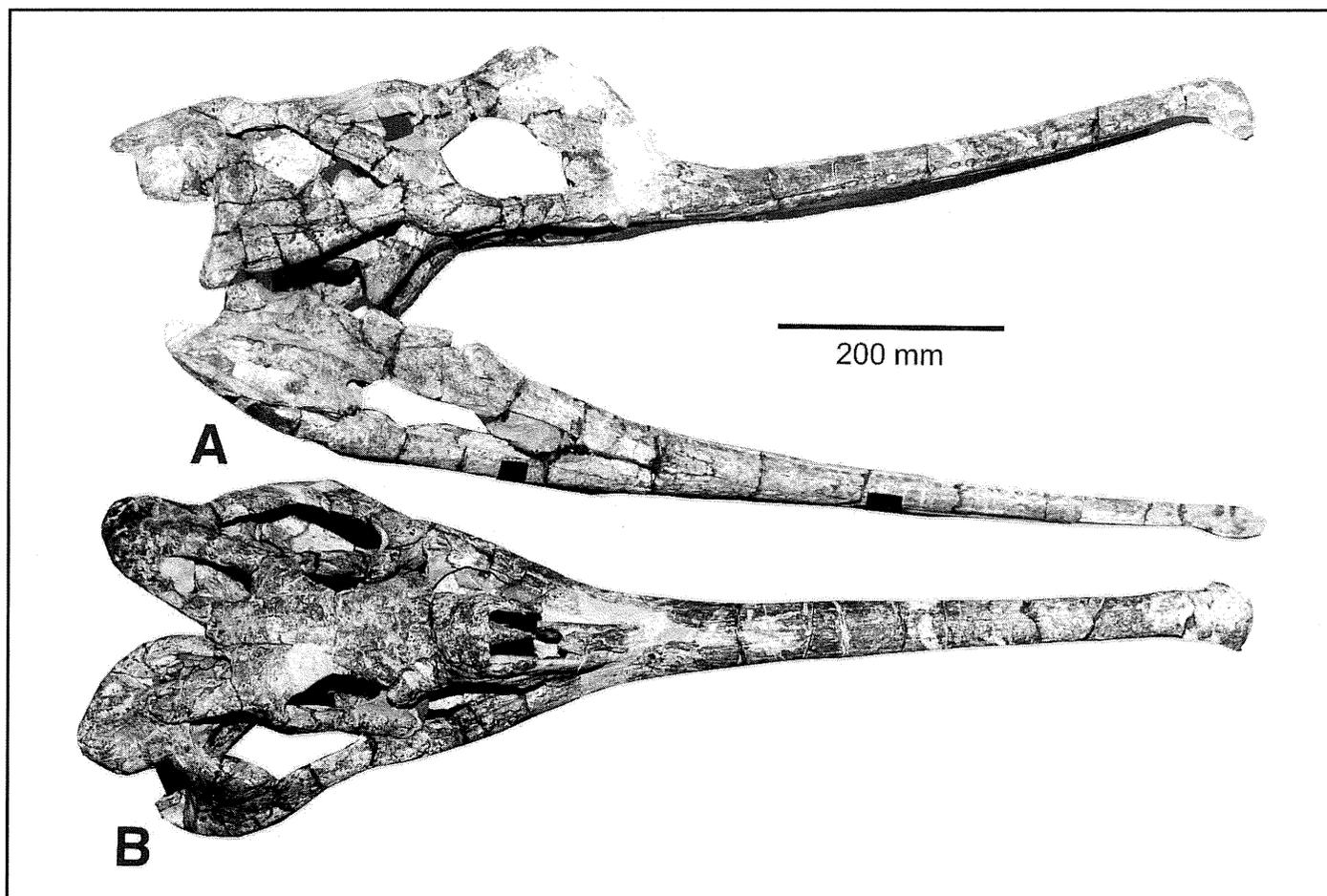


FIGURE 2. Skull and lower jaws of *Angistorhinus grandis* in A, lateral and B, dorsal views. Lower jaw appears longer than snout because it is not properly articulated.

