The Carboniferous Amphibian *Tuditanus* [*Eosauravus*] and the Distinction Between Microsaurs and Reptiles

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INTRODUCTION

The ancestry of reptiles has been subject to considerable dispute in recent years. One of the major problems involves the possibility that microsaurian amphibians may have given rise to some, if not all, members of the class. Because of the many similarities in skull and skeleton between captorhinomorph reptiles and microsaurs, a number of authors (Gregory, 1948; Westoll, 1942; Huene, 1948; Vaughn, 1960, 1962; Brough and Brough, 1967a, 1967b, 1967c) have suggested that the two groups are closely related.

This problem has been clouded by the general confusion as to the nature of microsaurs and the content of the Microsauria. Romer (1950) defined and delimited the group, clarifying the question considerably. Several of the genera, such as *Cephalerpeton*, *Petrobates*, and *Hylonomus*, which had been considered as microsaurs with possible reptilian affinities, were shown to be true captorhinomorph reptiles and to have little if any connection with the microsaurs as Romer defined them.

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This clarification does not entirely solve the problem, however, since there remain a number of species included among the Microsauria of which the anatomy has not been well enough known to state whether they are true microsaurs, reptiles, or forms transitional between the two groups. As Vaughn (1962) has pointed out, many of the features that have been used to separate microsaurs from reptiles may be only specializations of the few well-known members of the group and do not necessarily preclude relationship between less-specialized microsaurs and early reptiles.

This problem can be solved only by our gaining a thorough knowledge of all the forms that have been described as microsaurs. It must then be determined whether or not such forms constitute a taxonomically coherent assemblage, which can be defined by a consistent morphological pattern, and whether their morphological features support relationship with the reptiles.

Fortunately the early reptiles, particularly the captorhinomorphs (Price, 1935, 1937; Watson, 1954; Fox and Bowman, 1966; and Carroll, 1964b), are much better known than are microsaurs and do form a consistent taxonomic and morphological assemblage. A basis for comparison with the microsaurs is thus available.

A general redescription of all microsaur genera is now being undertaken by the senior author. The purpose of the present paper is to redescribe one of the most controversial genera in the entire group, and to survey the similarities and dissimilarities between microsaurs and reptiles in the light of its anatomy.

to examine the specimens of solenodonsaurids and adelogyrinids in their possession. Dr. Peter P. Vaughn of the University of California at Los Angeles also facilitated the work and provided stimulating discussion of controversial points.

MUSEUM ABBREVIATIONS

A.M.N.H., the American Museum of Natural History
B.M.(N.H.), British Museum (Natural History), London
C.G.H., Narodni Museum, Prague   .
D.M.S.W., D. M. S. Watson collection, Cambridge University
H.M., Hunterian Museum, Glasgow
M.C.Z., Museum of Comparative Zoology at Harvard College
N.M.C., National Museum of Canada, Ottawa
R.M., Redpath Museum, McGill University, Montreal
R.S.M., Royal Scottish Museum, Edinburgh
U.S.N.M., United States National Museum, Smithsonian Institution
U.T., University of Texas, Austin

TAXONOMIC HISTORY

Tuditanus punctulatus from the Middle Pennsylvanian of Linton, Ohio, has alternated in the literature between the Amphibia and the Reptilia ever since its discovery. The species is represented by two specimens, A.M.N.H. No. 6926 and U.S.N.M. No. 4457. The American Museum specimen, consisting of a skull and presacral skeleton, was described as a "batrachian" by Cope in 1874. In 1875 he erected a new family Tuditanidae for the genus. In 1896, however, Cope included *Tuditanus punctulatus* in his new reptilian order Cotylosauria, observed that he could not distinguish it from *"Isodectes"* (*Captorhinus* in modern terminology), and stated with emphasis that "this is the first identification of a true reptile in the Coal Measures." The United States National Museum specimen, consisting of a vertebral column and the hind limbs, was assigned by Cope in 1897 to *Isodectes punctulatus* with the notation, "This specimen is of importance as pertaining to the oldest known reptile, and the only one which has been thus far positively identified from the Coal Measures."

Williston (1908) concluded that the two specimens represented different genera. Classifying the type specimen of *Tuditanus punctulatus* by

Fig. 1. *Tuditanus punctulatus,* A.M.N.H. No. 6926, type, latex cast showing skull roof before preparation. ×4.

implication as a microsaur *sensu lato,* he renamed the United States National Museum specimen *Isodectes copei* and commented prophetically: "It is somewhat hazardous to say with assurance that the specimen really is that of a true reptile. . . . There are those who believe that the reptiles arose from two distinct groups of the amphibia, one from the Microsauria, the other from the Temnospondyli; and I must confess that *Isodectes* helps that theory materially, for its relationships with the Microsauria on the one side cannot be gainsaid."

