

## A new skeleton of *Ianthasaurus hardestii*, a primitive edaphosaur (Synapsida: Pelycosauria) from the Upper Pennsylvanian of Kansas

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A new specimen from the Upper Pennsylvanian of Garnett, Kansas, is referable to the edaphosaur *Ianthasaurus hardestii*. It is the second articulated skeleton known of this species, and possesses previously undescribed midline elements of the skull roof. This specimen features a new autapomorphy, an elongate cross-barred dorsal process on the axial neural spine. The presence of ventral webbing and multiple tubercles on several basal lateral protuberances of the presacral neural spines in this skeleton may represent a sexual dimorphism of *Ianthasaurus*. Two synapomorphies of sphenacodonts and edaphosaurs, the presence of a lateral lapper on the frontal and exclusion of the reduced quadratojugal from the ventral margin of the temporal bar, are confirmed in this specimen. The presence of these traits in *Ianthasaurus* supports the hypothesis that edaphosaurs and sphenacodonts form a clade more derived than other pelycosaur groups. New information provided by this specimen indicates that edaphosaurs can be recognized only by the morphology of their distinctive presacral neural spines. Small, problematical edaphosaur species assigned to the genus *Edaphosaurus* may be reinterpreted as insectivores, closely related to the Garnett edaphosaur and distinguishable from the large, bulky herbivore *Edaphosaurus*.

Un nouveau spécimen du site Garnett (Pennsylvanien supérieur) est assigné à l'édaphosaure *Ianthasaurus hardestii*. Il s'agit du second squelette articulé connu de cet édaphosaure. Ce squelette possède des éléments médians du toit crânien non préservés dans l'autre spécimen de ce genre. Ce spécimen démontre la présence d'une nouvelle autaporphie : l'épine neurale axiale possède un processus transverse dorsal allongé. La présence d'une palmure ventrale et de tubercules multiples sur plusieurs protubérances latérales proximales des vertèbres présacrées indiquent peut-être un dimorphisme sexuel. L'existence de deux synapomorphies des sphénacodontes et des édaphosaures, la présence d'un processus latéral du frontal et l'exclusion du quadratojugal du bord ventral de l'arc temporal, est confirmée par ce spécimen. L'édaphosaure de Garnett possède des caractères qui supportent l'hypothèse selon laquelle les édaphosaures et les sphénacodontes forment un clade plus dérivé que les autres pélycosaures. Ce nouveau spécimen indique que l'Edaphosauridae peut être définie seulement par la morphologie de leurs épines neurales présacrées. Les petites espèces d'édaphosaures d'affinités incertaines qui avaient été assignées au genre *Edaphosaurus* peuvent être réinterprétées comme étant des insectivores étroitement apparentés à l'édaphosaure de Garnett et distincts du grand herbivore *Edaphosaurus*.

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### Introduction

The pelycosaur family Edaphosauridae, represented by the genera *Edaphosaurus* and *Ianthasaurus*, spans the Upper Pennsylvanian and the Lower Permian strata of Europe and North America.

*Edaphosaurus* is one of the most widespread and successful of Permian reptiles. Eight species are currently recognized (Reisz 1986). Dental morphology indicates that *Edaphosaurus* probably fed upon plant material. The majority of differences between *Edaphosaurus* and *Ianthasaurus* are directly attributable to this adaptation to herbivory: large body size, barrel-shaped trunk, relatively small skull, enlarged temporal fenestrae, slightly bulbous marginal dentition, and massive crushing tooth plates on the palate and the medial surface of the mandible. *Edaphosaurus* is adequately represented by five North American species, four of these by cranial as well as postcranial material. In the absence of adequate specimens, the validity of two small European and a small North American species has been questioned by Reisz (1986).

*Ianthasaurus*, the smaller, earlier, and morphologically more primitive member of the Edaphosauridae, is known from a single species from the Upper Pennsylvanian of Kansas. *Ianthasaurus* is distinguished from later edaphosaurs by its small body and dorsal-sail size, slim trunk, relatively large skull, small temporal fenestrae, long and low maxillae with sharp, recurved teeth, caniniform teeth, and no tooth plates (Reisz and Berman 1986). On the basis of the morphology of its marginal and inferred palatal dentition, Reisz and Berman

(1986) suggested that this edaphosaur fed primarily upon soft-bodied insects. The small, elongate body, large head, and small temporal openings support this hypothesis. Therefore, *Ianthasaurus* differs from *Edaphosaurus* essentially in its adaptation to insectivory.

The description of *Ianthasaurus hardestii* (Reisz and Berman 1986) was based solely on material from Garnett, Kansas. The Garnett locality has produced an abundance of vertebrate, invertebrate, and plant remains, including taxa of great phylogenetic significance such as the oldest known diapsid *Petrolacosaurus kansensis* (Reisz 1977, 1981), the earliest sphenacodont *Haptodus garnettensis* (Currie 1977), and other unique, endemic amniote species (Reisz *et al.* 1982; Dilkes 1987). The specimens available to Reisz and Berman (1986) depicted a very primitive eupelycosaur with a single autapomorphy, the presence of at least 29 presacral vertebrae. The holotype also characterized *Ianthasaurus* as bearing a maximum of five pairs of lateral tubercles on each neural spine, with crossbars concentrated on the anterior two thirds of the sail. However, the palate, braincase, occiput, most of the skull table, and much of the pectoral girdle were absent from the known specimens or, in the case of the limb elements, too poorly preserved for descriptive purposes.

The description of the Garnett edaphosaur appeared soon after recent reevaluations of pelycosaur interrelationships. Brinkman and Eberth (1983) showed that the Edaphosauridae and the Sphenacodontidae form a clade defined by several synapomorphies. Reisz and Berman (1986) demonstrated that

*Ianthasaurus* possessed three of the 10 synapomorphies of the edaphosaur–sphenacodont clade, and they inferred the presence of two more.

The subject of this paper is a well-preserved and partially articulated skeleton of *Ianthasaurus* collected by G. MacDonald and M. Heaton from Garnett. The significance of this specimen lies in the presence of most of the skull-roof elements. Closely associated with the skull is an assemblage of 23 presacral vertebrae, including the axis, and a number of other disarticulated elements. The new information provided by this specimen allows for a revised diagnosis of the genus and more complete reconstructions of the skull and sail than those offered by Reisz and Berman (1986).

The nearly complete skull roof also permits more thorough comparisons with later members of the family. *Ianthasaurus* is compared with *Edaphosaurus novomexicanus* and *Edaphosaurus boanerges* not only because these species are the oldest and most primitive members of the genus *Edaphosaurus*, but also because specimens of these species are available for direct comparisons.

The new material prompts a discussion of edaphosaur phylogeny and the probable identity of the small, poorly known edaphosaur species.

