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Ianthasaurus hardestii n. sp., a primitive edaphosaur (Reptilia, Pelycosauria) from the Upper Pennsylvanian Rock Lake Shale near Garnett, Kansas

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A new, small pelycosaur, **Ianthasaurus hardestii**, has been discovered in the well-known, richly fossiliferous locality in the Upper Pennsylvanian (Missourian) Stanton Formation, near Garnett, Kansas. It is represented by a partial, semi-articulated skeleton and scattered elements of at least three other individuals. The small, insectivorous *Ianthasaurus* possesses a number of primitive pelycosaurian features but also shares several derived characters with the large Early Permian herbivore *Edaphosaurus*, justifying its inclusion in the family Edaphosauridae and its recognition as the oldest and most primitive member of that group.

Un nouveau petit pélycosaure, **Ianthasaurus hardestii**, a été découvert dans la localité abondamment fossilifère bien connue de la formation de Stanton, Pennsylvanien supérieur (Missourien), près de Garnett, Kansas. Il est représenté par une partie d'un squelette semi-articulé et par des éléments éparpillés appartenant à trois autres individus. Le petit *Ianthasaurus* insectivore exhibe un nombre de particularités pélycosauriennes primitives, mais il présente plusieurs caractères dérivés communs avec le grand *Edaphosaurus* herbivore du Permien inférieur, ce qui justifie sa place dans la famille des Edaphosauridés et de le considérer comme le membre le plus ancien et le plus primitif de ce groupe.

[Traduit par la revue]

Introduction

At a site near Garnett, Kansas, commonly referred to as the Garnett quarry, the Upper Pennsylvanian (upper Missourian) Rock Lake Shale Member of the Stanton Formation has produced a rich thanatocoenosis of plants (macrofossils, ovules, and miospores), invertebrates (arthropods, molluscs, brachiopods, corals, bryozoans, and foraminiferans), and vertebrates. This unusual assemblage was preserved as a result of the gradual flooding of a stream valley during a regressive−transgressive sequence (Reisz *et al.* 1982). The Garnett quarry, sporadically worked during the 1930's and 1940's, was intensively quarried only in 1953 and 1954 by the late F. E. Peabody. Following further sporadic collecting, a 4 year program of excavation was begun by the senior author in 1979, yielding additional specimens of forms already known from this site, as well as new taxa.

Vertebrate remains collected from the Garnett quarry include fish, amphibians, and reptiles. The fish are represented by numerous specimens of a small coelacanth, named *Synaptotylus newelli* by Echols (1963) but probably attributable to *Rhabdoderma* (Forey 1981), a scattered skeleton of a very large, unidentified coelacanth, and a few isolated xenacanth shark spines. Only two amphibians have been described: the fragmentary remains of the embolomere *Hesperoherpeton* (Peabody 1958) and the skull and partial postcranial skeleton of the rhachitome *Actiobates* (Eaton 1973). Not only are most of the Garnett vertebrate remains those of terrestrial reptiles, but also they represent the most diverse and advanced assemblage for any Pennsylvanian locality. The best known and most common reptile is *Petrolacosaurus kansensis* (Lane 1945; Peabody 1952; Reisz 1977, 1981), a small diapsid known only from this site. It is represented by more than 50 specimens, including complete and nearly complete, articulated skeletons. A small specimen of a probable protorothyri-

did captorhinomorph, consisting of a few vertebrae and a hind limb, has been discovered recently; positive identification, however, is best deferred until additional materials are found.

All other reptiles collected from the Garnett quarry are mammal-like reptiles of the order Pelycosauria. *Haptodus garnettensis*, first described by Currie (1977) on the basis of a fragmentary skull and an incomplete, partially articulated skeleton, is now represented by an additional dozen partial skulls and lower jaws, two articulated partial verebral columns, and a nearly complete but disarticulated skeleton. *Haptodus garnettensis* is the oldest known sphenacodont, and the genus is considered to be closely related to the ancestry of the therapsids, the advanced mammal-like reptiles (Currie 1979). A small, enigmatic pelycosaur, originally described as *Edaphosaurus ecordi* (Peabody 1957) and recently renamed *Xyrospondylus ecordi* (Reisz *et al.* 1982), is represented by a single cervical vertebra. A third small pleycosaur that was collected and briefly mentioned by Peabody (1954, 1957) is an ophiacodont. The articulated skeleton that Peabody found was thought to be similar to *Clepsydrops*, but subsequent preparation and the discovery of additional specimens of more mature individuals now indicate that this ophiacodont is probably the oldest known representative of the genus *Ophiacodon*.

Examination of all the fossil materials collected by Peabody from the Garnett quarry has disclosed the presence of yet another undescribed small pelycosaur, which is the subject of this paper. A series of poorly preserved neural spines without centra was briefly noted and tentatively attributed by DeMar (1970) to an immature, *Dimetrodon*-like sphenacodont. Reisz *et al.* (1982) showed that this specimen is an edaphosaurid, rather than a sphenacodontid pelycosaur, and they tentatively assigned it to *Edaphosaurus*. Their determination was based on the discovery of an additional portion of the specimen that included neural spines possessing the lateral tubercles that are so typical of the genus. Further, they collected fragmentary