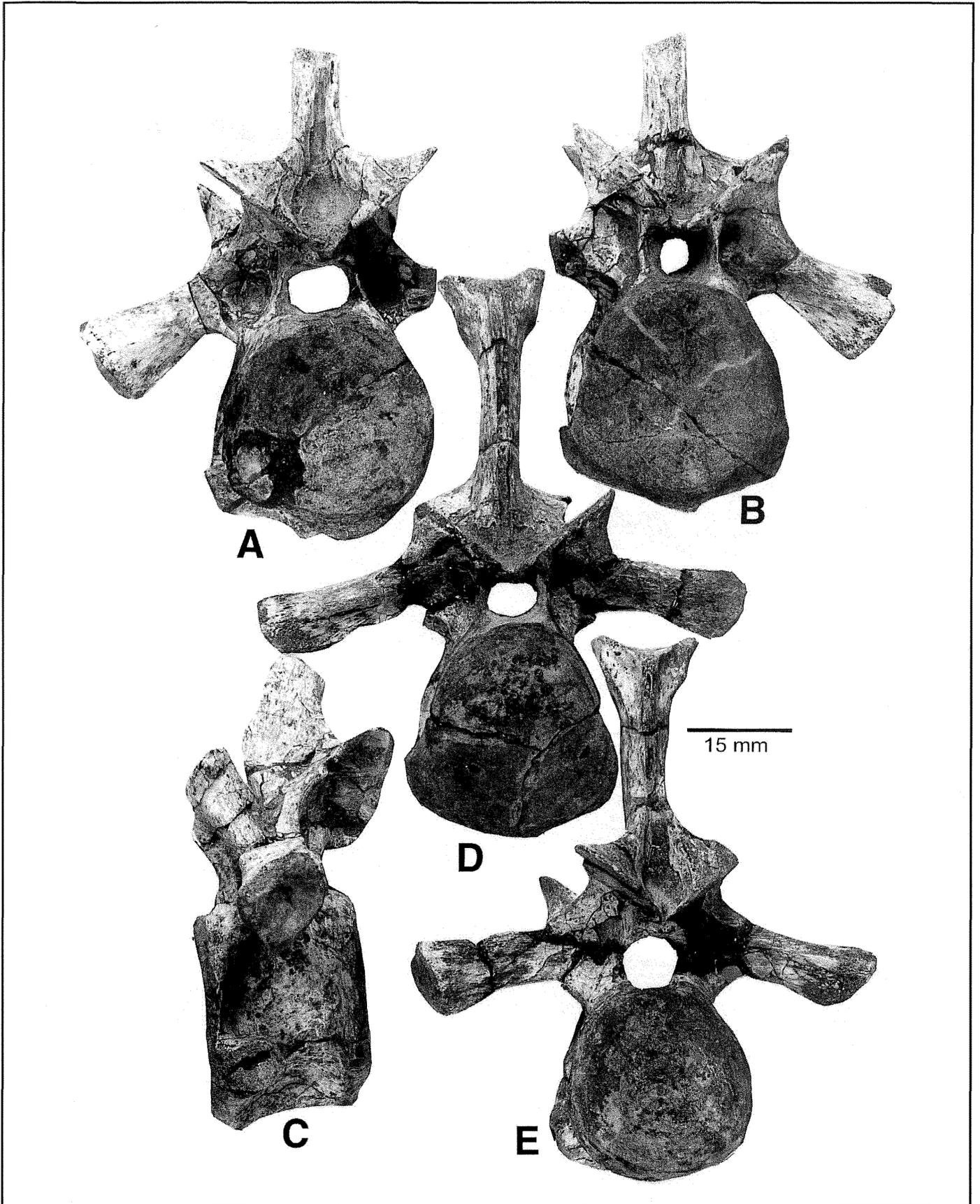


FIGURE 3. Cervical vertebrae of *Angistorhinus grandis*. A-C, Cervical 4 or 5? in A, anterior, B, posterior, and C, lateral views; D-E, Cervical 5 or 6?, in D, anterior and E, posterior views.

