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Charles D. and Mary Vaux Walcott Research Fund

THE OLDEST KNOWN REPTILE, EOSAURAVUS COPEI WILLISTON

(WITH 1 PLATE)

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Los Angeles, Calif.

(PUBLICATION 4377)

CITY OF WASHINGTON
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FOREWORD

Dr. Frank E. Peabody died on June 27, 1958, leaving several manuscripts in various stages of completion. The one published here, based on a specimen in the collections of the United States National Museum, was complete except for final touching up of some of the illustrations; these illustrations have been finished by Miss Madeline M. Peabody with the help of Dr. Theodore H. Eaton, Jr. The manuscript has been edited by Dr. Eaton and myself. Dr. Peabody's paper presents a welcome clarification of the relationships of an important, and heretofore much misunderstood, early reptile.

PETER P. VAUGHN

Charles D. and Mary Vaux Walcott Research Fund

THE OLDEST KNOWN REPTILE, EOSAURAVUS COPEI WILLISTON

By FRANK E. PEABODY

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(With One Plate)

One of the most tantalizing examples of Carboniferous tetrapods is the posterior part of a small skeleton from Linton, Ohio, described by Cope in 1897 as the earliest known reptile. Some 60 years later, and after many taxonomic vicissitudes, the specimen seems in danger of slipping into obscurity among the microsaur Amphibia. Meanwhile no more reptiles have been found at Linton or in earlier horizons.[1] Various students have described Cope's specimen, but most have tended to discount its importance because the anterior part of the skeleton, including the skull, is missing, and have tended to accept the early descriptions with little question. Present high interest in the origin of reptiles during the Carboniferous prompted a restudy of Cope's historic specimen. It was found that strong lighting from a very low angle, and directed from various positions, revealed much new detail that can be demonstrated by photographic enlargements. The result is a new interpretation, particularly of the vertebrae and tarsus, which reaffirms the reptilian affinities of the specimen and furthermore strongly suggests a captorhinomorph relationship.

I am indebted to Dr. Peter P. Vaughn of the United States National Museum for permission to borrow Cope's specimen, and to Miss Madeline M. Peabody, my sister, for assistance with the illustrations.

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[1] [*Cephalerpeton ventriarmatum,* apparently a captorhinomorph reptile (see Gregory, 1950), is known from the nodule beds at Mazon Creek, Ill., which represent a somewhat earlier horizon (but still within the Allegheny series). —Ed.]

SYSTEMATIC DESCRIPTION

EOSAURAVUS COPEI Williston

Plate 1; Text Figures 1-3

Isodectes punctulatus Cope, Proc. Amer. Philos. Soc., vol. 36, pp. 88-90, pl. 3, fig. 3, 1897; Williston, Journ. Geol., vol. 16, pp. 395-400, text fig. 1, pl. 1, 1908; Moodie, Proc. U. S. Nat. Mus., vol. 37, pp. 11-16, pls. 4-5, 1909.

Eosauravus copei Williston, Bull. Geol. Soc. Amer., vol. 21, p. 272, 1910; Case, Carnegie Inst. Washington Publ. 145, pp. 31-32, text fig. 8, 1911.

Tuditanus punctulatus Romer, Bull. Amer. Mus. Nat. Hist., vol. 59, pp. 134-135, 1930; Bull. Mus. Comp. Zool., Harvard Coll., vol. 99, p. 300, 1947; Amer. Journ. Sci., vol. 248, p. 641, 1950; Huene, Paläontologie und Phylogenie der niederen Tetrapoden, p. 163, 1956.

?*Tuditanus* Romer, Osteology of the reptiles, p. 483, 1956.

Type.—U.S.N.M. No. 4457; posterior $\frac{2}{3}$ of a reptilian skeleton preserved belly-down on a slab of coal from Linton, Ohio.

Horizon.—Allegheny group, Middle Pennsylvanian (Westphalian).