FIG. 1. *Ianthasaurus hardestii,* n. gen. et sp. Holotype (KUVP 69035) includes partial vertebral column, cranial elements, and humerus. Scale = 5 cm.
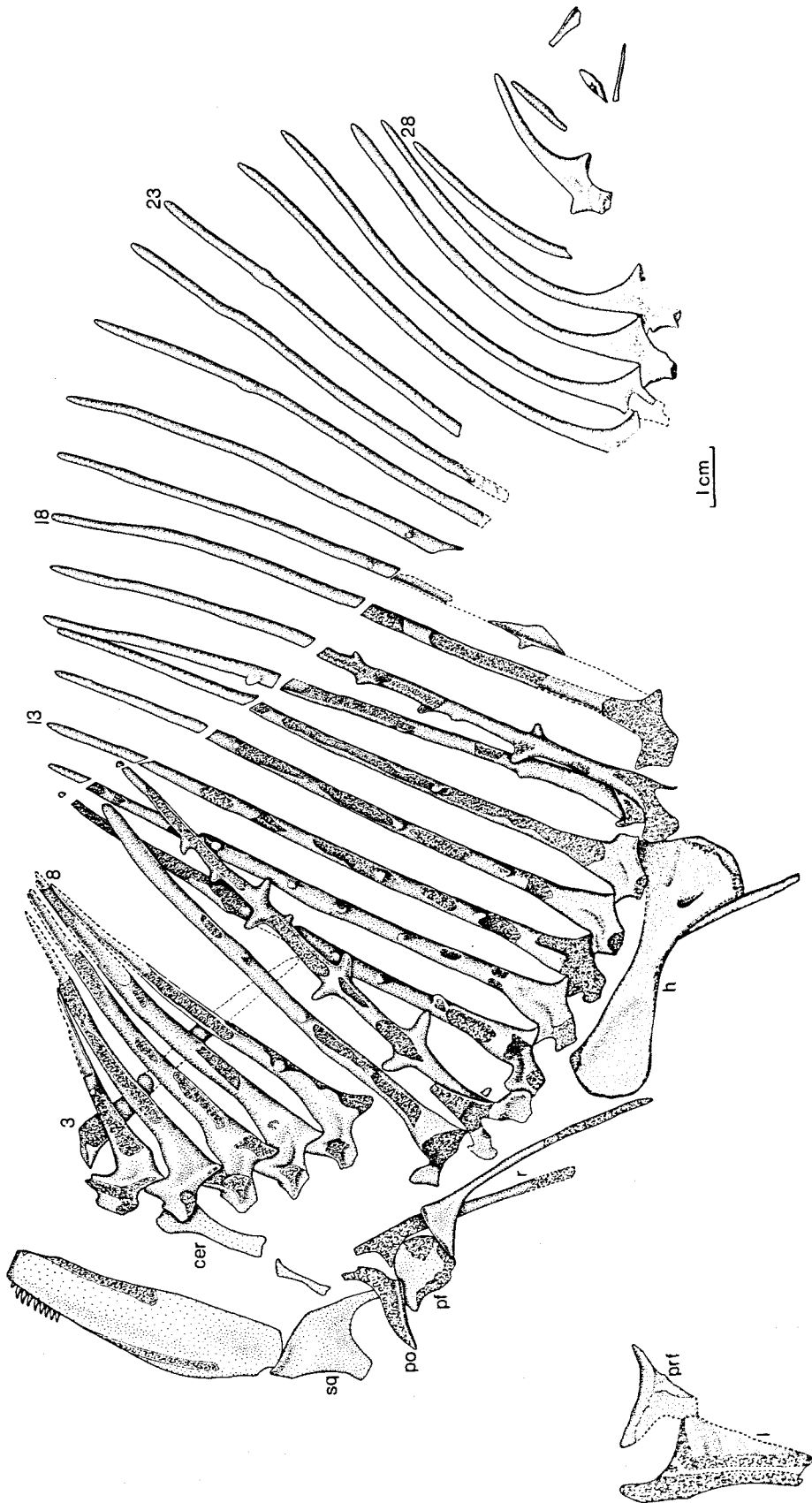
FIG. 2. *Ianthasaurus hardestii*, n. gen. et sp. Left side of holotype sail, KUVP 69035. Abbreviations: cer, cervical rib; h, humerus; l, lacrimal; pf, postfrontal; po, postorbital; prf, prefrontal; r, dorsal rib; sq, squamosal; 3–28, presacral vertebrae.
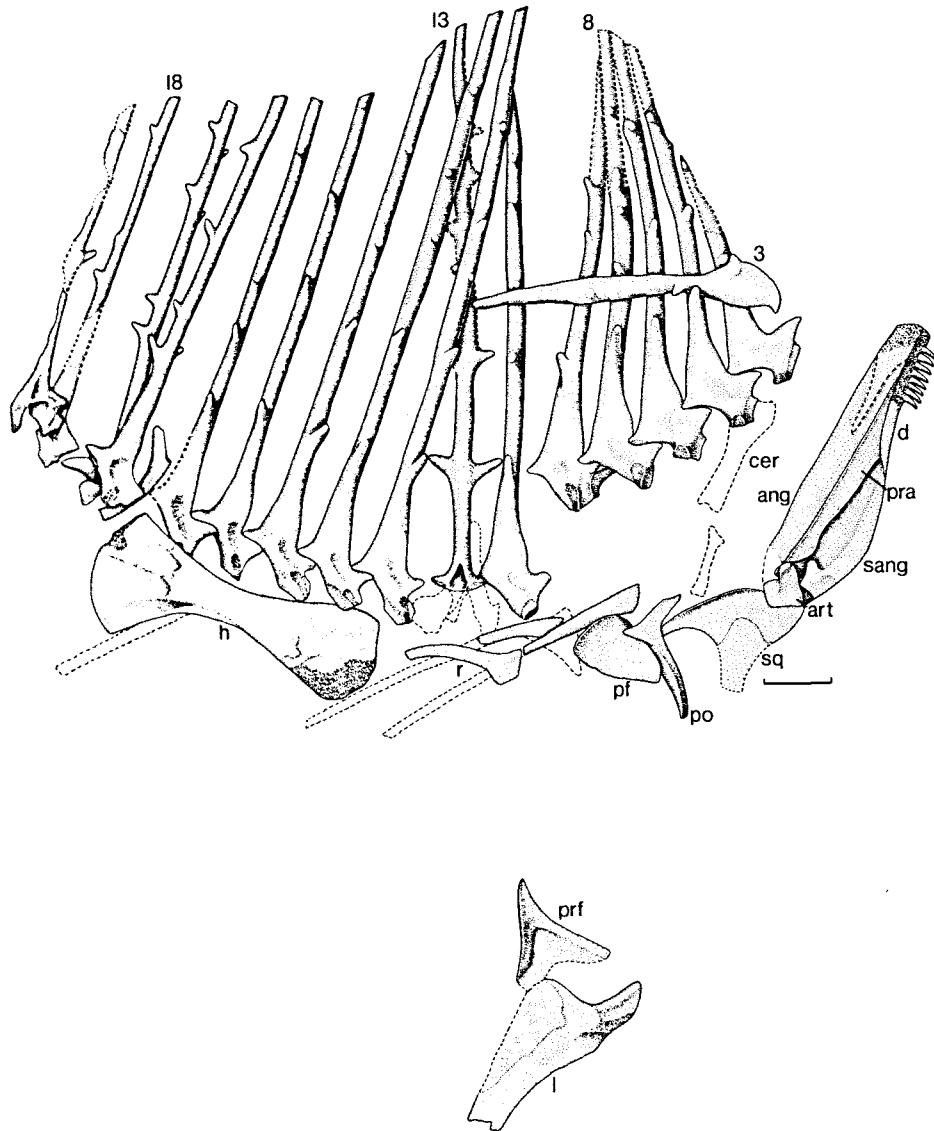
FIG. 3. *Ianthasaurus hardestii*, n. gen. et sp. Right side of holotype sail, KUVP 69035. Abbreviations: ang, angular; art, articular; cer, cervical rib; d, dentary; h, humerus; l, lacrimal; pf, postfrontal; po, postorbital; pra, prearticular; prf, prefrontal; r, dorsal rib; sq, squamosal; 3–19, presacral vertebrae. Scale = 1 cm.

remains of other skeletons from the Garnett quarry that possessed *Edaphosaurus*-like neural spines, which they also attributed to this genus. This study reveals that the Garnett edaphosaur is sufficiently different from the well-known, large Early Permian representatives of that genus to warrant the erection of a new genus and species, *Ianthasaurus hardestii*. The Garnett species provides enough information about the primitive edaphosaur morphology to permit the reevaluation of the fragmentary remains of other small edaphosaurs from the Late Pennsylvanian of North America and the Permo-Carboniferous of Europe.

Systematic paleontology

SUBCLASS Synapsida
ORDER Pelycosauria
FAMILY Edaphosauridae
GENUS *Ianthasaurus* n. gen.

Type species
Ianthasaurus hardestii n. sp.
Diagnosis

A small edaphosaurid pelycosaur distinguished from other members of the family in the following features: skull long, equal in length to about eight dorsal centra; elongate maxilla, with 27–29 sharply pointed, slightly recurved teeth; caniniform-like teeth present; no development of enlarged tooth plates on inner surface of lower jaw; at least 29 presacral vertebrae; lateral surfaces of neural arches of presacral vertebrae excavated; centrum lengths of postaxial cervical vertebrae slightly greater than those of rest of presacral column; maximum of five lateral tubercles per side of neural spine; neural spines of posterior region of presacral column lacking lateral tubercles; transverse processes of presacral vertebrae short; trunk ribs not strongly curved and with normally developed tubercula; ilium possessing well-developed, posterior blade-like expansion.

FIG. 4. *Ianthasaurus hardestii*, n. gen. et sp. Disarticulated skeletal remains, ROM 29942. Abbreviations: acor, anterior coracoid; c, centrum; f, femur; j, jugal; m, maxilla; pf, postfrontal; po, postorbital; r, rib; sc, scapula; x, unidentified limb element; i–vi, neural spines. This figure and Fig. 5 show parts of ROM 29942 in part and counterpart relationship, with neural spines iv, v, and vi partially preserved on two blocks.
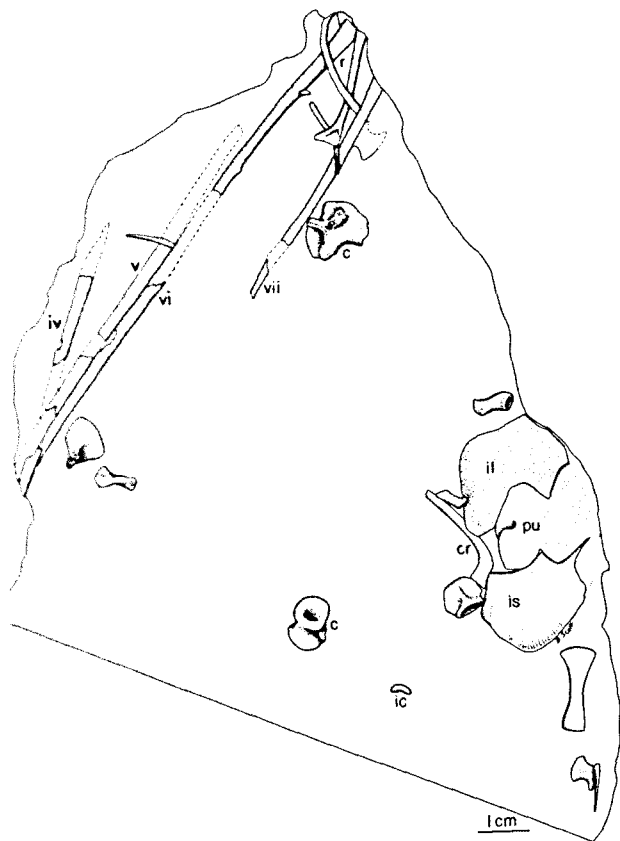
FIG. 5. *Ianthasaurus hardestii*, n. gen. et sp. Disarticulated skeletal remains, ROM 29942. Abbreviations: c, centrum; cr, caudal rib; ic, intercentrum; il. ilium; is, ischium; pu, pubis; iv–vii, neural spines. Parts of neural spines iv, v, and vi are also present on the block shown in Fig. 4.