### Systematic paleontology

SUBCLASS Synapsida

ORDER Pelycosauria

FAMILY Edaphosauridae Cope, 1882

#### Revised diagnosis

Small to large pelycosaurs with greatly elongated presacral neural spines, which are subcircular in cross section except for a short, laterally compressed proximal portion. Neural spines of the cervical region lean anteriorly, whereas those of the lumbar region curve posteriorly. Most presacral neural spines possess lateral tubercles of regular distribution and development; basal lateral tubercles are always paired.

GENUS *Ianthasaurus* Reisz and Berman, 1986

*Ianthasaurus hardestii* Reisz and Berman, 1986

#### Revised diagnosis

A small edaphosaur characterized by an elongate, cross-barred dorsal process on the axis and at least 29 presacral vertebrae. *Ianthasaurus* differs from other edaphosaurs in the following features: skull long, equal to eight dorsal centra; frontal long and broad anteriorly, with lateral lappet located just posterior to midpoint; parietal with greatest breadth at level of pineal foramen; maxilla elongate with 27–29 sharply pointed, slightly recurved teeth; caniniform teeth present; no development of enlarged tooth plates on the lower jaw; postaxial cervical vertebrae slightly longer than succeeding presacral vertebrae. neural arches of presacral vertebrae laterally excavated and bearing short transverse processes; maximum of five lateral tubercles on each side of neural spine, with some proximal tubercles supported ventrally by slight webbing; no tubercles on neural spines of the posterior region of presacral column; trunk ribs strongly curved proximally and bearing well-developed tubercula; ilium with well-developed, blade-like posterior process.

#### Holotype

KUVP 69035 (University of Kansas Museum of Natural History) consists of a nearly complete series of articulated

presacral vertebrae, several disarticulated dorsal ribs, and several disarticulated skull-roof elements of the right side of the skull. A humerus is also present, as is the posterior two thirds of the lower right jaw.

#### Attributed specimens

ROM 29942 (Royal Ontario Museum) includes several scattered cranial and postcranial bones (also present is an amphibian ilium and several poorly preserved and unidentifiable limb elements). ROM 29941 consists of three isolated vertebrae assigned to a single catalogue number for convenience only. ROM 29940 consists of a first sacral rib, seven caudal ribs, and a partial dorsal neural arch with a fragmented but complete neural spine. ROM 37751, the subject of this study, consists of a semiarticulated skull roof, left angular, both ilia, left pubis, left ischium, 23 presacral vertebrae, several caudal vertebrae, and dorsal and caudal ribs on three closely associated blocks.

#### Horizon and locality

Rock Lake Shale Member of the Stanton Formation, Lansing Group, Missouriian Series, Upper Peusylvauian, NW 1/4, sec. 5, tp. 19E, Putnam Township, Anderson County, Kansas.

### Description

Although not perfectly articulated, ROM 37751 (Figs. 1–3) undoubtedly represents the remains of a single animal; all of the elements lie on the same bedding plane, there is no duplication of cranial and appendicular elements, and the preservation of all elements is identical.

The skeleton is that of an immature animal: none of the neural arches are fused to their centra, the preserved pelvic girdle elements are not coossified, and the cranial elements are of comparable size to those present in the holotype, which has also been shown to be immature (Reisz and Berman 1986).

The skull roof is nearly completely preserved except for the tooth-bearing elements. Problems associated with the removal of the specimen from the quarry resulted in its separation into three small blocks. Consequently, some bone was lost from the skull roof, primarily from the right prefrontal, left postfrontal, and both frontals. Otherwise, most cranial elements are undamaged and the paired dorsal elements have retained their midline sutural contacts. We achieved precise realignment of the separated skull table by measuring the undisturbed distances between the frontal–postfrontal suture at the orbital border and two different points on the midline along the right frontal and repositioning the two blocks in such a way that the complementary measures were restored on the left side.

A revised reconstruction of the skull roof in lateral aspect is shown in Fig. 4a. This reconstruction differs from that offered by Reisz and Berman (1986) in three respects: (1) the orbit is slightly larger than in the original description because of the undetected absence of a posterior process on the holotypic prefrontal; (2) the jugal is more slender; and (3) the temporal fenestra is smaller. These corrections in the reconstruction of the skull of *Ianthasaurus* in lateral aspect result in a much more gracile skull than that suggested by Reisz and Berman (1986). The presence of most of the skull-roof bones permits a reconstruction of the skull in dorsal perspective (Fig. 4b). The exact width of the skull roof, however, remains conjectural because palatal elements are unknown. A partial reconstruction of the skeleton (Fig. 5) provides new information on the nature