Diagnosis.—Small reptile with a minimum of 28 presacral vertebrae of generally captorhinid structure, with broad, swollen neural arches, low neural spines, zygapophyseal facets in horizontal plane, and small intercentra; free ribs on all vertebrae except distal caudals; distal caudal vertebrae with low neural arches and probably without haemal spines, centra occasionally fused forming relatively stiffened axis; one principal and one accessory sacral rib; hind limb with prominent internal trochanter, with relatively short epipodial (=zeugopodial) segment having relatively massive fibula; primitive, well-ossified tarsus of basic captorhinid or pelycosaurian plan with separate median and lateral centrale and with a 6th distal tarsal (=postminimus); phalangeal formula 2-3-4-5-4, terminal phalanges blunt-ended. No gastralia present; possibly with body scales, having striae radiating from anterior margin of scale. No obvious aquatic adaptations of well-ossified skeleton. Anterior skeleton unknown.

Taxonomic notes.—The taxonomic history of Cope's specimen is so devious and confusing that a short explanation is necessary to supplement the synonymy listed above. Cope (1897) described the posterior skeleton and believed it to be conspecific with another small vertebrate represented by a skull and anterior two-thirds of a skeleton. The latter had been described by Cope (1874, p. 271) as *Tuditanus punctulatus,* but in his 1897 paper, it was referred along with the posterior skeleton to the genus *Isodectes.* Williston (1908) and Moodie (1909) offered new descriptions of the posterior skeleton, treating it as distinct from the anterior skeleton, but tending to overlook the fact that the anterior skeleton is the type of *Isodectes* *punctulatus.* (Moodie's plate description (p. 28) in fact refers to the posterior skeleton as "the type specimen of *Isodectes punctulatus,*" which, of course, it is not.) Later, Williston (1910) and then Case (1911) established the posterior skeleton as a new genus and species, *Eosauravus copei* Williston. Unfortunately, the European genus *Sauravus* to which Williston related the posterior skeleton is clearly an amphibian with nectridian vertebrae, so the name *Eosauravus* is inappropriate morphologically but remains valid taxonomically.

Romer (1930) restudied the Linton fauna and, in a commendable attempt to reduce the large number of artificial species, referred Cope's posterior skeleton again to the anterior skeleton now designated as *Tuditanus punctulatus.* The synonymy of *Tuditanus* with *Isodectes* had proved to be wrong since the latter genus now appears to be a captorhinomorph (Gregory et al., 1956, p. 2), and the former genus is a microsaur. Romer's decision apparently rested mainly on the improbability that there might be more than one reptile at Linton, and that there was the distinct possibility that the smaller, less ossified anterior skeleton merely represents a more immature individual than the posterior skeleton. The two specimens were regarded by Romer as reptilian with no recognizable ordinal characters. Later, Romer (1947, p. 300) suggested that the two specimens together represent either a seymouriamorph or cotylosaur on the basis of a stemmed interclavicle, seemingly broad-arched vertebrae, and a pes with a phalangeal formula 2-3-4-5-4. Still later, Romer (1950, p. 641) discounted the importance of the stemmed interclavicle and phalangeal formula, and, while noting a presumed high presacral count of vertebrae, long, slender body proportions, apparent lack of caudal chevrons, and long postorbital region of the skull, concluded that *Tuditanus punctulatus* (based on anterior and posterior skeletons) "is not improbably a microsaur." This conclusion, undoubtedly influenced by increased understanding of microsaurs, was followed by both Piveteau (1955) and Huene (1956) in their valuable compendia of vertebrate paleontology. Meanwhile, Romer (1956, p. 483) apparently turned once more toward Williston's opinion of the posterior skeleton as shown by the lone entry "[Reptilia] Incertae sedis. ?Seymouriamorpha. *?Tuditanus* Cope 1874 (*Eosauravus* Williston 1910)." Thus at present, the posterior skeleton designated as *Eosauravus copei* by Williston, is in an obscure position both taxonomically and phylogenetically. The anterior skeleton is best considered a probable microsaur amphibian under the designation *Tuditanus punctulatus.* In any case it is difficult to demonstrate distinctive reptilian characteristics in

T. punctulatus, and especially difficult to demonstrate any real affinities with *Eosauravus copei.*

Description.—The specimen consists of the posterior two-thirds of a postcranial skeleton preserved belly-down on a coal stratum. Neither the opposing slab, probably containing a dozen thoracic vertebrae and caudal neural arches, nor adjoining blocks of matrix containing the tip of the tail, some terminal phalanges of the left pes, and the anterior end of the skeleton, were collected. The remaining parts of the skeleton have undergone very little deterioration since Cope's time, judging from the excellent photograph presented by Williston (1908) and republished (with inaccurate retouchings) by Moodie (1909).