Ianthasaurus hardestii n. sp.

Etymology

Iantha refers to the Iantha River, 1 km northwest of the type locality; *sauros* is Greek for lizard. Specific name recognizes Mr. and Mrs. C. A. Hardesty on whose property the type locality is located.

Holotype

University of Kansas Museum of Natural History, KUVP 69035, consists of portions of the cranial, axial, and appendicular skeleton (Figs. 1–3). The axial skeleton is represented by a nearly complete and articulated series of 27 presacral vertebral neural arches with spines believed to include the third cervical through the last, or second to last, lumbar; one cervical, three anterior dorsal, and fragments of four posterior dorsal ribs lie near the column. Closely associated with the vertebral sail are the disarticulated lacrimal, prefrontal, postfrontal, postorbital, and squamosal of the right side of the skull, and the posterior two thirds of the right mandible. A left humerus also lies near the column.

KUVP 69035 is preserved on three small blocks (Fig. 1): one block contains the anterior portion of the presacral column, cranial elements, and the humerus; a second block has the posterior portion of the presacral column; and the third and smallest block possesses the fragments of the four posterior dorsal ribs. Much of the holotype is poorly preserved as a

result of *in situ* leaching of the bone and extensive damage to the bone surfaces during collection and original preparation of the specimen. Prior to this study the block containing the anterior portion of the presacral vertebral series, as well as the cranial elements and humerus, was exposed so as to show the left side of the column, and the block containing the posterior portion of the presacral vertebral series was exposed showing its right side. These exposures of the holotype were prepared further by the authors, using a cyano-acrylate ester or "super glue" product to reinforce the bone, and then thoroughly impregnated and embedded with a clear polyester resin so that the skeleton could be exposed from the opposite sides of the blocks.

Referred specimens

Royal Ontario Museum, ROM 29942, preserved on two blocks (Figs. 4, 5) that have a partial part and counterpart relationship, consists of the following disarticulated and randomly scattered elements of the skull and postcranial skeleton: maxillae, left jugal, postfrontals, postorbital, probable anterior coronoid, several fragmentary neural arches and spines, three dorsal and a caudal centrum, an intercentrum, fragmentary presacral ribs, a caudal rib, a right scapula and anterior coracoid, nearly complete left pelvis, a femur, and a portion of manus. In addition to a small amphibian ilium, there is a long, poorly preserved limb element and several unidentifiable bones that cannot be safely assigned to *Ianthasaurus*. The limb element is preserved on a lower bedding plane than the other elements.

ROM 29941 includes a cervical vertebra, a dorsal vertebra with associated right rib, and a lumbar vertebra with an attached rib (Fig. 6). Although all three vertebrae are contained on a single block, only the cervical and lumbar lie on the same bedding plane; assignment to a single catalog number is for convenience, because there is no evidence that they belong to a single individual.

ROM 29940 includes a partial dorsal neural arch, with essentially complete neural spine, and a first sacral and seven caudal ribs preserved on a single block (Fig. 7); it is not certain that the vertebra and ribs belong to the same individual.

A poorly preserved, isolated left pelvis, KUVP 1425 (Fig. 8), collected near the Garnett quarry, has been mistakenly assigned by Peabody to *Petrolacosaurus* (1952) and to *Edaphosaurus ecordi* (1957). Its assignment to *Petrolacosaurus* predates the discovery of well-preserved pelves of articulated skeletons of this genus (Reisz 1981), and its assignment to *Edaphosaurus* was based on similarities in the shape of this pelvis to those of the large Early Permian species (Peabody 1957; Reisz *et al.* 1982). Although the identity of KUVP 1425 will remain uncertain until this type of pelvis is found as part of a skeleton, it can be stated that it is not like the pelvis of *Ianthasaurus*. The pelvis of ROM 29942 differs from that of KUVP 1425 in possessing a well-developed posterior process of the iliac blade.

Horizon and locality

Rock Lake Member, Stanton Formation, Lansing Group, Missourian Series, Upper Pennsylvanian; NW 1/4, NE 1/4, sec. 5, tp. 20 S, rge. 19 E, Putnam Township, Anderson County, Kansas.
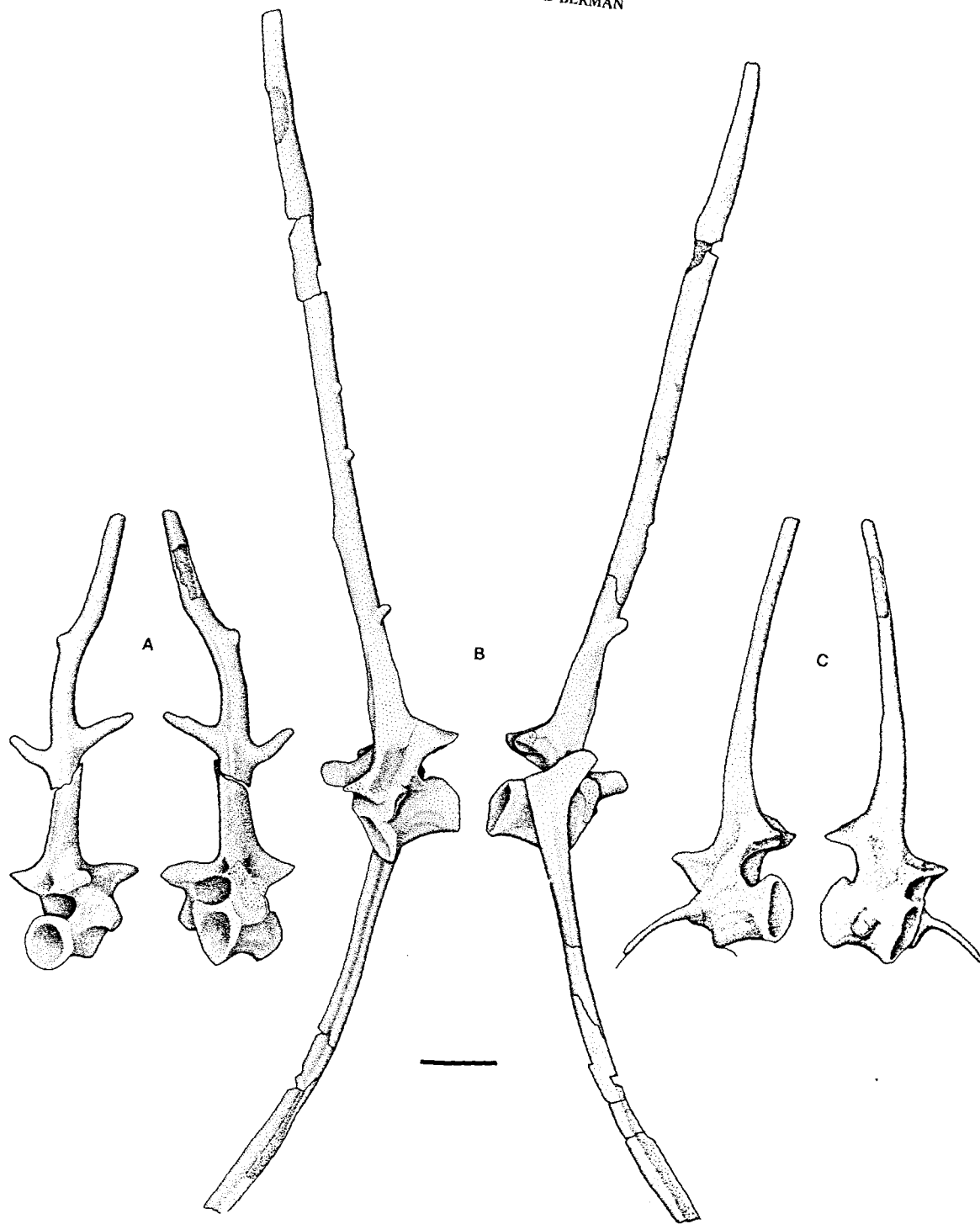
Diagnosis

Only known species of *Ianthasaurus*.