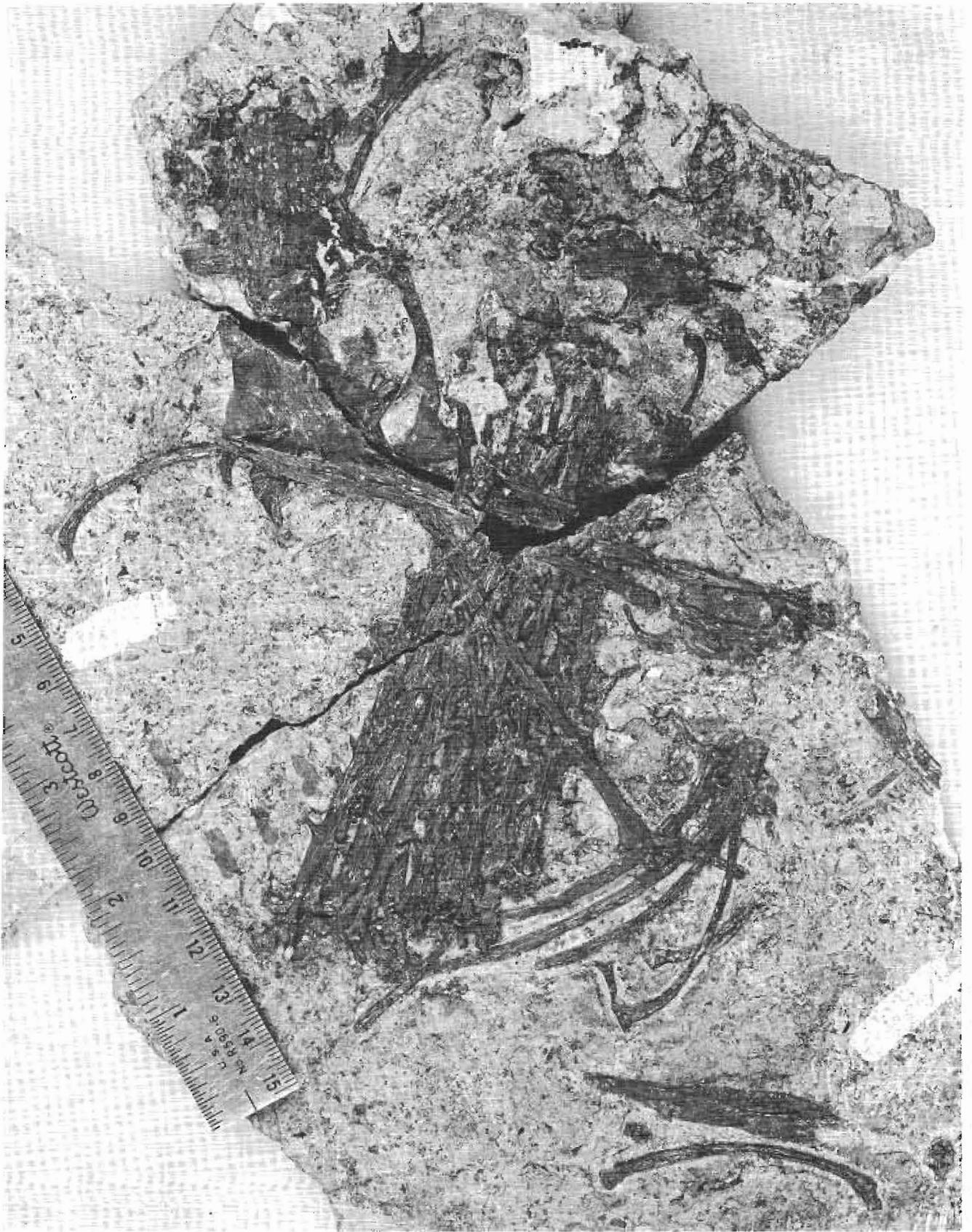


FIG. 1 *Ianthasaurus hardestii*, ROM 37751. Partial skull roof in ventral view, angular, partial vertebral column, and pelvic girdle elements. Scale is in centimetres.

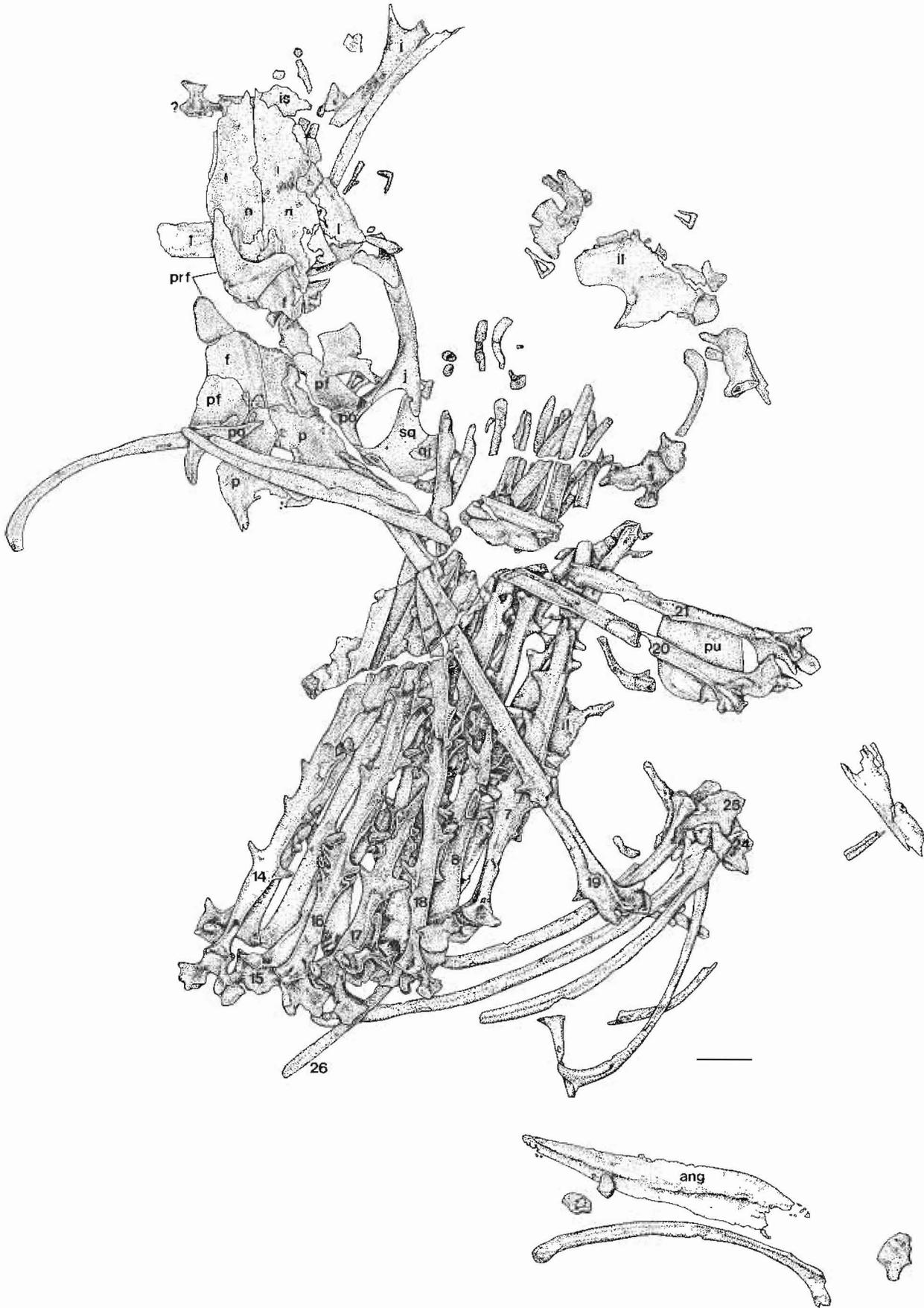


FIG. 2. *Ianthasaurus hardestii*, ROM 37751, referred specimen. Partial skull roof exposed in ventral view, angular, partial vertebral column, and pelvic girdle elements. Abbreviations: ang, angular; ax, axis; f, frontal; il, ilium; is, ischium; j, jugal; l, lacrimal; n, nasal; p, parietal; pf, postfrontal; po, postorbital; pp, postparietal; prf, prefrontal; pu, pubis; qj, quadratojugal; r, dorsal rib; sq, squamosal; 3–21, 24–26, presacral vertebrae. Scale = 1 cm.