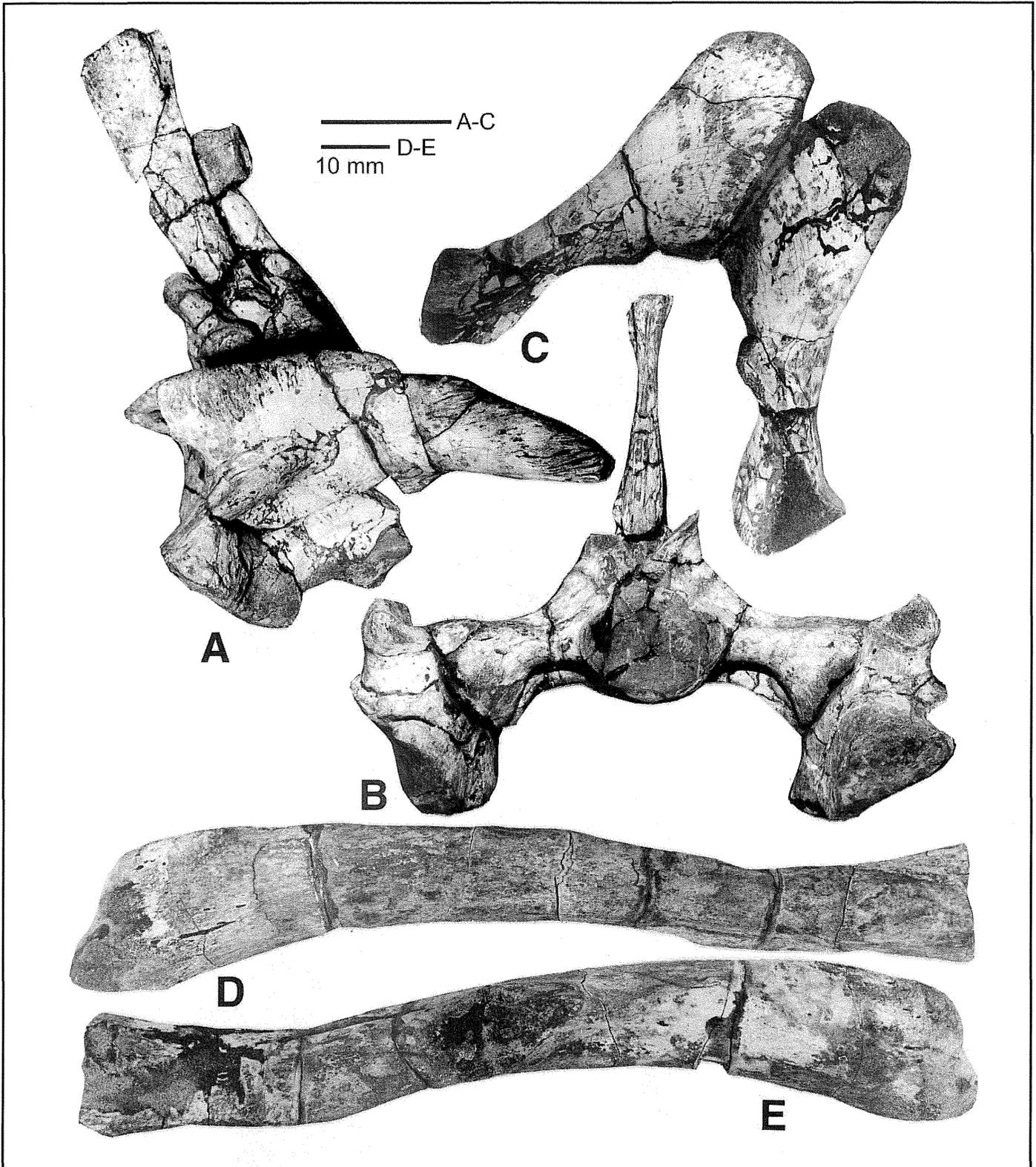


FIGURE 4. Sacrum, ilium, ischia and fibula of *Angistorhinus grandis*. A-B, Sacrum and ilia in A, left lateral and B, anterior views; C, Ischia in ventral view, D-E, Incomplete left fibula in D, lateral and E, medial views.