Fɪɢ. 6. *Ianthasaurus hardestii*, n. gen. et sp. Isolated vertebrae, ROM 29941, shown from both sides. (A) Cervical vertebra. (B) Dorsal vertebra with associated rib. (C) Lumbar vertebra with attached rib. Scale = 1 cm.

Description

The skull elements and partial lower jaw of the holotype KUVP 69035 and referred specimen ROM 29942 exhibit some striking differences from those of the well-known *Edaphosaurus* species of the Early Permian (Romer and Price 1940). It might, therefore, be argued that they do not belong to the same individual or species represented by the *Edaphosaurus*-like vertebrae with which they are closely associated. Supporting this view are the observations that in the Garnett quarry deposits it is not uncommon for partial skeletons of several taxa to be intermingled on the same bedding plane and that

several types of pelycosaurs occur at Garnett that are difficult to identify solely on the basis of isolated cranial elements. Several reasons can be offered, however, for accepting the assignment of the skull and vertebral elements of KUVP 69035 and ROM 29942 as belonging to the same species. (1) Each specimen appears to represent a single individual; in both there is no duplication of any of the cranial elements, and they are all of an appropriate size to have belonged to a single individual. (2) In the holotype the skull elements are preserved near the anterior end of the vertebral column, and they remain in the proper sequence to suggest that the head had been rotated backward from its original articulation with the vertebral
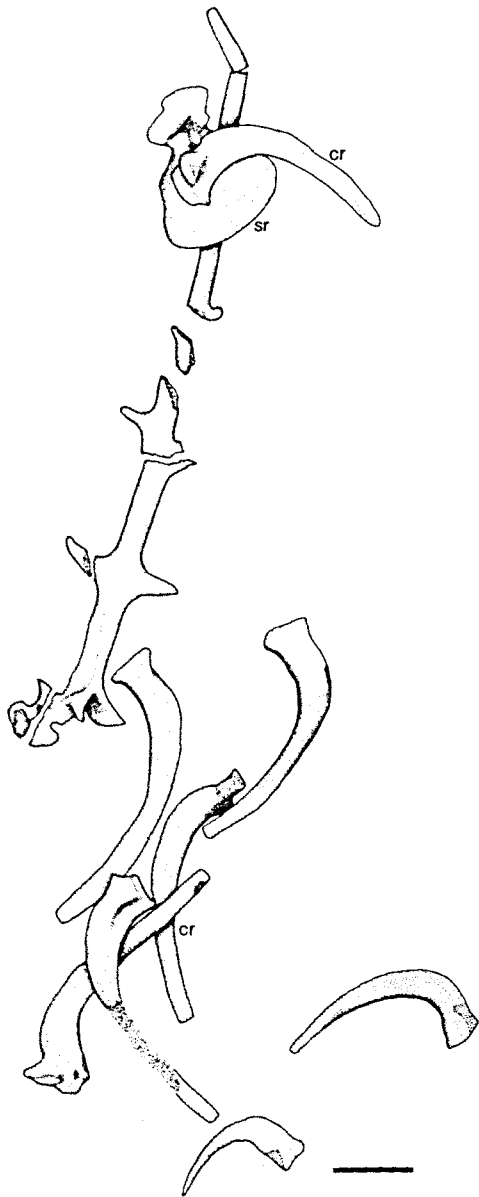
FIG. 7. *Ianthasaurus hardestii*, n. gen. et sp. Partial dorsal neural arch with neural spine, first sacral and seven caudal ribs, ROM 29940. Abbreviations: cr, caudal rib; sr, sacral rib. Scale = 1 cm.

column. (3) Cranial elements duplicated by the two specimens are identical in size and morphology. (4) The mandibular dentition of the holotype is similar to that of the maxillae of ROM 29942, and the well preserved maxillary dentition of ROM 2994 is unlike that of any other reptile known from the Garnett deposits. (5) In KUVP 69035 the degree of ossification, the relative size, and the orientation to the vertebral column of the humerus suggest that they are part of a single individual.

The holotype and ROM 29942 are considered immature, whereas the vertebrae of ROM 29941 are viewed as those of adults. Comparisons of the vertebral materials suggest that the former pair may be as much as 30—40% smaller than the latter. The loss or disassociation of the centra from the neural arches of the holotype and ROM 29942 reflects incomplete ossification, a feature commonly attributed to immaturity; in ROM 29941 the vertebrae are well ossified, with no trace of a suture between the neural arch and centrum.

Skull and lower jaw

Dermal elements of the skull are found only in the holotype and referred specimen ROM 29942. Many of the dermal roof bones are not represented, particularly the midline elements, yet those that are present provide sufficient information for a tentative reconstruction of the skull in lateral view (Fig. 9).

The maxilla is represented by the closely associated pair in ROM 29942 (Fig. 4); both are exposed in lateral view, but much of their surface has been damaged. The right maxilla appears to be essentially complete. It is low throughout its length and exhibits a short, slightly concave, dorsal emargination at its anterior end that probably formed the posteroventral border of the external naris. The dentition is best preserved in the right maxilla, which possesses 23 teeth with spaces for about five more, giving a total of about 28. The teeth increase in size posteriorly to the fifth preserved tooth, which, although noticeably larger than the rest of the series, is still too small to be considered a true canine. Posterior to the caniniform-like fifth tooth there is a series of 14—17 teeth that are subequal in size; the last six teeth of the series exhibit a steady decrease in size. The teeth appear to be subcircular in cross section and are sharply pointed and slightly recurved. The maxilla probably extended posteriorly a short distance beyond the midlength level of the orbit. The dorsoventrally broad lacrimal of the holotype is sufficiently preserved to indicate that it extended from the orbit to the external naris. A stout suborbital process of the lacrimal projected posteriorly along the ventral rim of the orbit. At the medial surface of the base of this suborbital process is a massive, medially directed buttress that abutted against the alveolar shelf of the maxilla. Loss of the lateral bone surface has exposed the lacrimal duct.

The holotypic right prefrontal is preserved in part as impression because of the loss of the thin bone at its anterior end during preparation. It has the outline of an equilateral triangle; the margins of two sides of the triangle, one contributing to the orbital margin and the other to the dorsal roof of the skull, are supported by internal ridges. There was probably a considerable amount of overlap of the lacrimal onto the prefrontal, greatly reducing the lateral exposure of the orbital margin of the prefrontal. It is also obvious that the prefrontal made little contribution to the dorsal skull roof.

Of the three postfrontals preserved, only the right of ROM 29942 (Fig. 4), exposed in dorsal view, is complete. It is a relatively large sheet of bone that is roughly trapezoid in outline and slightly arched laterally; the orbital margin, identified by its greater thickness and scalloped sculpturing, greatly exceeds the other margins in length. The thickened orbital margin is slightly convex, indicating that it was a major contributor to a well-developed supraorbital shelf. As a result of its great mediolateral width, the postfrontal encroached significantly on the posterolateral margin of the frontal. It is therefore likely that the anterolateral margin of the frontal would have been expanded, extending laterally between the prefrontal and postfrontal to reach the dorsal rim of the orbit in the form of a long, winglike flange or lappet. The lateral lappet of the frontal was probably very broad anteroposteriorly, judging from the insignificant contribution of the prefrontal to the dorsal skull roof.