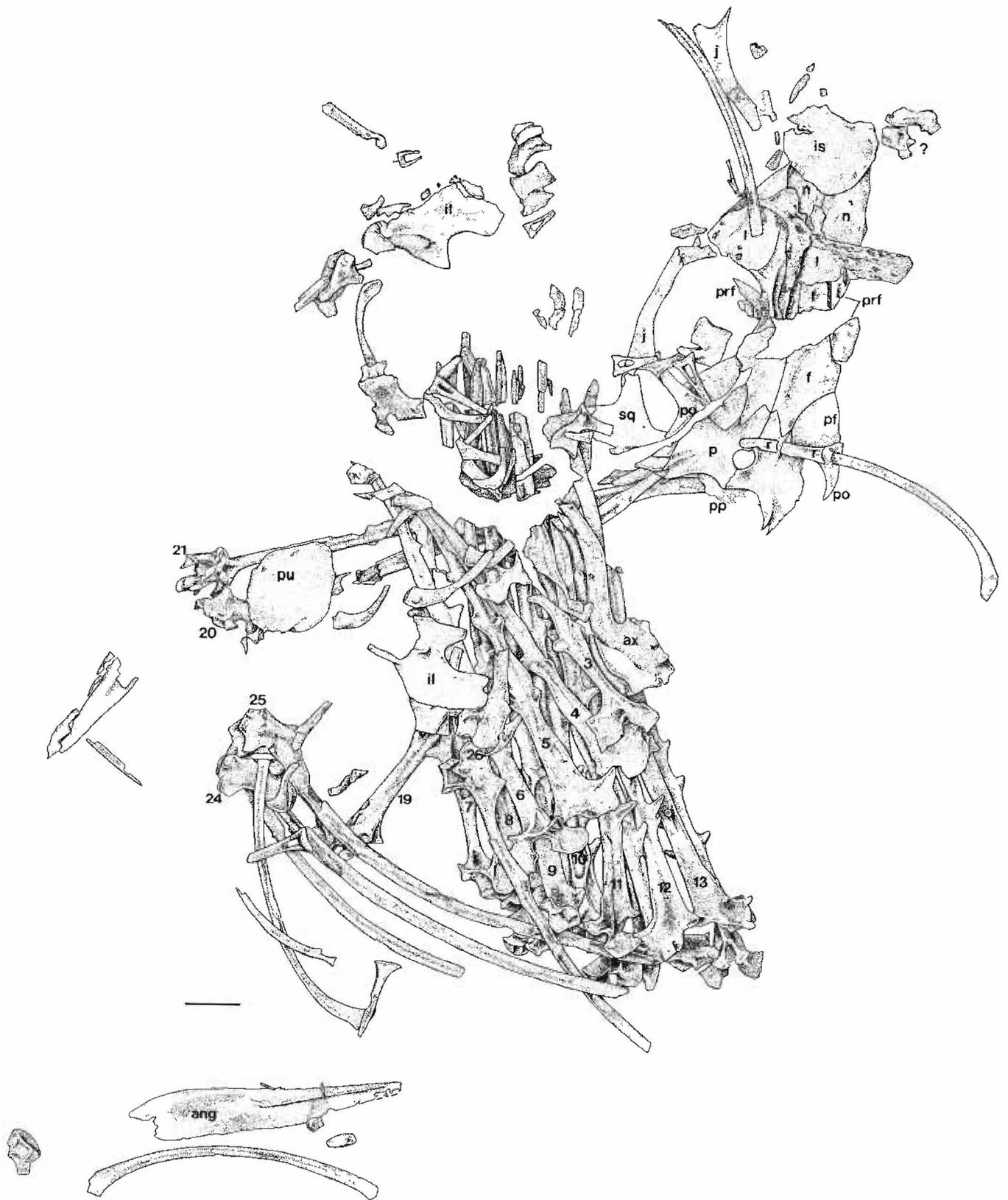


FIG. 3. *Ianthasaurus hardestii*, ROM 37751, referred specimen. Partial skull roof exposed in dorsal view, angular, partial vertebral column, and pelvic girdle elements. See Fig. 2 for abbreviations. Scale = 1 cm.

of the crossbars and illustrates the relationship between head and sail.

The following descriptions refer to the specimens seen in Figs. 2 and 3. For those elements that are not described in detail below refer to the initial description (Reisz and Berman 1986).

The well-preserved nasals are large, long, trapezoidal sheets of bone that dominate the snout (Fig. 2). The nasal is almost as long as the frontal at the midline. The bone is slightly convex in transverse section, becoming progressively flatter anteriorly. A small oval foramen on the ventral surface, its long axis aligned anteroposteriorly, probably represents the egress of the orbito-nasal vein. Laterally, the nasal articulates with the prefrontal and lacrimal along a faintly sigmoidal suture. A small anterior process of the nasal abuts its fellow and forms half of a small wedge between the dorsal processes of the premaxillae. To what extent the premaxilla overlapped this process remains unknown because the overlying ischium obscures this part of the nasals in dorsal view (Fig. 3). A slight concavity on the anterolateral border of the nasal probably represents the posterodorsal margin of the external naris. The nasal–frontal contact, obscured by the lacrimal in dorsal view (Fig. 3) and only partially visible in ventral view (Fig. 2), is a strongly interdigitating suture. The nasal underlies a long, tongue-like process of the frontal (Fig. 3).

Both lacrimals are present but poorly preserved. In each the lacrimal duct has been exposed through loss of the lateral surface.

The frontals are well preserved, except for the loss of bone explained above (Figs. 2, 3). The strongly developed lateral lappet lies approximately two thirds back from the nasals and on its dorsal surface features very shallow but perceptible transverse scalloping. The free lateral border of the lappet is approximately one quarter of the length of the frontal at the midline. An interdigitating suture between frontal and parietal is evident in dorsal view (Fig. 3), but ventrally this interdigitation is not pronounced (Fig. 2). Medially, the frontal receives a small, tongue-like anterior process of the parietal. Lateral to this, the frontal bears a long posterior process that is received by the parietal and contributes significantly to the central parasagittal ridge of that element. Articulation with the postfrontal is long and concave. The anterior process of the frontal tapers to a truncated edge that contacts the nasal. This process is approximately twice as long as the posterior process and bears distinctive striations that suggest that growth at this stage was occurring primarily to the front.

Both prefrontals differ from the description of the holotype (Reisz and Berman 1986) in possessing a well-developed posterodorsal process that bears shallow scalloping on its dorsal surface. Accompanying postdepositional crushing, separation of the main bodies of the prefrontals in ROM 37751 from their posterodorsal processes occurred. These processes retain their respective sutures with the frontals, and presumably this may also be the case with KUVV 69035. Therefore, the prefrontal contributes more to both the dorsal skull roof and the orbital margin than Reisz and Berman (1986) have suggested.

Both postfrontals are present and do not differ significantly from those seen in KUVV 69035 and ROM 29942, except that the scalloping observed by Reisz and Berman (1986) is more pronounced and occupies the lateral two thirds of its dorsal surface. The large anterior expansion of the postfrontal interpreted for ROM 29942 by Reisz and Berman (1986) is actually the posterior portion of that element.