The presacral, sacral, and anterior caudal vertebrae lie on their right sides (as observed by Cope, 1897) in such a manner as to cover the proximal tips of the right ribs while the proximal ends of the left presacral ribs are pressed against the upper (left) surfaces of their corresponding centra. The outline of successive neural spines is clearly visible on the right side between successive ribs. The caudal vertebrae posterior to the rib-bearing caudals are preserved with ventral side down and have lost their neural arches, thus exposing the neural canal as a longitudinal groove in the dorsal surface of the centra. Unfortunately, Moodie (1909, pl. 5) illustrated the entire column as though it were oriented with the dorsal side uppermost (figure reproduced by Case, 1911, fig. 8). The result is an erroneous picture of the vertebrae from anterior caudals forward. Cope's illustration (1897, pl. 3) shows the correct orientation, but is only slightly suggestive of the true form of the vertebrae.

The true form of the presacral and anterior caudal vertebrae may be reconstructed with reasonable accuracy from a composite of details exhibited along the column. Specifically the impression of the anterior presacrals clearly shows the contour of the centrum; the first 5 presacrals and anterior caudals preserve details of swollen neural arches as well as of the centra and intercentra. The position of intervertebral foramina is clearly indicated by a series of circular pits. Figure 1 is presented as a reconstruction based on composite detail.

There seems to be little doubt that the neural arch is low and broad as mentioned by Romer (1947, p. 300), has a low spine, and has a perceptible swelling above the posterior zygapophysis; also that small intercentra are present. The latter are indicated between the first several presacral centra, between the 1st and 2d caudal centra, and by a haemal wedge between the 3d and 4th caudal centra. In the presacral series the left ribs appear to have been crushed precisely against