Neither the postorbital of the holotype nor that of ROM 29942 is complete, and only the former exhibits the relationships of this bone with adjoining elements. The postorbital does not appear to have contributed to the dorsal margin of the orbit. A very long ventral process formed most of the thin
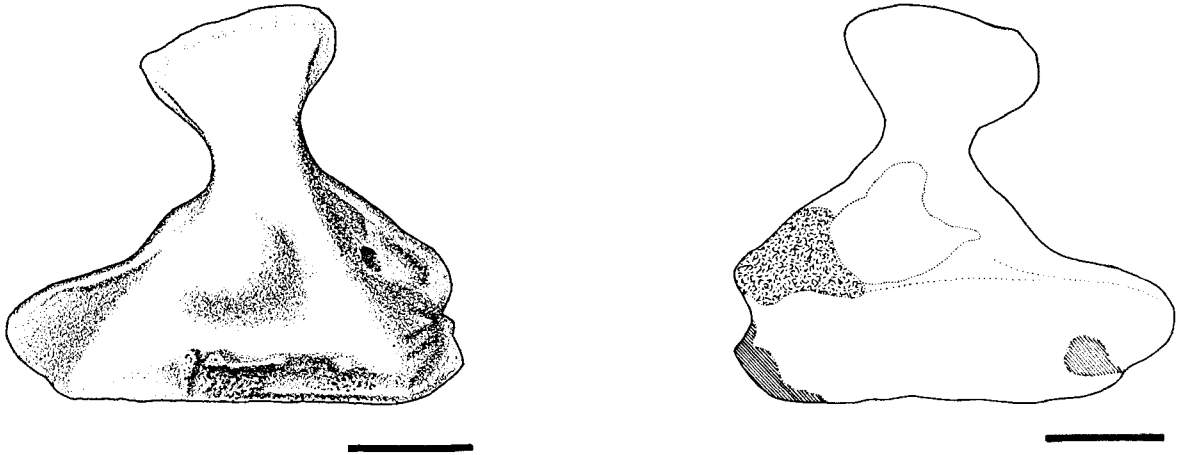
FIG. 8. Isolated left pelvis, KUVP 1425, formerly attributed to *Edaphosaurus*. See text ("Referred specimens") for explanation. Scale = 1 cm.

postorbital bar and extended along the anteromedial surface of the dorsal process of the jugal. The posterior process of the postorbital probably contacted the squamosal along the dorsal margin of the temporal fenestra.

The jugal of ROM 29942, exposed in lateral view (Fig. 4), appears to be complete. It is basically triradiate in structure. A long, narrow anterior process must have formed much of the ventral border of the orbit and contacted the posterior process of the lacrimal. A short, pointed dorsal process joined the ventral process of the postorbital, and another short, bladelike posterior process probably contacted the zygomatic process of the squamosal. The jugal, therefore, formed the anteroventral corner of the temporal fenestra. Available evidence indicates that the jugal had a very wide entrance into the ventral rim of the skull. There is no direct evidence about the shape or size of the quadratojugal.

The squamosal of the holotype (Figs. 2, 3) is nearly complete, and its major contribution to the fenestra is obvious. The orientation of the squamosal in the reconstruction of Fig. 9 was determined by its presumed contacts with the postorbital and jugal, and the restored relationships of the three elements to each other suggests the following cranial features: (1) the temporal fenestra was oblong, with the long axis directed anteroventrally; (2) the ventral margin of the skull beneath the fenestra was slightly arched dorsally; and (3) it is likely that the jaw articulation was at about the same level as the tooth row.

In ROM 29942 there is a long, narrow bone that supports a series of small teeth. This element appears too long to be the vomer, and it may be an anterior coronoid or part of the anterior process of the pterygoid.

The lower jaw (Figs. 1–3) is represented by the posterior two thirds of the right mandible of the holotype (KUVP 69035). The mandible appears to have been shallow, mainly because of the modest development of the coronoid eminence of the surangular. Sutures are detectible only on the medial surface of the mandible. The coronoids appear to be absent, thereby exposing the dentary medially along the superior margin of the mandible. The angular is low dorsoventrally, and its ventral margin curves abruptly upward at the posterior end of the mandible without any sign of an angular notch or flange. The prearticular is typically pelycosaurian in its size and extent. It is important to note, however, that the posterior end of the bone twists ventromedially so as to form a sheathlike

covering of the ventral surface of the pterygoideus process of the articular. The articular is too poorly preserved to describe in detail except to note that the internal or pterygoideus process is well developed and resembles that of edaphosaurs and sphenacodonts. Only the posteriormost eight marginal teeth of the dentary are present. They are equal in size and are similar to the maxillary teeth.

Vertebrae and ribs

The holotype includes a nearly complete and articulated series of 29 presacral neural arches with spines (Figs. 1–3); no central elements are present. An accurate reconstruction of the series can be made (Fig. 10) despite the absence of various portions of some of the arches and spines. The series of 27 vertebrae is believed to include the third cervical through the last, or possibly second to last, lumbar. This estimate is based on a comparison of the serial changes in the dorsal sail of *Ianthasaurus* with those in well-known *Edaphosaurus* species (Romer and Price 1940). If correct, then *Ianthasaurus* possessed a minimum of 29 presacral vertebrae, unusually large for a pelycosaur. Additional vertebral materials of the referred specimens include (1) neural arch with partial neural spine, numerous incomplete spines, and four centra, including a caudal, of ROM 29942 (Figs. 4, 5); (2) essentially complete cervical, dorsal, and lumbar vertebra of ROM 29941 (Fig. 6); and (3) nearly complete neural spine with partial neural arch of ROM 29940 (Fig. 7). Crushing and incomplete preservation have made accurate measurements of the centra impossible.

The proximal portions of the presacral neural spines (below the basal tubercle) are laterally compressed, with the greatest anteroposterior length just above the zygapophyses; the proximal portion of the spine tapers quickly in this dimension distally and is subcircular in cross section at the level of the basal tubercle. The remainder of the spine is subcircular in cross section, gradually narrowing to its bluntly pointed terminus. The only exception to this pattern is seen in the neural spines of the cervical and anterior dorsal vertebrae, where there is a distinct demarcation or anteroposterior "shoulder" just below the level of the basal tubercles. In the holotype the noticeable swelling of the spine of the displaced vertebra three is due to crushing. Not only are the neural arches of the cervicals slightly more massive than those of the dorsals and lumbars, but also they have a noticeably greater anteroposterior length. There is often a small, longitudinal ridge on the anterior and posterior faces of the proximal portion of the spine. The recon-
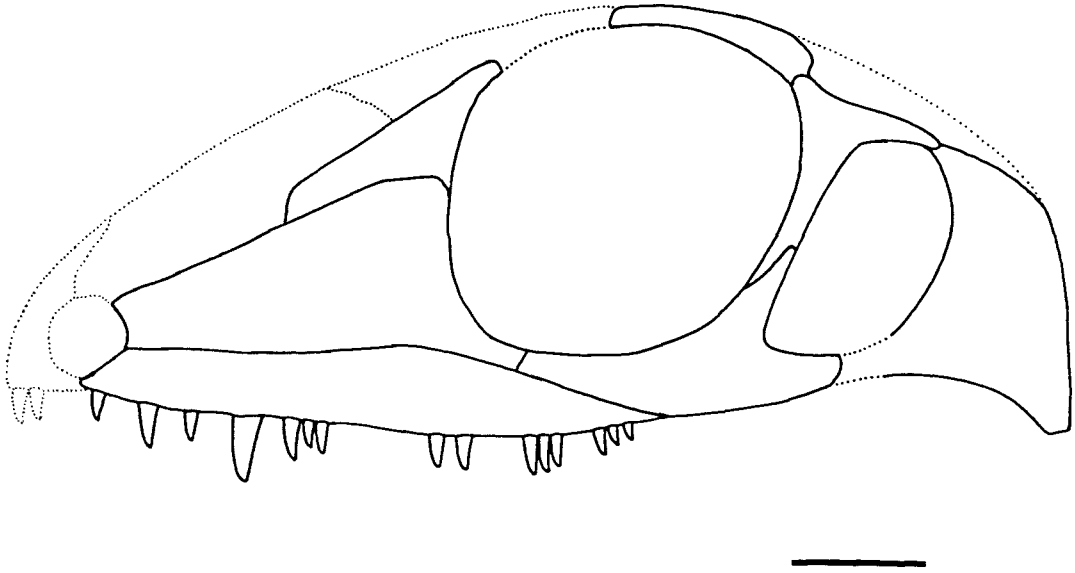
FIG. 9. *Ianthasaurus hardestii*, n. gen. et sp. Tentative composite reconstruction of skull in lateral view. Scale = 1 cm.

structed dorsal sail (Fig. 10) reaches its greatest height at about vertebra 17; from this point the curvature of the dorsal edge of the sail is greater posteriorly than anteriorly. The spines of the cervicals and first few dorsals exhibit an anterior inclination of as much as 20° from a position vertical to the long axis of the centra, as well as a slight posteriorward curvature. More posteriorly, the spines gradually become straight and vertically oriented except for the last eight or nine, which exhibit an increasing posteriorward curvature with successive spines.