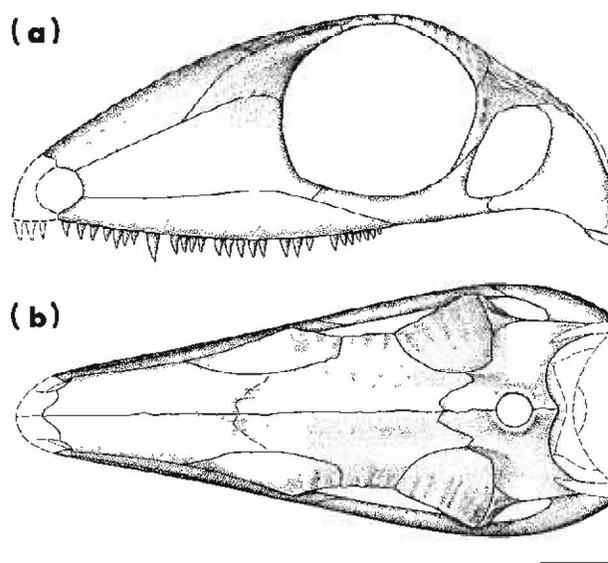


FIG. 4. *Ianthasaurus hardestii*. Composite reconstruction of skull in lateral (a) and dorsal (b) views, based mainly on ROM 37751. Scale = 1 cm.

The postorbitals assume the same outline as that in the holotype. The left element, the best preserved of the pair, shows three characteristics not previously observed. Weak scalloping is present on the lateral surface of the raised orbital margin, and the posterior process has a distinct ridge along the edge articulating with the parietal. The most surprising feature is the small size of the posterior process. The sutural pattern of this process with the squamosal and parietal indicates that the postorbital did not contact the supratemporal.

The parietals remain fully articulated with both frontals and postfrontals. The parietal is approximately two thirds of the length of the frontal. The subcircular pineal opening lies just posterior to the midpoint of the interparietal suture. The pineal foramen features a slight dorsal lip, which contributes posteriorly to a broadly rounded ridge formed by both parietals at the midline. This ridge may have anchored an anterior extension of connective tissue from the neural spine of the axis. The lateral edge of the parietal, overlapped anteriorly by the postfrontal, is moderately convex in dorsal view, with the parietal reaching its greatest width at the level of the pineal opening. The posterolateral wing of the parietal is approximately one fifth of the total anteroposterior length of the bone and bears a relatively deep, narrow groove for the supratemporal. Lateral to this groove, the parietal has a small lateral flange that overlies the postorbital. The posterior margin of the parietal is strongly concave and bears a shallow shelf for receiving the tabular. A parasagittal ridge extends posteriorly from the point where the frontal and postfrontal meet, curves laterally at the level of the pineal foramen, and becomes progressively rounded until it dissipates at the level of posterior edge of the pineal opening.

The single median postparietal, unusually thin, contacts the parietals anteriorly but is imperfectly defined posteriorly and laterally.

Both jugals are present, but only the left element is well preserved and retains most of its sutural contacts. Neither differs from that described by Reisz and Berman (1986) except in having the anterior edge of the dorsal ramus slightly thickened and continuous with the orbital rim on the postorbital.

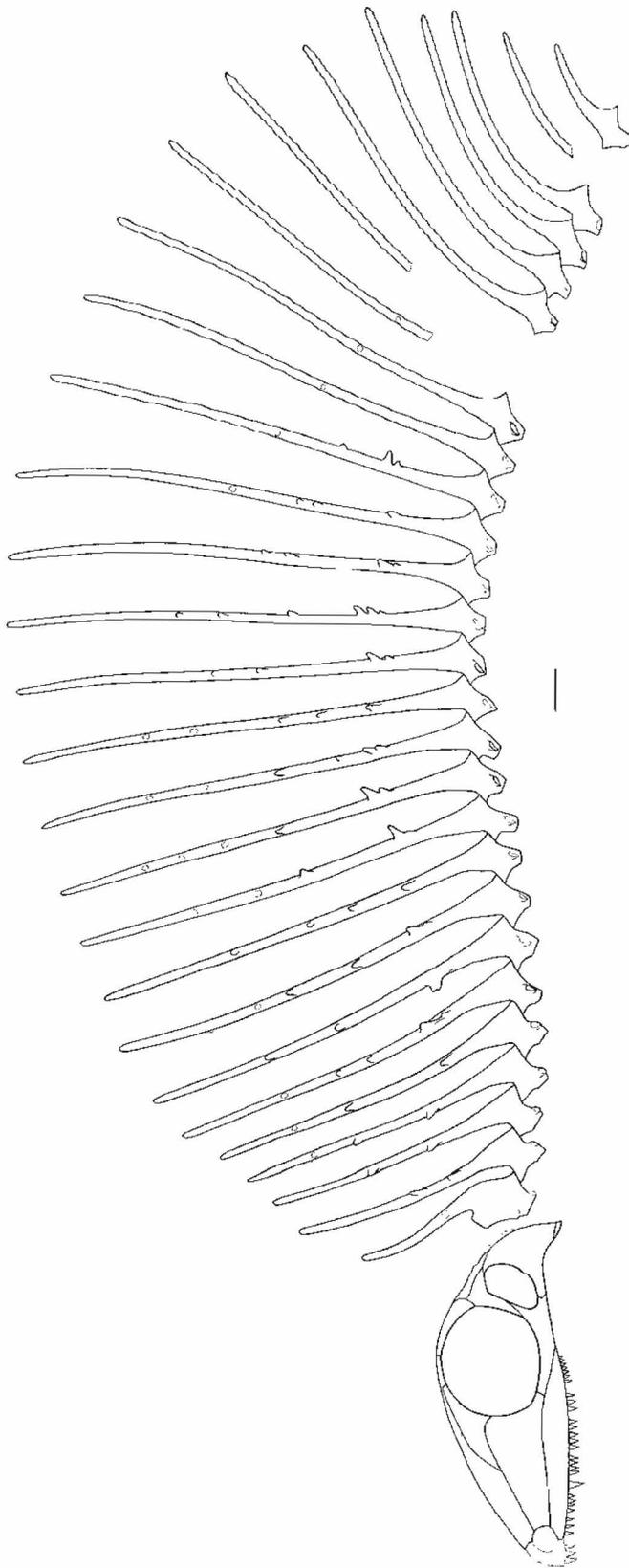


FIG. 5. *Ianthasaurus hardestii*. Composite reconstruction of skull and dorsal sail in left lateral view, based mainly on ROM 37751. Scale = 1 cm.