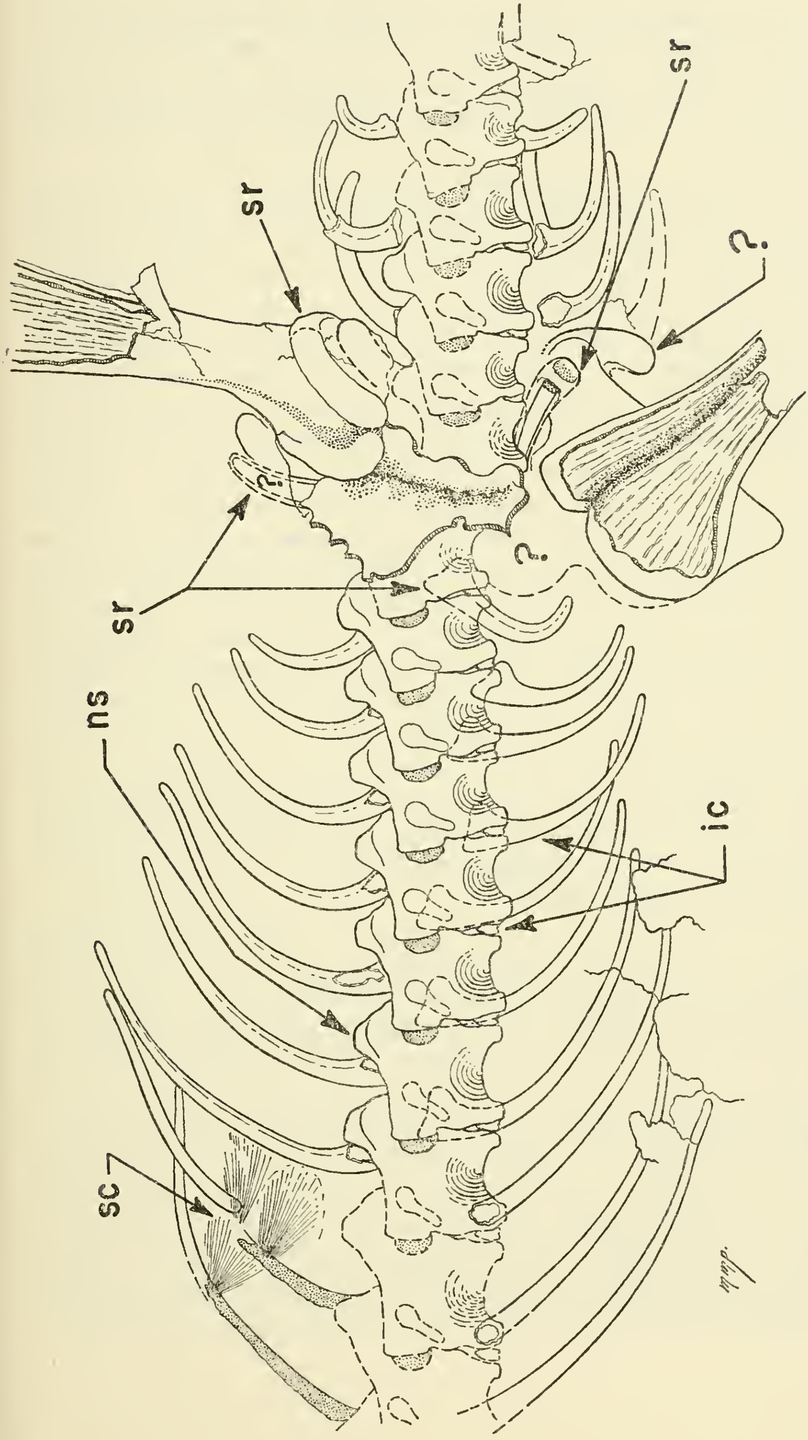

Fig. 1.—Lumbar, sacral, and anterior caudal region of *Eosauravus copei*, reconstructed from composite detail of type specimen. Possible body scales (sc), neural spine (ns), sacral ribs (sr), intercentra (ic).

the intervertebral area; thus the supposed intercentra here may be parts of the ribs. However, there appears to be a distinct intercentral space coincidental with the position of the ribs, and, in any case, the evidence for intercentra in the anterior caudals is clear and unobscured by ribs.

Evidence of 24 presacral ribs on the left side is fairly clear, although the first presacral is difficult to see, and only the distal tip of the 24th presacral is preserved on the edge of the slab. The general pattern and number of the presacral ribs and the far anterior position of the left manus have led to the opinion (Romer, 1950, p. 641) that the presacral count is significantly higher than the 25-27 vertebrae usually found in the most primitive reptiles. However, the 5 most anterior ribs are clearly more massive than following ribs, and the distal ends are slightly spatulate—all indicative of an extreme anterior thoracic position related to serrati muscles of the pectoral girdle. Also, the successive positions of the distal ends of the 5 anterior ribs suggest a progressive shortening in a forward direction as might be expected in a smooth transition to the cervical region. Accordingly, a reconstruction will show that the total number of presacrals may have been as few as 28. The forward position of the left manus as an indicator of a far anterior position of the pectoral girdle is probably misleading. The girdle probably shifted forward or to the right side away from its life position lateral to the 5 anterior ribs.

Rib heads are obscured in the presacral series generally, but the 3d to 8th left presacral ribs appear to have a proximal expansion commensurate with the elongate diapophysis of the neural arch. Certainly these ribs are not single-headed as in lizards, but bear a general resemblance to captorhinid ribs.