The tubercles or crossbars of the neural spines are in most respects identical to those of *Edaphosaurus* (Romer and Price 1940). They tend to be arranged in bilaterally symmetrical pairs that occur at rather regular intervals along the spine and form longitudinal rows with those of successive spines. This pattern becomes increasingly irregular toward the distal end of the spines and the anterior end of the column. The basal pairs of tubercles are always considerably larger than the more distal tubercles, which steadily decrease in size distally along the spine until they become mere nubbins. In the holotypic sail the greatest number of tubercles on the side of any neural spine is five (vertebrae 9–12), and five is also the highest count for any of the spines of the referred specimens. The holotypic sail exhibits a very unusual feature in the overall distribution of the tubercles. Beginning at about the midlength of the sail, there is a progressive decrease posteriorly in the number and distal extent of the tubercles along the spines until there is a complete absence of tubercles from spine 23 or 24 to the end of the presacral column. It could be argued that the wide area of the sail without tubercles is a juvenile feature inasmuch as the holotype is considered immature. The vertebrae of ROM 29941, however, probably represent mature individuals, and yet the same pattern is present in two of them: the dorsal vertebra possesses only three pairs of lateral tubercles that occupy the proximal half of the spine, and tubercles are absent in the lumbar vertebra.

The zygapophyseal planes of the presacral vertebrae slope only moderately inward from the horizontal; in the cervical of ROM 29941 the slope is about 30°, whereas that of the dorsal of ROM 29941 appears to be slightly greater. The lateral surfaces of all of the presacral neural arches are excavated to some extent just above the transverse process. As seen in the holotype, at the anterior end of the column the neural arch excavations are shallow but extend over much of its surface, whereas in the dorsal portion of the column they become considerably deeper, more prominent, and restricted to the anterior half of the arch; the excavations are broad in the lumbars. The transverse processes are well developed and exhibit significant serial variations in their shape and size. The processes of the cervicals extend only a short distance laterally and are directed posterolaterally and ventrally; this changes rather abruptly at the beginning of the dorsal series, where they extend farther laterally and are directed anterolaterally and only slightly ventrally. More posteriorly, the size and orientation of the processes change gradually, until in the middorsal region they are directed laterally and slightly ventrally and extend laterally just beyond the level of the zygapophyses. The articular facets of the cervical and dorsal processes, as in pelycosaurs generally, have an outline of an inverted teardrop.

Features of the presacral centra are by necessity based almost entirely on the cervical, dorsal, and lumbar vertebra of ROM 29941 (Fig. 6). The lateral surfaces of the centra are moderately concave, flaring outward at the ends of the centra to form liplike rims. The ventral longitudinal ridge of the centrum is only weakly developed. The centrum lengths of the cervical and lumbar exceed slightly the centrum widths; the length of the dorsal centrum appears to be somewhat greater than its estimated width. The centra are subcircular in end view. There is no obvious bevelling of the ventral margins of the centra to accommodate intercentra. What appears to be well-developed anterior centrospheres are seen on the dorsal margin of the centrum rim of the cervical. A single anterior caudal centrum with an attached rib and exposed in ventral view can be identified in ROM 29942 (Fig. 5). The width and length of the centrum appear to be subequal, and a narrow, rounded ventral ridge is clearly visible. A single, crescentic intercentrum is preserved in ROM 29942 (Fig. 5).

Of the numerous ribs associated with the holotype and referred specimens, only a few are complete enough to warrant description. What is suspected of being a nearly complete, anterior cervical rib lies beside the fourth cervical of the holotype. The head, which is partially hidden from view, appears
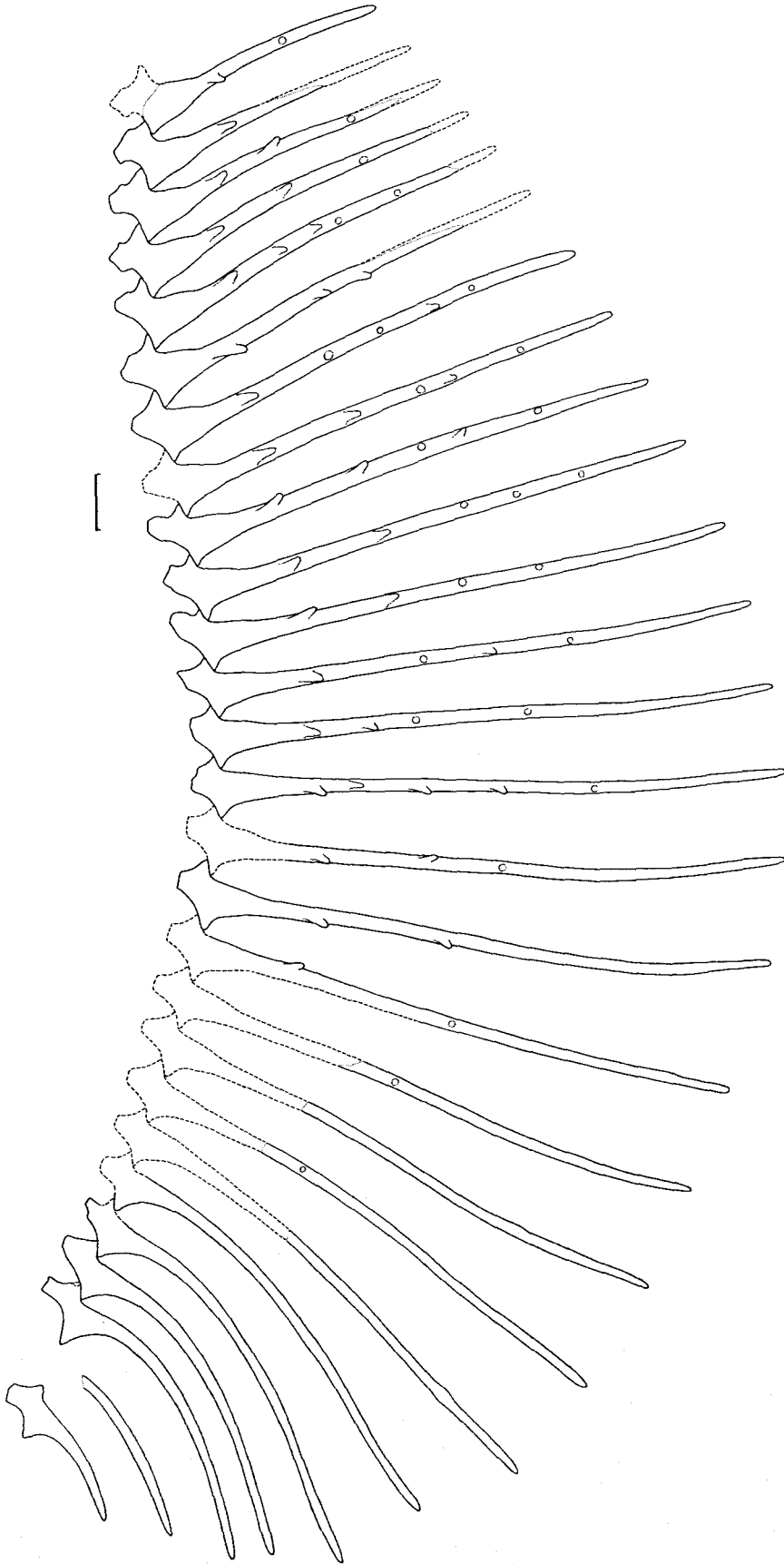
FIG. 10. *Ianthasaurus hardestii*, n. gen. et sp. Reconstruction of dorsal sail, based on KUVP 69035. Scale = 1 cm.

to be holocephalous, with the capitulum and tuberculum set close together; the very short and wide shaft widens slightly at its abruptly truncated distal end. In the same area is an essentially complete rib from the cervical–dorsal transition. The broadly triangular head is holocephalous, and the narrow shaft is only slightly curved. A single sacral rib is associated with the dorsal spine of ROM 29940 (Fig. 7). It exhibits the typical, primitive pelycosaurian form, having a stout, short neck that joins the short, expanded proximal head with the ventrally directed, very broadly expanded distal portion. The great anteroposterior expansion of this rib suggests that there may have been room for attachment of only two sacral ribs to the ilium. The caudal rib associated with the centrum in ROM 29942 (Fig. 5) is like those of other pelycosaurs. The head is very short and slightly expanded. The shaft extends outward only a short distance before curving abruptly posteriorly, is relatively short, and tapers to a blunt point. Seven similar caudal ribs are associated with the dorsal neural spine of ROM 29940 (Fig. 7); they exhibit a distinct, double articular facet of the head.