The left squamosal is preserved in articulation with the postorbital, whereas the suture with the jugal has been displaced slightly. This squamosal differs little from the squamosal of the holotype (Reisz and Berman 1986), except that the posterior flange of bone that supports the supratemporal is preserved in ROM 37751. The flange arises from the posteriormost point of the squamosal–parietal contact and ends directly opposite the ventral margin of the subtemporal ramus.

The left quadratojugal is preserved in articulation with the squamosal. Although the quadratojugal is obscured to some extent by a neural spine medially and a caudal neural arch laterally, the trapezoidal outline of the quadratojugal can be discerned. Ventrally the quadratojugal is relatively thick where it probably abutted against the condylar process of the quadrate. Dorsally the quadratojugal becomes progressively thinner, terminating with a rounded dorsal border confluent with the medial surface of the squamosal. The element is well removed from the lower temporal bar.

Only the left angular remains of the lower jaw; it appears to be essentially complete. It is a long, moderately deep element whose ventral edge is straight for much of its length but curves gently upwards about one fifth from its posterior end. The medial surface of the ventral keel bears weak striations that suggest growth was occurring downwards, deepening the keel. Notably absent is the area associated with the articular. Laterally, the anterior half of the angular is divided into dorsal and ventral portions by a prominent ridge (Fig. 3). The dentary was probably sutured to the anterior region dorsal to this ridge.

Approximately 23 presacral and eight caudal vertebrae are preserved. Centra are absent except for those of two distal caudal vertebrae. Most of the vertebral arches and their spines suffered some crushing and distortion. The neural arches of the second cervical through to the twenty-sixth vertebra lie closely associated and are posterior to the skull. They were laid down in what appears to be a semiarticulated state, preserved as though the sail membrane that once held the vertebrae together had been folded at three points. The first series of vertebrae (Fig. 3) consists of the axis through to the seventh vertebra, at which the first fold occurs. The second series overlies the first (Fig. 3). It consists of the eighth vertebra through to the thirteenth, after which the second fold occurs. Passed back directly over the second series, the third series (Fig. 2) comprises the fourteenth vertebra through to the twenty-first. The orientation of the last three (Fig. 3) is the reverse of that of the other vertebrae. The preservation of both the dorsal surface of the skull and the first vertebral series on the same level, coupled with the close proximity of the axis to the posterior end of the skull, supports the hypothesis that the skull and axial neural spine were connected by an anterior extension of the sail. Prior to entombment and after the decomposition of the soft tissues, the skull of ROM 37751 apparently moved away from the axis, and the neural spines were rearranged as indicated above.

The neural arches and spines are similar in most respects to those described by Reisz and Berman (1986). The dorsal sail of ROM 37751 differs from the holotypic sail in that the 12 neural spines posterior to the axis are approximately 20–25% taller. The remaining neural spines differ little in height from those of the holotype. This difference may result from a period of differential growth in the sail or possibly sexual dimorphism. Lateral excavations of the neural arches are preserved in those vertebrae that did not suffer extensive distortion from being crushed against underlying vertebrae.

The axial neural arch (Fig. 3) is readily identified by the presence of small anterior zygopophyses that project only slightly from the lateral surface of the arch and the anteroposteriorly expanded spine that presumably projected over the posterior end of the atlas neural arch and served for attachment of nuchal ligaments. The posterior border of the anteroposteriorly expanded portion of the spine is relatively thick, whereas the anterior margin is quite thin. Directly above the posterior zygopophyses, a tall neural spine similar to those borne by the postaxial neural arches extends dorsally. This spine, although broken at the tip, appears typically edaphosaurian in nature, being subcircular in cross section and curving forward at the base and slightly backwards distally. A small lateral tubercle can be seen on the right side (Fig. 3), approximately at the same level as basal tubercles of the postaxial neural spines.

The postaxial spines show the typical edaphosaurian arrangement of laterally projecting crossbars that form longitudinal rows along the dorsal sail. The postaxial series of ROM 37751 conforms closely to that described by Reisz and Berman (1986) for the holotype. Lateral tubercles are rare on the posterior dorsals and totally absent on the lumbar neural spines. The anterior dorsals have no more than five pairs of crossbars, with mid-dorsals exhibiting crossbars only on the proximal two thirds of the spine. As in other specimens of this genus, the tubercles project laterally and slightly dorsally, with the largest lateral tubercles located proximally on the spine. Some of the largest tubercles feature small, web-like ventral sheets, which may have served to strengthen the tubercle. The webbing is considerably thinner than the tubercle itself and tapers to a rounded edge. This feature was not observed in the holotype or ROM 29942, possibly because of the manner of exposure of the spines or because the feature may have been so poorly developed as to elude observation. In addition to the webbing, accessory tubercles are borne by several basal tubercles. The seventh vertebra is interesting: it features both multiple tubercles and ventral webbing. As in the holotype and other specimens, the tubercles distal to the basal pairs are less prominent and accordingly may feature weaker webbing. The pairing of lateral tubercles becomes more irregular distal to the basal pair, occasionally assuming a staggered appearance.

Several ribs from the dorsal, lumbar, and caudal regions are preserved but do not add new information to the original description of the genus (Reisz and Berman 1986).

A pubis, an ischium, and both ilia are preserved. The ilia (Fig. 3) appear well preserved with the exception of some loss of bone along the anterior edge; both exhibit the blade-like posterior process observed by Reisz and Berman (1986). Neither element possesses a well-defined ventral border because of the immaturity of the animal. The left pubis underlies two posterior dorsal neural spines. An overlapping fold along the posterior edge of this bone probably represents the location of the obturator foramen. The contribution to the acetabulum may be represented by a slightly thickened, smooth region of bone at the margin next to the obturator foramen. The remainder of the element is otherwise nondescript. The ischium, identified by its thick, concave dorsal margin, underlies the anterior portion of the skull. Because of crushing, marginal distortion, and loss of bone, its assignment to the left side is tenuous.

### Discussion

In 1940 Romer and Price suggested that edaphosaurs and the younger caseids were two distinct herbivorous lineages of the

suborder Edaphosauria. Four decades later Kemp (1982) and Reisz (1980), employing cladistic analysis, hypothesized that edaphosaurs were more closely related to the carnivorous ophiacodontids and sphenacodontids. Following a more rigorous analysis, Brinkman and Eberth (1983) hypothesized that edaphosaurs and sphenacodonts formed a clade defined by several synapomorphies. The latter theory implies that herbivory had evolved within the Edaphosauridae, suggesting that the group must have passed through a carnivorous stage, possibly as insectivores. This was confirmed by the discovery of the insectivorous edaphosaur *Ianthasaurus* (Reisz and Berman 1986). The osteology of *Ianthasaurus* also provides direct evidence for the hypothesis of close relationships between edaphosaurs and sphenacodonts (Brinkman and Eberth 1983).