The pelvic girdle and sacral vertebrae are distorted beyond certain recognition of salient features, although the spacing of vertebral segments and disposition of lumbar and caudal ribs suggest the presence of two sacral vertebrae. A short, thick element lying across the adductor fossa of the right femur may be a right second sacral rib; an obscure spatulate structure immediately anterior to the anteriormost left caudal rib may be the first or principal sacral rib. Except for a general outline of the acetabular regions of the girdle, little can be demonstrated here except that the mass lying between the heads of the femora probably constitutes a pelvic girdle and sacrum of primitive reptilian plan. According to my interpretation, Moodie (1909, pl. 5) included the internal trochanter of the left femur in his outline of the left acetabular region, thus giving the left pelvis a more distinct outline than is warranted. A thin plate lying anterior to the head of the right femur may represent the left ilium broken over to the right. Although the thin plate may be regarded as a patch of overlying matrix such as obscures the centrale of the left tarsus (see below), there is a definite anterior border that looks much like the anterior edge of an iliac blade. Nowhere is there evidence of a long posterior process of the ilium like that of *Eogyrinus.*

The anterior 4 or 5 caudal vertebrae are associated with 3 pairs of sharply curved ribs. In addition, there are short structures faintly shown on the left side that are not curved and probably represent short haemal spines nearly in the correct position. Also, there is a distinct haemal wedge between the 3d and 4th caudal centra. Certainly there is enough evidence to question seriously earlier observations (Cope, 1897, p. 89; Romer, 1950, p. 641) that there are no haemal spines in the tail.

The caudal series becomes twisted, possibly 180 degrees, at the position of the 7th vertebra, which appears to be lying on its left side. Posteriorly the series is oriented with ventral side down—an unusual position if neural and haemal arches were at all well developed here, or if there was any lateral compression of the centra. Under these conditions the vertebrae would be almost certainly lying on one side or the other as in the anterior column. However, the caudal centra appear broader than high, and occasional fusion of neighboring centra seems to have occurred. All features of the tail, including the orientation, suggest some specialized function—perhaps a prehensile action in the dorsoventral plane. A special aquatic function does not seem possible, insofar as a lateral sculling motion is concerned, although the fused vertebrae may suggest a stiffened axis serving as the foundation for a rudder.

Part of the left manus (omitted in Cope's figure, 1897, pl. 3) lies disarticulated near the anterior end of the vertebral column. Enough is shown to indicate that the carpus was definitely as fully ossified as the tarsus, and less surely that the phalangeal formula was comparable to the reptilian count in the pes.

Both limbs are complete except for the loss of some terminal phalanges on the left side. The left femur is preserved with the dorsal surface uppermost—the right femur with the ventral surface uppermost. Thus the whole contour of the bone can be recognized in composite. The femoral head, internal trochanter, adductor fossa, and distally the tibial and fibular condyles resemble those of primitive reptiles such as ophiacodonts and captorhinids. The trochanter is especially prominent and extends proximally nearly in line with the femoral head. Ossification is fully developed in the femur as well as in the more distal elements.

The tibia and fibula are short, stout bones of generally primitive contour; the fibula appears relatively more massive than is usually the case in the tetrapod limb. The distal end of the left tibia appears to have slipped slightly upward from the life position and now rests on the neck of the astragalus. Otherwise, the left femur, tibia, and fibula are in normal articulation.

The right pes is twisted so as to obscure details of the tarsus, but details of the digits help to complete a restoration of the left pes. The left pes is preserved dorsal side uppermost and exhibits one of the most perfect preservations of tarsal structure known from the Carboniferous, indeed, from the Paleozoic, as will be demonstrated presently. The pes has been given several superficial descriptions (Cope, 1897; Williston, 1908; Moodie, 1909) which fail to recognize the extent of ossification in the tarsus, but nevertheless establish two proximal elements in the tarsus and a phalangeal formula of 2-3-4-5-4. A main difficulty lies in the interpretation of tarsal elements distal to the presumed astragalus and calcaneum, especially in the medial region of the tarsus where no one has been able to recognize central elements. Moodie's figure (1909, pl. 5), republished by Case (1911), is particularly misleading in that the tarsus appears to have an enigmatic pattern, doubtfully reptilian. (Also, in Moodie's figure a nonexistent element is added distal to the lateralmost distal tarsal, although none is shown in Moodie's retouched photograph—his pl. 4). My photographs (pl. 1A, B), taken under low-angle light from first one direction and then from the opposite direction, demonstrate the wealth of detail making possible text figure 2. The two proximal bones of the tarsus are clearly the astragalus and calcaneum which enclose between them a perforating foramen, not previously noted. The astragalus has a small but definite tibial facet directed mostly preaxially. There is no evidence of tripartite structure such as exhibited by *Captorhinus* (Peabody, 1951). The preaxial border between the astragalus and the first metatarsal clearly exhibits two bones that must be a median centrale and distal tarsal 1. A thin veneer of matrix obscures part of the dorsal surface of these bones, but the oblique lighting (pl. 1A) clearly brings out their contours in the preaxial border. Lateral to these bones and median to the large distal tarsal are at least 2 and probably 3 separate bones that are identifiable as the lateral centrale and distal tarsals 2 and 3. A slight proximal jamming (see fig. 2) has forced distal tarsals 2 and 3 slightly out of position. The existence of two separate centralia seems certain although the separation between the lateral centrale and distal tarsal 2 is not clear—probably because of a slightly overriding relationship due to jamming. A unique feature of the tarsus is a postminimus or distal tarsal 6 in the postaxial border. Such an element is unknown in reptiles but is found in the tarsal pattern of the urodele, *Salamandrella,* by Holmgren (1933, p. 217).