Appendicular skeleton

The appendicular skeleton is represented by the right scapulocoracoid, left pelvis, and partial manus of ROM 29942 (Figs. 4, 5) and a left humerus of the holotype (Figs. 1–3). The scapula and anterior coracoid are essentially complete and exposed in medial view; the posterior coracoid is absent. The scapula and anterior coracoid appear to be slightly separated along their sutural contact. The scapular blade is rectangular except for the posteroventral expansion into the supraglenoid buttress. The glenoid is too poorly preserved to comment on, and it is not possible to determine whether or not the absence of the supraglenoid foramen is due to inadequate preservation. At the base of the anterior margin of the blade is a deep notch that is similar to that seen in many pelycosaurs. The anterior coracoid is greatly expanded anteriorly into a broadly convex anteroventral margin. There is an anteroposteriorly oriented ridge in the center of the coracoid plate.

All three elements of the left pelvis are represented and exposed in medial view (Fig. 5). They are disarticulated but closely associated; the ilium is complete, whereas important parts of the pubis and ischium were lost during collecting. The well-developed iliac blade has a large posterior extension, as in primitive pelycosaurs. The pubis lacks its anterior portion, whereas parts of its free dorsal and ventral margins are overlapped by the ilium and ischium. The clearly defined obturator foramen is located at the posterior edge of the pubis, and its posterior border appears to have opened onto the posterior margin of the pubis by way of a narrow notch, a clear indication of immaturity. The ischium is of the typical pelycosaurian configuration. The anteroposterior extent of this element is difficult to establish, because the posterior portion has been lost; it appears, however, to have been a long element. Articulated, the pubis and ischium would have had only a narrow contact just below the ventral lip of the acetabulum; ventromedial to this they would have been separated by a widening gap that was the result of incomplete ossification along the puboischiadic suture.

The holotypic humerus is featureless because of poor ossification and preservation. The distal end is rather narrow as a result of the poor development of the entepicondyle and the apparent absence of the supinator process. The long, narrow shaft appears to be almost round in cross section. There is no indication that the expanded ends of the bone were strongly twisted about the shaft. What is believed to be a partial manus is preserved with the materials catalogued at ROM 29942. The elements are loosely articulated and tentatively identified as the ulnare, intermedium, medial and lateral centrale, and a metacarpal. No useful information can be added to that offered by their illustration in Fig. 4.

Discussion

Ianthasaurus hardestii is one of the smallest known pelycosaurs and appears to show none of the dental specializations that characterize the large Early Permian forms. Yet it possesses several derived cranial and axial features found only in one other pelycosaur, the highly specialized and advanced herbivore *Edaphosaurus*. There is a large, well-developed supraorbital shelf in both *Ianthasaurus* and *Edaphosaurus*. In *Edaphosaurus pogonias* (Romer and Price 1940, Pl. 17) this shelf is formed mainly by a very large anterior expansion of the postfrontal and a large lateral lappet of the frontal. The frontal is not preserved in the *Ianthasaurus* specimens, but the postfrontal, seen in both the holotype and ROM 29942, is very similar to that of *E. pogonias*. In *Ianthasaurus* the lateral lappet of the frontal was probably present and had a broad entrance into the orbital rim, judging from the insignificant contribution of the prefrontal to the dorsal skull roof. Spenacodonts also have a supraorbital shelf, but of far lesser development, and the postfrontal is not greatly enlarged anteriorly. Although the temporal region of the skull of *Ianthasaurus* is poorly preserved, judging from the configurations of the postorbital, jugal, and squamosal, there can be little doubt that the temporal fenestra was enlarged, especially vertically. The actual outline of the fenestra, particularly the extent of its horizontal expansion, is difficult to determine, because the sutural surfaces of the circumfenestral bones are not sufficiently preserved to allow a precise reconstruction.

In *Ianthasaurus* and *Edaphosaurus* the neural spines of the presacral vertebrae are greatly elongated, subcircular in cross section, and possess crossbars or lateral tubercles. Although large pelycosaurs such as *Secodontosaurus*, *Dimetrodon*, and *Lupeosaurus* have greatly elongated neural spines that are subcircular in cross section, they do not possess any lateral tubercles. The pattern of distribution and the development of the lateral tubercles on the vertebral neural spines in *Ianthasaurus* and *Edaphosaurus* are very similar except for the far lower maximum number of lateral tubercles per spine and the absence of tubercles in the posterior portion of the presacral column in the former. As in *Edaphosaurus*, the neural spines of the cervical region lean forward and those of the lumbar region curve strongly backward in *Ianthasaurus*. Although this feature is not seen in the sphenacodonts that have well-preserved sails, the condition in *Ctenospondylus* and *Lupeosaurus* is not known because the relevant parts of the sail are not preserved.

Romer and Price (1940) recognized that *Edaphosaurus*, best known from the three consecutively occurring species, *E. boanerges*, *E. cruciger*, and *E. pogonias*, from Lower Permian strata of north-central Texas, occupies an isolated position among pelycosaurs, with no known genus that is closely related to it. *Edaphosaurus* was, therefore, placed in its own family, the Edaphosauridae. The presence of these derived features only in *Ianthasaurus* and *Edaphosaurus* justifies their close systematic association within the family

Edaphosauridae. The inclusion of *Ianthasaurus* within the Edaphosauridae, however, necessitates a revision of the familial diagnosis from that which has been historically the same as the generic (*Edaphosaurus*) diagnosis to one limited to the shared derived features of both genera. We offer the following revised familial diagnosis.

Edaphosauridae Cope, 1882

Diagnosis

Small to large advanced pelycosaurs with enlarged temporal fenestra, large supraorbital shelf in which the postfrontal is greatly enlarged anteriorly, and a narrow skull table. Presacral neural spines are greatly elongated, subcircular in cross section except for a short, laterally flattened proximal portion, and possess lateral tubercles that exhibit a regular pattern of distribution and development. The neural spines of the cervical region lean anteriorly, whereas those of the lumbar region curve posteriorly.

Eight species of *Edaphosaurus* are recognized from the Upper Pennsylvanian and Lower Permian strata of North America and Europe. The better known Early Permian species from North America, *E. boanerges*, *E. cruciger*, and *E. pogonias* from Texas, *E. novomexicanus* from New Mexico, and *E. colohistion* from West Virginia, provide a clear understanding of the morphological pattern that characterizes this genus. On the basis of these species alone it is possible to provide the following revised generic definition.

Edaphosaurus Cope, 1882

Diagnosis

Edaphosaurid pelycosaur characterized by reduced skull size, reduced marginal homodont dentition, and short, deep mandible. Well-developed tooth plates present on the palate and the inner surface of the mandible. Densely packed teeth cover most of the palatal surfaces of the pterygoid, ectopterygoid, and palatine. The denticulated plate on the inner surface of the mandible is formed by the anterior coronoid, coronoid, and prearticular. Centrum lengths of the dorsal and lumbar vertebrae are significantly longer than those of the cervical vertebrae. The anterior caudal vertebrae have slightly elongated neural spines with longitudinal ridges on their sides.