The initial description (Reisz and Berman 1986) showed that *Ianthasaurus* possesses the following derived features of edaphosaurs and sphenacodonts: (1) a prearticular twisted posteriorly as to underlie the pterygoideus process of the articular, (2) a pterygoideus process formed by the articular alone, and (3) excavation of the lateral surfaces of the neural arches.

Reisz and Berman (1986) inferred the presence of two additional synapomorphies shared with sphenacodonts: a small quadratojugal excluded from the temporal bar, and a frontal lateral lappet. A small quadratojugal located medial to the squamosal in ROM 37751 confirms the first. The quadratojugal of *Ianthasaurus* is similar to that of *Haptodus* in its configuration and small size. Reisz and Berman (1986) deduced the presence of the frontal lateral lappet from the wide gap between the prefrontal and postfrontal elements in their tentative reconstruction of the skull. The contribution of the frontal to the orbital margin in ROM 37751 is approximately that postulated by Reisz and Berman (1986). This is so despite the observation that the absent posterodorsal process of the holotypic prefrontal was not detected by Reisz and Berman (1986). The frontal lappet of *Ianthasaurus* assumes the most primitive state observed in edaphosaurs, being broad anteroposteriorly and shallow in transverse dimension. The frontal lappet of *E. novomexicanus* extends farther laterally and has a reduced contribution to the orbital margin (S. P. Modesto and R. R. Reisz, personal observation). In *E. boanerges* this apparent trend is continued and the frontal contribution to the orbital margin is greatly reduced (personal observation).

In addition to the shallow lateral lappet, the frontal of the Garnett edaphosaur is primitive in featuring a relatively long and broad anterior process, approximately half the length of the frontal at the midline. The frontal of *Ianthasaurus* is also primitive in featuring weak yet discernible sculpturing. The long anterior process, the transversely short lateral lappet, and weak sculpturing give the frontal an appearance similar to that observed in *Haptodus*, the most primitive known sphenacodont.

The parietal of the Garnett edaphosaur resembles the parietal of *Haptodus* and *Ophiacodon* more closely than that of *Edaphosaurus*. The lateral edge of the parietal is convex in dorsal aspect and the posterior process is directed posteriorly, unlike the condition seen in *Edaphosaurus*, where dorsal expansion of the temporal fenestra embayed the parietal laterally, and the posterior process of the parietal became posterolaterally directed following lateral expansion of the posterior cheek. In addition, the parietals form a posterior median wedge in *Ianthasaurus* probably because of the relatively large size and posterior location of the pineal foramen. Although the parietal

of *Ianthasaurus* is similar to that of *Haptodus* (Currie 1977, 1979) in the respective convexity and concavity of its lateral and posterior edges, the parietal of the Garnett edaphosaur is distinct in that it contacts the squamosal lateral to the supratemporal.

The postorbital of *Ianthasaurus* bears a small posterodorsal process which is excluded from contacting the supratemporal by the parietal. A short posterior process is also present in both *E. novomexicanus* and *E. bounerges* (personal observation), and as in *Ianthasaurus*, there is no evidence indicating contact with the supratemporal posteriorly. A postorbital-supratemporal contact may have indeed strengthened the union between the cheek and skull table in a short-cheeked animal such as *Procolophon* (Carroll and Lindsay 1985), but the absence of such a contact in edaphosaurs implies that a long posterior process of the postorbital did not necessarily develop in association with the development of a lateral temporal opening as suggested by Carroll (1986).

Other aspects of the skull table imply a primitive morphological grade for *Ianthasaurus*. The postfrontal of *Edaphosaurus* has a broad anterior expansion, probably resulting from the lateral expansion of the supraorbital shelf and possibly also from the dorsal expansion of the temporal fenestra. Reisz and Berman (1986) interpreted the postfrontal of *Ianthasaurus* as having a large anterior expansion as in *Edaphosaurus*. Unfortunately, the orientation of the isolated postfrontal in ROM 29942 was misidentified by Reisz and Berman (1986). ROM 37751 reveals that the posterior portion of the postfrontal is more transversely broad than the anterior portion. This pattern is also observed for the postfrontal in *Haptodus*, *Archaeothyris*, and *Eothyris*. In relative size and configuration, the temporal fenestra of *Ianthasaurus* (Fig 4a) resembles closely that of *Haptodus*. The size of the temporal fenestra relative to the cheek in *Ianthasaurus* is not significantly enlarged when compared with the same opening in *Edaphosaurus*. The primitive configuration of the postfrontal, the short lateral lappet of the frontal, the small size of the temporal opening, and the transversely broad parietals necessitate the revised familial diagnosis given in the Systematic Paleontology section. Until materials presently unknown for *Ianthasaurus* are available and provide information that may expand diagnosis offered here, the family must be defined only by the morphology of the distinctive presacral neural spines.

The presence of a dorsal sail in the small pelycosaur *Ianthasaurus* requires a reconsideration of the possible functions of the distinctive edaphosaur dorsal sail. General consensus holds that the pelycosaur sail served for heat exchange rather than for protection or sexual display. This hypothesis is supported by a correlation between body volume and sail area in sphenacodontids (Romer 1948). If the dorsal sail served as a thermoregulatory device in edaphosaurs, one would expect a correlation between sail area and body volume similar to that seen in sphenacodonts. The reverse is true for *Edaphosaurus*, in which relative sail area decreases with increasing body volume (Romer and Price 1940; Berman 1979). *Ianthasaurus* is distinguished among edaphosaurs in possessing the smallest sail relative to body size, a characteristic Reisz and Berman (1986) considered primitive for the family. In addition, the heat-exchange theory does not account for the presence of the distinctive lateral tubercles of the neural spines. The pattern of the crossbars suggests that the sail may have also served for individual recognition. This hypothesis is supported by the observation that although the crossbars are distinctly set both vertically on

the same neural spine and horizontally across the series, the pattern observed for ROM 37751 differs from that for KUV 69035. Lastly, the edaphosaur sail may have had a defensive purpose or served to make the animal appear larger and more formidable. This is supported by four observations: (1) the anterior and posterior neural spines sweep over the neck and hips, respectively; (2) the sail bears an imposing array of lateral projections; (3) the lateral tubercles typically reach their greatest length proximally, projecting over the epaxial musculature; and (4) the cervical and anterior dorsal presacral neural spines are anteroposteriorly expanded in the most advanced members of the family. To what degree the above hypotheses accurately account for the function of the edaphosaurid sail remains highly speculative.