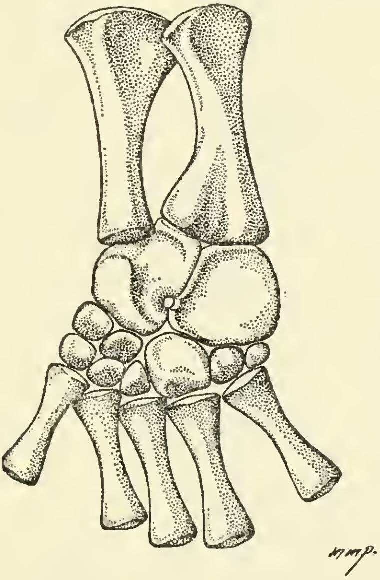

Fig. 2.—Left pes of *Eosauravus copei* showing primitive reptilian pattern with separate median and lateral centrale, and with unique postminimus or distal tarsal 6 on postaxial border.

There is no doubt that the tarsal pattern is generally comparable to primitive captorhinids and pelycosaurs.

The metatarsals are all well developed as indicated in figure 2. No special features seem to be present except for a generally robust ossification (like that of more proximal bones) that contrasts markedly with a seemingly delicate ossification of the phalanges.

The phalanges may be confidently restored with a 2-3-4-5-4 formula, using the evidence from both feet. The terminal phalanges are not acutely pointed and cannot be considered as definitely bearing claws. The relative length of the 5th digit suggests no obvious aquatic adaptation—in the obviously aquatic *Mesosaurus,* the 5th digit is longer than the 4th. This condition may also be noted in nothosaurs.