In light of the description given here for *Ianthasaurus*, the generic assignments of three species of very small edaphosaurs, *Edaphosaurus raymondi*, *E. mirabilis*, and *E. credneri*, have to be considered uncertain because of their incomplete and fragmentary nature (Romer and Price 1940). *Edaphosaurus raymondi*, from the Upper Pennsylvanian strata of southwestern Pennsylvania (Case 1908), consists of a small spine fragment with a pair of tubercles, and *E. mirabilis*, from the Upper Pennsylvanian strata of Kounova, Czechoslovakia (Fritsch 1895), consists of a poorly preserved, incomplete dorsal vertebra that lacks the distal portion of the spine. Both species surely represent small edaphosaurs comparable in size to *Ianthasaurus*, but their fragmentary nature does not provide morphological grounds for comparisons with either *Edaphosaurus* or *Ianthasaurus*. Further, as Romer and Price (1940) pointed out, *E. raymondi* and *E. mirabilis* are not separable on morphological grounds. It is, therefore, recommended here

that *E. raymondi* and *E. mirabilis* be considered as *nomina dubia*. In contrast, *E. credneri*, from the Lower Permian strata of Germany, is based on a partial skeleton, and its taxonomic position may eventually be resolved. In the original description Jaekel (1910) indicated that its delicately constructed neural spines had few lateral tubercles. In this feature *E. credneri* appears to be similar to *Ianthasaurus hardestii*, indicating a possible close relationship between the two taxa, but this can only be determined through a reexamination of the holotype of the former. Vaughn (1969) has described fragments of edaphosaur spines from the Upper Pennsylvanian strata of Colorado as *Edaphosaurus* aff. *E. raymondi*, but unfortunately his description provides no information that would resolve the uncertainty of its generic assignment.

If a comparison between *Ianthasaurus* and *Edaphosaurus* is limited to only the well-known North American species of the latter, then it can be demonstrated clearly that *Ianthasaurus* is much more primitive. The skull of *Ianthasaurus* exhibits several primitive pelycosaurian features relative to *Edaphosaurus*. As the reconstruction of Fig. 9 indicates, the skull of *Ianthasaurus* is much more elongate, particularly the preorbital region, than that of *Edaphosaurus*. In contrast to the short, deep jaw of *Edaphosaurus*, that of *Ianthasaurus* is long and shallow. It is likely that this difference in proportions is related to the unique development in *Edaphosaurus* of a large, massive tooth plate on the inner surface of the mandible that opposed a similar tooth plate on the palate. The unspecialized marginal and palatal dentitions of *Ianthasaurus* suggest an insectivorous diet, whereas the blunt, bulbous homodont teeth of the jaw margins and tooth plates of the palate and inner surface of the lower jaws in *Edaphosaurus* indicate specialization for a herbivorous diet.

There are several features of the axial skeleton of *Ianthasaurus* that set it apart as more primitive than *Edaphosaurus*. The postaxial cervical vertebrae of *Ianthasaurus*, in contrast to those of *Edaphosaurus*, are slightly longer than those of the rest of column. This feature of *Ianthasaurus*, which is typical of most pelycosaurs, is easily demonstrated in the column of the holotype, even though the centra are missing. As an example, the total length of the articulated series of vertebrae 4−8 is about 5.0 cm (measured at the level of the zygapophyses), whereas that for the series 11−15 is about 4.6 cm. In *Edaphosaurus*, as Romer and Price (1940) have shown, the centra of the dorsal and lumbar vertebrae are greatly elongated, being about 25% longer than those of the postaxial cervicals.

The dorsal sail of *Ianthasaurus* appears to be relatively much smaller than those of any of the *Edaphosaurus* species in which this structure is adequately known. In comparing relative sizes of structures of closely related species, it has become common practice to employ the orthometric linear unit formulated by Romer and Price (1940) (Currie 1978). In this procedure linear measurements are expressed in values relative to the animal's overall size by dividing them by the orthometric linear unit of the specimen, which is defined as equal to the radius of the average-sized dorsal centrum to the 2/3 power. Although the centra of the holotype of *Ianthasaurus* are missing, a rough approximation can be made for the value of the radius by comparison of the neural arches with those associated with centra. Using greatest spine length as an index to overall sail size, the maximum height of the sail of the holotype is roughly estimated at about 40 units and the spine height of the mid-dorsal of ROM 29941 is about 36 units. This is considerably smaller than those of the well-known Early

Permian *Edaphosaurus* species, *E. colohistion*, *E. boanerges*, *E. cruciger*, and *E. pogonias*, in which the longest spines of the sails are 85, 108, 109, and 92 orthometric linear units in length, respectively. Although comparisons of neural spine height, a size-dependent feature, may not be valid when animals of different adult size are considered, the dramatic differences noted here suggest that the relatively smaller size of the dorsal sail of *Ianthasaurus* is a significant feature. As Romer (1948) noted, though there was a dramatic and steady evolutionary increase in overall body size in the Texas species, their sails increased only slightly in absolute size. In terms of orthometric linear units, sail size remained essentially constant, with the largest member of the series actually possessing the smallest sail relative to body size. Despite the possibility that in the Early Permian *Edaphosaurus* species there was a trend toward decreased relative sail size, which may have been reversed in the *Edaphosaurus* series in the eastern United States (Berman 1979), the relatively small sail of *Ianthasaurus* is considered a primitive feature. This is supported not only by the early occurrence of *Ianthasaurus* in the history of the pelycosaurs but also by the assumption that there must have been a period in the evolution of the edaphosaurs in which there was relative increase in sail size.

The absence of tubercles in the posterior portion of the sail of *Ianthasaurus* may be considered a primitive feature, although this suggests, without direct evidence, that the primitive state is a sail devoid of tubercles. A primitive feature of the sail of *Ianthasaurus* that would appear to be related to its small size is the low maximum number of five lateral tubercles per side of a spine; in all *Edaphosaurus* species in which this feature is known, the maximum number of tubercles ranges from about 12 to 14.

There are three features of the axial skeleton of *Edaphosaurus* that are related to its broad and greatly rounded trunk and are primitively absent in *Ianthasaurus:* (1) the transverse processes of the vertebrae are elongate; (2) the rib shafts are curved throughout their length; and (3) tubercula of dorsal ribs are reduced to mere rugose areas on the shafts.

Finally, the pelvis of *Ianthasaurus,* in contrast to that of *Edaphosaurus,* is primitive in exhibiting a posterior bladelike expansion and a somewhat wider neck of the ilium.

All the available evidence suggests that *Ianthasaurus* should be considered as an ideal antecedent to *Edaphosaurus*. It is, therefore, reasonable to ask whether *Ianthasaurus* can be utilized to reevaluate the relationships of edaphosaurs in general and their proposed close relationship with the sphencodonts in particular (Brinkman and Eberth 1983). *Ianthasaurus* indicates that edaphosaurs probably arose from a carnivorous pelycosaur stock that ate soft-bodied invertebrates. There are certain general similarities between *Ianthasaurus* and the oldest known and most primitive sphenacodont, *Haptodus garnettensis,* but the latter is already too advanced in specializations of the skull and its dentition toward a predaceous habit to suggest a direct ancestor–descendant relationship. Brinkman and Eberth (1983) have presented a long list of shared derived characters that support the concept of a close relationship between *Edaphosaurus* and sphenacodonts. Because of the incompleteness of the *Ianthasaurus* specimens, only a few of these characters can be considered here: (1) frontal with a well-developed lateral lappet; (2) prearticular twisted so as to underlie the pterygoideus process of the angular; (3) presence of a pterygoideus process formed by the angular; and (4) lateral surfaces of the neural arches excavated. There is no doubt that the

second, third, and fourth features are present in *Ianthasaurus,* and the presence of the first feature is inferred. The first three shared, derived features support the hypothesis of a close relationship between edaphosaurs and sphenacodonts, but the fourth is of doubtful value in evaluating relationships. Excavated neural arches also occur in the varanopseids, and it is likely that this feature, as in the elongation of neural spines, developed several times within the pelycosaurs. Thus, while the osteological evidence afforded by the known specimens of *Ianthasaurus* provides some support for a close relationship between edaphosaurs and sphenacodonts, a thorough test of this hypothesis must await the discovery of more complete skeletons of this small edaphosaur.

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