The elongate dorsal process on the axial neural spine represents the second autapomorphy known for *Ianthasaurus*. This process increases the forward extent of the dorsal sail in the Garnett edaphosaur (Fig. 5). The axial neural spine in *Ianthasaurus* apparently compensates for the cervical spines that are less strongly swept forward than in other edaphosaurs. The dorsal process of the axial neural spine probably had minimal interference in the flexibility of the neck, outside that allowable by the presence of the remaining cervical spines, yet may have provided additional protection from predators in the anterior region of the neck. In addition, the rugose ridge formed posterior to the pineal opening on the parietals and the close proximity of the axial neural spine to the skull surface suggest that the dorsal sail may have extended to the dorsal surface of the skull, to the posterior edge of the pineal opening.

The significant proportion of multiple tubercles and ventral webbing on the basal tubercles of ROM 37751 and the observation that the anterior presacral neural spines are 25% longer than those of the holotypic sail raise the possibility that *Ianthasaurus* may have been sexually dimorphic. These differences, however, are not great enough to merit a separate specific diagnosis. Multiple tubercles are not unique to *Ianthasaurus*. Carnegie Museum specimen CM 8540, attributed to *Edaphosaurus cruciger* by Romer (1952), features a lateral tubercle that clearly bears a small accessory process (see also Berman 1979). However, no other cases of multiple tubercles of this nature have been reported for *Edaphosaurus*.

Available dentition suggests that *Ianthasaurus* fed primarily on soft-bodied insects (Reisz and Berman 1986). The sharp, recurved teeth are not capable of shredding plant material as leaf-shaped teeth are; the later are common to herbivorous reptiles lacking massive, crushing tooth batteries. The skull and mandible appear too lightly built to suggest a small carnivore role for *Ianthasaurus* (Reisz and Berman 1986). The adaptation to insectivory in a small, primitive member within a group comprising mostly large herbivores is strong testimony that herbivory had evolved within the Edaphosauridae.

Current evidence accordingly suggests that the edaphosaurs evolved first as small insectivores, bearing the characteristic cross-barred sail that distinguished them from primitive sphenacodonts with which they shared a recent common ancestor. The phylogenetic progression seen in the edaphosaurs is the evolution of adaptations associated with herbivory. These adaptations include modified dentition, the development of a barrel-shaped trunk (containing an enlarged, possibly compartmentalized gut with endosymbiotic microorganisms), and the evolution of large body size. These modifications are common to extant herbivorous lizards and are not shared with carni-

vorous lizards (Zimmerman and Tracy 1989). The increase in body size also may have been driven by intraspecific competition. On the other hand, the trend towards large size may have instead been a response to a similar increase in body size of their main predators, the sphenacodonts. This hypothesis is supported by the presence of a primitive sphenacodont at Garnett, slightly larger than *Ianthasaurus* and well advanced towards a predaceous lifestyle (Reisz and Berman 1986). Conversely, the trend towards large body size in sphenacodonts may have been a response to the trend seen in edaphosaurs.

Consequently, it should be possible to identify edaphosaur material, in the absence of dental indicators, as belonging to either an insectivore or a herbivore. The postcrania of insectivorous edaphosaurs may be identified by small body size, elongate trunk, trunk ribs that are curved mainly proximally and bear well-developed tubercula, and cervical centra of slightly greater lengths than dorsal centra. Herbivorous edaphosaurs may be identified in the absence of cranial material by large size, cervical centra with lengths less than those of dorsal vertebrae, and strongly curved trunk ribs lacking proper tubercles. The strong curvature of the ribs implies the presence of an enlarged, possibly compartmentalized digestive tract bearing cellulolytic microflora.

Four edaphosaur species are represented by fragmentary postcranial material. Because the family is no longer monogeneric, possession of long neural spines with lateral tubercles cannot be used to assign material to the genus *Edaphosaurus*. An edaphosaur of medium size from the Lower Permian of West Virginia, of which no cranial material is known, has been confidently identified as *Edaphosaurus colohistion* on the basis of strongly curved ribs and neural spine morphology characteristic of the better known Texan edaphosaurs (Berman 1979). A spine fragment from Pennsylvania, identified by Case (1908) as *Edaphosaurus raymondi*, possesses no diagnostic characters and is in all likelihood a *nomen vanum*. A partial vertebra from Czechoslovakia, assigned to *Edaphosaurus mirabilis*, may belong to the genus *Ianthasaurus*, for it is also Late Pennsylvanian in age and of small body size. A partial skeleton of the Early Permian *Edaphosaurus credneri*, from the German Democratic Republic is diminutive in size and features few tubercles on the posterior presacral neural spines. It may also belong to *Ianthasaurus* because of its small size and the rarity of tubercles on the posterior neural spines. *Edaphosaurus raymondi*, *E. mirabilis*, and *E. credneri* need to be restudied. If these species are reassigned to *Ianthasaurus* the geographic and temporal ranges of this genus will be greatly increased, perhaps equal to those of *Haptodus*.

The information provided by *Ianthasaurus* supports the hypothesis that the poorly known pelycosaur *Lupeosaurus* is an edaphosaur. Recently, Sumida (1989) described new material of this unusual pelycosaur. He noted that *Lupeosaurus* shares several derived features with *Ianthasaurus* and *Edaphosaurus* yet remains distinct from the latter two genera in the absence of lateral tubercles of the neural spines and the possession of an exaggerated, enlarged clavicular plate and a flared dorsal scapular blade. Because of the absence of cranial materials, Sumida (1989) tentatively referred the genus to the Edaphosauridae, recognizing that the lack of lateral tubercles is possibly a primitive condition for edaphosaurs that may not necessarily bar the inclusion of *Lupeosaurus* in the Edaphosauridae. However, ROM 37751 reveals that no derived cranial characters are known for edaphosaurs and suggests that if *Lupeo-*

*saurus* cranial materials were to become available they would be informative only at the subfamilial level. Nevertheless, confident assignment of *Lupeosaurus* to the family must await a thorough phylogenetic review of the Edaphosauridae.

*Ianthasaurus* plays an important role in our understanding of the adaptation to herbivory in early amniotes. The Garnett edaphosaur possesses features that support the hypothesis that herbivory had developed within the family Edaphosauridae. The known material of *Ianthasaurus* exhibits a number of derived characters that support the hypothesis of an edaphosaur-sphenacodont clade. This is further supported by the observation that the skull-roof elements of this primitive edaphosaur ostensibly resemble those of the most primitive sphenacodont, *Haptodus garnettensis*. The information provided by the skull-roof elements has shown also that the Edaphosauridae can be defined only by the morphology of the presacral neural spines. This study has stressed the need for the reexamination of other early edaphosaur material. Future studies may reveal *Ianthasaurus* to be as geographically and temporally widespread as its sphenacodont counterpart *Haptodus*.

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