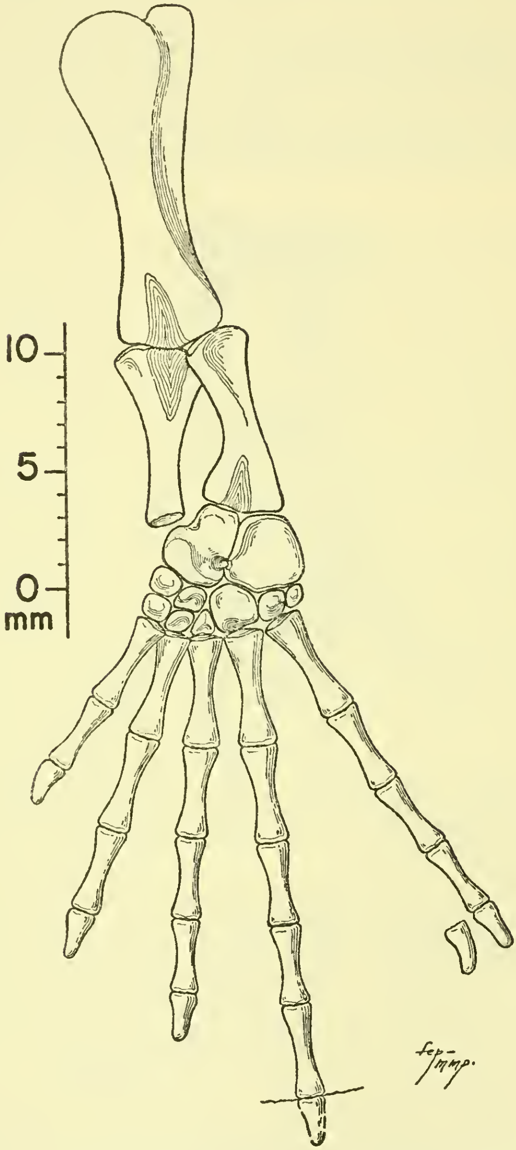

FIG. 3.—Left limb of *Eosauravus copei* reconstructed in fully extended position.

The surface surrounding the skeleton seems devoid of structures resembling gastralia as indicated by early descriptions. However, a problematical object that may be an unidentified bone from the anterior skeleton lies just to the left of the distal tail. Possibly of more importance, an enlarged view of the surfaces near the skeleton reveals a number of delicate, ovoid areas with fine striae radiating from a point near one border. The striated areas occur only close to the skeleton; an example of the striated areas can be seen clearly between the right ribs in plate 1C. It is possible that these striated areas represent body scales developed from the epidermis of *Eosauravus.* No bone is indicated in the delicate impressions

Conclusions.—It is concluded that Cope's historic specimen from Linton, Ohio, is surely a reptile that has evolved beyond the seymouriamorph level. The broad-arched, cotylosaurian vertebrae possess small intercentra, and the narrow space between successive pleurocentra is in decided contrast with the wide, unossified gap seen in seymouriamorphs. Here, the pedicel of the neural arch has a marked overhang above the intercentral gap. The tarsus has a characteristic reptilian astragalus and calcaneum, with enclosed perforating foramen in the usual position. The astragalus is fully developed with no indication of a compound origin as in the relict *Captorhinus aguti* of Early Permian age (Peabody, 1951). The whole structure of the pes is of basic reptilian pattern except for the 6th distal tarsal or postminimus. The latter may be considered an amphibian feature rather than a supernumerary element that widens the pes surface in correlation with aquatic adaptations—an untenable point of view considering the general lack of characteristics suggesting aquatic habits of *Eosauravus.* The combination of vertebral and tarsal characteristics is consonant with other features of the skeleton; together they strengthen the evidence that the astragalar bone, originating from a fusion of tibiale, intermedium, and proximal centrale of the amphibian foot, may be regarded as a reliable osteological indication of the attainment of the amniote level of organization—at least until conflicting evidence is found.

If it be granted that *Eosauravus* is a reptile, there is a question as to its subgroup affiliation. Current evidence strongly suggests that early ophiacodont pelycosaurs and captorhinomorphs are very close to the root of the reptilian stock. The tarsus of *Eosauravus* is exceedingly primitive in the possession of separate median and lateral centrale, and of the postminimus. Only early pelycosaurs have separate centralia—they are fused in *Captorhinus* and *Limnoscelis.* No reptiles presently known have a postminimus. The nature of the vertebrae of *Eosauravus* would indicate that its affinities probably lie with the captorhinomorphs. No pelycosaur is presently known to possess vertebrae of a pure cotylosaur type such as is evident in *Eosauravus.* In view of the primitive pattern of the tarsus, a position near the base of the captorhinomorphs is indicated.

Establishment of a true reptile of captorhinomorph affinities deep in the Middle Pennsylvanian helps to clear away some of the uncertainty surrounding the time of origin of reptiles. The varied reptiles found in the Upper Pennsylvanian of Kansas (Peabody, 1954) and more fragmentary remains from elsewhere indicate that the evolution of pelycosaurs and captorhinomorphs (if petrolacosaurs be considered an offshoot of the captorhinomorphs as suggested by Vaughn, 1955, p. 446) was well advanced. *Eosauravus* appears to have been at an evolutionary stage which could be ancestral to any known later reptile.

The particular adaptations of *Eosauravus* to life in a coal swamp are difficult to assess. Moodie (1909, p. 12) suggests that the reptile was aquatic or semi-aquatic mainly on the basis of an "expanded foot" similar to the broad foot of the obviously aquatic mesosaurs. However, the foot of *Eosauravus* and the rest of the preserved skeleton have little to suggest even semi-aquatic habits, but do allow the possibility that this small reptile spent most of its time in the "upper story" of the coal forest at Linton.