Westphal, 1976, p. 102) cannot be determined with certainty. Both vertebrae have tall neural spines that have a convex, blade-like anterior edge and a concave, longitudinal posterior groove. The vertebra with a complete neural spine has its dorsal tip broadened to a v-shaped surface that supported a pair of dorsal scutes. The neural spines of both vertebrae are nearly vertical and antero-

posteriorly thin, which, by comparison with Camp (1930, pl. 3), suggests these are probably cervicals 3, 4 or 5 of the series.

The neural canals are relatively small and round in cross section. The centra are slightly amphicoelous and round to slightly trapezoidal in cross section. They have weak ventral keels. The transverse processes are long, blunt-tipped rods that are inclined

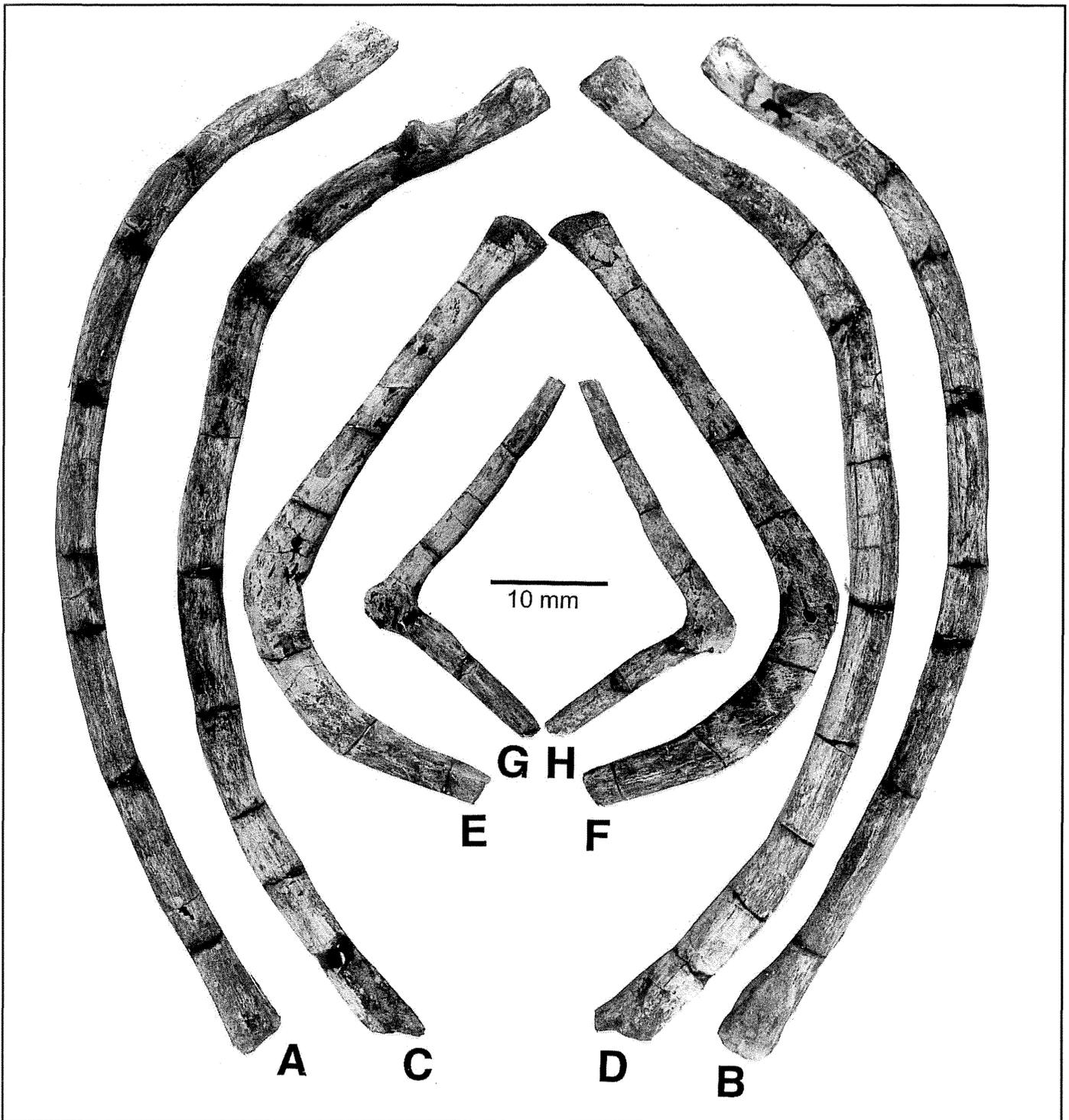


FIGURE 5. Representative ribs and gastralia of *Angistorhinus grandis*. A-D, Ribs. E-H, Gastralia.

slightly ventrally and arise from near the dorso-lateral edge of the neural arch. The parapophyses are on the antero-ventral end of the lateral aspect of the centra and are nearly round, concave depressions. The anterior and posterior zygapophyses are at the base of the neural spine and just above the neural canal as inclined, nearly flat surfaces. The two vertebrae illustrated (Fig. 3) articulate with each other. Both centra measure about 47 mm long, 56 mm wide (both anteriorly and posteriorly), and 59 mm tall. These cervical vertebrae of *Angistorhinus* closely resemble those of other phytosaurs (e.g., McGregor, 1906, fig. 14, pl. 8, fig. 9; Camp, 1930, pl. 3; Westphal, 1976, fig. 4; Long and Murry, 1995, fig. 47)

and thus present no distinctive characteristics of *Angistorhinus*.

Sacrum

The sacrum (Fig. 4A-B) consists of two fused vertebrae, as is the case in all other phytosaurs for which the sacrum is known (Westphal, 1976). The centra are amphiplatyan and have no ventral keels. The neural spines are long, distally thickened and inclined posteriorly. The auricular processes (mass) are distinctly unfused but strongly articulate laterally to the ilia. The thin, distally expanded neural spines of the *Angistorhinus* sacral vertebrae differ from those of "*Machaeroprosoopus*" *adamanensis* (Camp, 1930,