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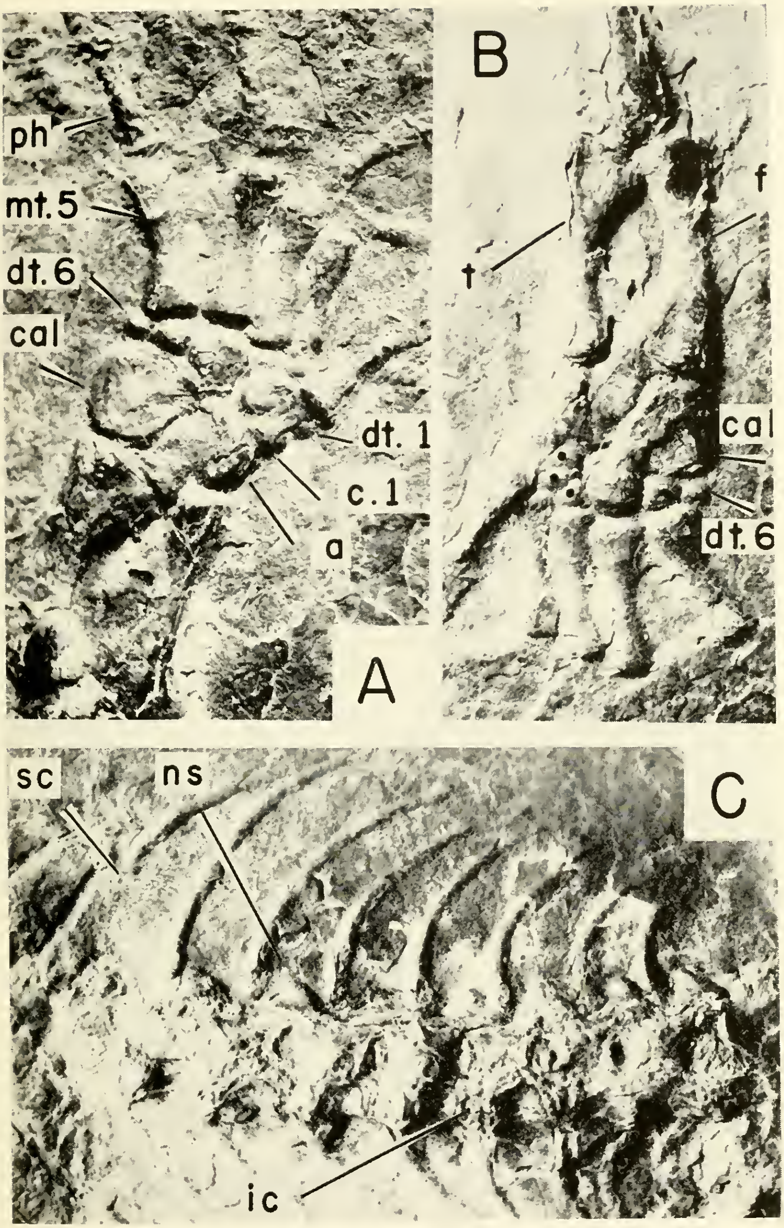
EXPLANATION OF PLATE 1

Left pes and lumbar region of *Eosauravus copei* seen under low-angle illumination.

A. Pes, lighted from distal direction, showing clearly: Two elements—median centrale (c. 1) and 1st distal tarsal (dt. 1)—lying between astragalus (a) and 1st metatarsal; and 6th distal tarsal (dt. 6) lying between calcaneum (cal) and 5th metatarsal (mt. 5).

B. Pes, lighted from proximal direction, showing 3 distinct elements (indicated by black dots) lying median to large 4th distal tarsal.

C. Presacral vertebrae of lumbar region, lighted from anterior direction, showing low neural spine (ns), presence of intercentrum (ic), and striated patches (sc) possibly representing body scales.



(For explanation, see p. 14.)