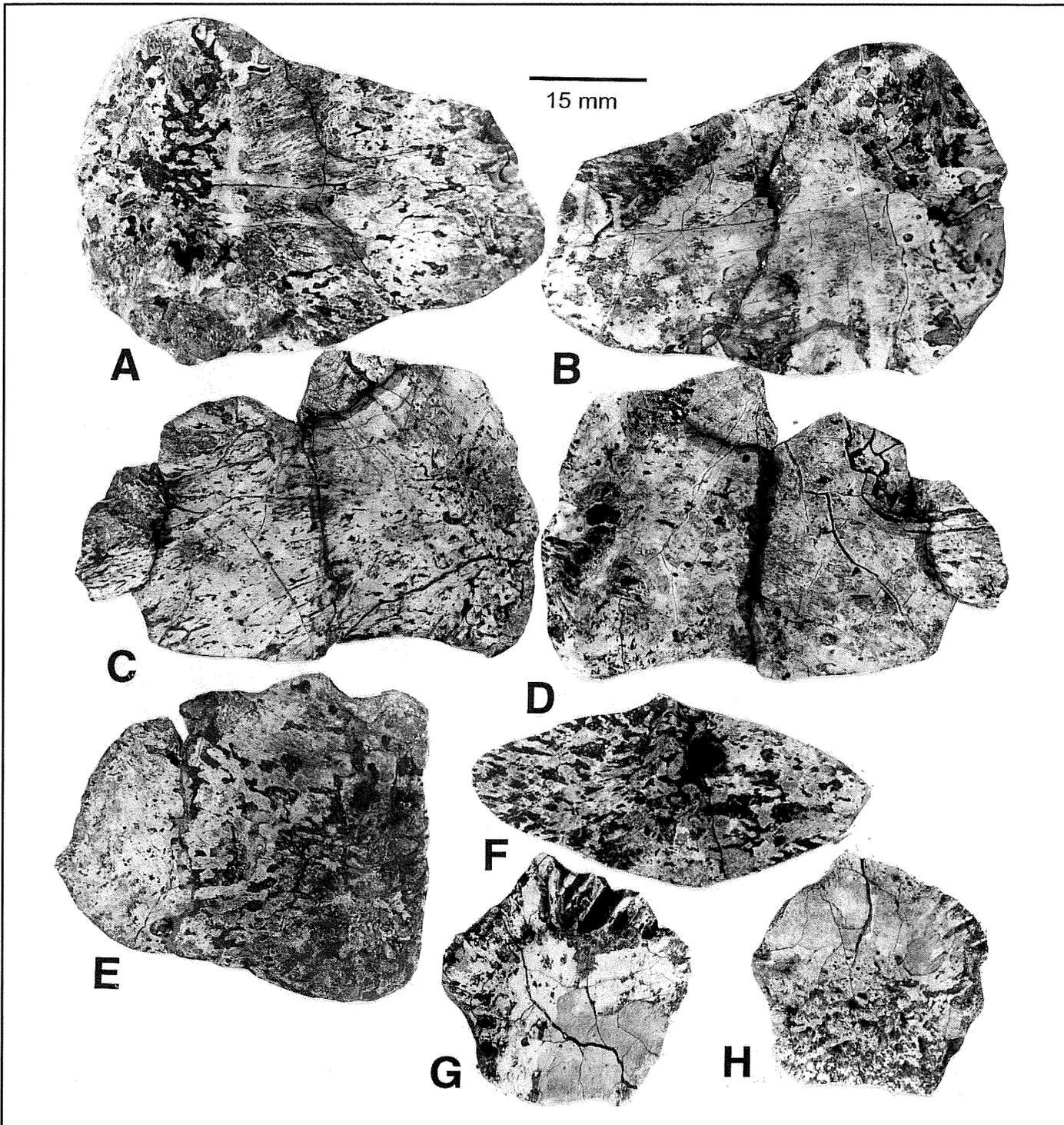


FIGURE 6. Selected osteosclerites of *Angistorhinus* in dorsal (A, C, E-G) and ventral (B, D, H) views.

pl. 3, pl. 4, figs. M-O), *Rutiodon* (McGregor, 1906, pl. 10, figs. 40-40a), *Nicrosaurus* (Huene, 1922, fig. 11) and *Mystriosuchus* (Huene, 1922, fig. 12). This may be a feature unique to *Angistorhinus*.

Ilium

Both ilia are present, sutured to the sacral vertebrae (Fig. 4A-B). The posterior process is long and pointed at its posterior edge. The anterior process is short and has a blunt antero-dorsal edge. The dorsal iliac blade thus is thickened, and broadly convex dorsally. The superior acetabular ridge is strongly developed along the anterior half of the acetabular border, but weak to non-

existent posterior to that. The ilium is generally similar to, although somewhat more elongate than, that of *Angistorhinus* (?) illustrated by Mehl (1928, pl. 39, fig. 3)

Camp (1930, table 5) tabulated differences between phytosaur ilia described up to the time of his work. The *Angistorhinus* ilia illustrated here are essentially identical to those of "*Machaeropsopus*" in the UCMP collection described by Camp in all the characteristics he scored: (1) there is a small "muscular process" on the anterior portion of the crest; (2) the length of the acetabulum is greater than its height; (3) the posterior iliac process is longer than the crest anterior to the post-iliac notch; (4) the

length across the ischio-pubic border is nearly equal to total iliac height; (5) the ischio-pubic border is below the pre-iliac notch; (6) the pubic and ischial articular surfaces are of nearly equal length; (7) the pre-iliac process is less than half as long as the pubic border; (8) the crest just behind the pre-iliac process is bowed upward; (9) the ischial suture bows inward; (10) total length divided by height is about 1.8; and (11) height divided by length across the pubo-ischial suture is about 1.0. Indeed, the ilia illustrated here closely resemble that of "*M.*" *adamanensis* illustrated by Camp (1930, fig. 16, pl. 3). This similarity casts doubt on Hunt's (1994, p. 112, fig. 16) contention that *Angistorhinus* has ilia distinct from those of other phytosaur genera.

Ischium

Both ischia are preserved, fused along a midline suture (Fig. 4C). The proximal end of the ischium is a thick, pyramidal peduncle that articulates with the ilium dorsally and the pubis anteriorly. The ischium's contribution to the acetabulum is thus restricted to the antero-proximal portion of the bone. The distal end is a broad, flat rounded blade that is slightly concave ventrally and slightly convex dorsally. Total length is 210 mm. These ischia well resemble those of other phytosaurs (e.g., Camp, 1930, fig. 16; Long and Murry, 1995, fig. 34D-E).

Ribs and Gastralia

There are parts or all of 12 ribs and 30 gastralia (abdominal ribs) preserved, and those illustrated here (Fig. 5) are representative. All the ribs appear to be double headed, anterior dorsal or posterior cervical ribs (cf. Camp, 1930, fig. 21, pl. 3). They are broadly arcuate with round to elliptical cross sections and not distally broadened. The gastralia preserve mostly the v-shaped central chevron elements and are broadly similar to those of other phytosaurs (McGregor, 1906, pl. 11; Huene, 1922, p. 83-84; Camp, 1930, p. 87; Long and Murry, 1995, figs. 42, 45).

Fibula

An incomplete left fibula (Fig. 4D-E) has a preserved length of 205 mm and a maximum distal width of 37 mm. This bone is missing the proximal end, has a slightly sinusoidal curve to the shaft and an expanded distal end. It closely resembles other illustrated phytosaur fibulae (e.g., Huene, 1922, figs. 53-54; Westphal,

1976, fig. 5c; Long and Murry, 1995, fig. 53b-d). We believe that this is the first illustration of the fibula of *Angistorhinus*.

Dermal Armor

A total of 32 armor plates (scutes) are present, and those illustrated are representative (Fig. 6). Most appear to be dorsal armor, and are characteristic of phytosaur plates in being polygonal in outline with a relatively smooth, concave interior surface and a rugose, convex external surface. Most significant, though, is the generally sparse pitting or absence of pitting on the dorsal surfaces. This condition is very different from the scutes of other phytosaurs (e.g., McGregor, 1906, fig. 11; Huene, 1922, figs. 87, 88, 112, 113, 135b; Camp, 1930, p. 89, pl. 3; Long and Murry, 1995, figs. 26, 44-46). This lack of pitting appears to be unique to *Angistorhinus* and is a feature alluded to earlier by Hunt (1994).

DISCUSSION

Although the specimen described here preserves less than half of the postcranial skeleton, it is significant for the following reasons:

1. The thin neural spines of the sacral vertebrae and the lack of pitting on the dermal armor appear to be features unique to *Angistorhinus*. The latter characteristic may be particularly significant, facilitating identification of *Angistorhinus* from fragmentary material.

2. The ilium of *Angistorhinus* does not appear to differ significantly from that of *Rutiodon* (= "*Machaeropsopos*"), casting doubt on the taxonomic use of differences in phytosaur ilia.

We anticipate that future discoveries and descriptions of associated postcrania of phytosaurs will continue to shed light on their systematics and taxonomy, and may help resolve the confused state of phytosaur taxonomy at the genus level. Of particular interest are autapomorphic features such as the lightly pitted scutes of *Angistorhinus*, which may render possible identification of this genus from fragmentary material, something not currently possible with most phytosaur taxa.

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