In 1910, still groping toward a classification, Williston divided "what are called Microsauria" into two groups: one amphibian, the other "more nearly allied, possibly identical, with the reptilia in a wide sense." To the latter group he assigned *Isodectes copei,* giving it the new generic name *Eosauravus.*
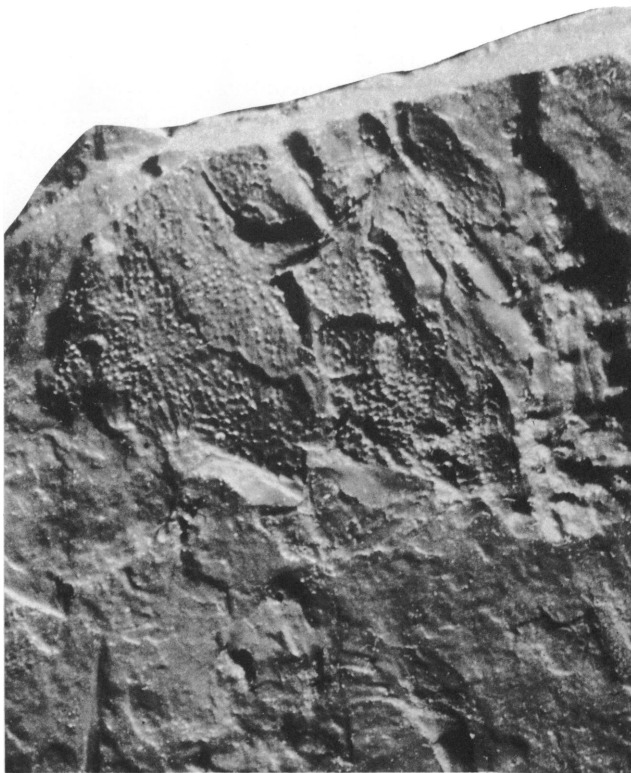
FIG. 2. *Tuditanus punctulatus,* counterpart of specimen shown in figure 1, latex cast of skull roof after preparation. Upper edge corresponds to crack crossing figure 1. ×4.

Moodie (1909a) redescribed the United States National Museum skeleton in the mistaken belief that it was the type specimen of *Isodectes punctulatus;* he asserted unequivocally its reptilian status. In 1916 he cited it as *"Eosauravus copei* Williston, which is . . . clearly a reptile," at the same time assigning the American Museum specimen to "the microsaurian family Tuditanidae" of the class Amphibia as *Tuditanus punctulatus* Cope.

Romer (1930), in his revision of the Linton fauna, returned to Cope's usage by assigning both specimens to *Tuditanus punctulatus,* which he regarded as "almost unquestionably . . . a primitive reptile." In 1950, however, he considered the genus to be "not improbably a microsaur." Shortly afterward, (1956), he tentatively classified *Tuditanus* and its synonym *Eosauravus* as Reptilia *"Incertae sedis,* ?Seymouriamorpha."

Two years later Baird prepared the American Museum type for the first time, making latex casts before and after dissolving out the bone with hydrochloric acid and reconstructed its skull from enlarged photographs assembled over a plasteline form. On the basis of similarities to *Limnoscelis* he classified the Tuditanidae as reptiles (Baird, 1958). During this same period a restudy of the still-unprepared United States National Museum specimen by the late Frank E. Peabody was being edited for posthumous publication. In this paper Peabody (1959) again separated the two specimens taxonomically, designating *Tuditanus punctulatus* as "a probable microsaur amphibian" while championing *Eosauravus copei* as "the oldest known reptile," the affinities of which "probably lie with the captorhinomorphs."

After Peabody's conclusions had been announced at a scientific meeting, Baird borrowed and prepared the United States National Museum specimen and recognized that it is a microsaur and unquestionably conspecific with *Tuditanus punctulatus*. A preliminary notice of the new findings has since been published (Baird, 1965), along with illustrations of the reconstructed skull.

The type specimens of other species assigned to *Tuditanus* by Cope (1874, 1875, 1877) and Moodie (1909a, 1909b) are not microsaurs but include labyrinthodonts of three families, a nectridean, and a romeriid reptile.

CLASS AMPHIBIA

SUBCLASS LEPOSPONDYLI

ORDER MICROSAURIA

FAMILY TUDITANIDAE COPE, 1875

TUDITANUS COPE, 1874

Figures 1–10

Tuditanus punctulatus (*nomen nudum*) COPE, 1871, p. 177.
Tuditanus punctulatus COPE, 1874, p. 271.
Isodectes punctulatus (Cope): COPE, 1897, p. 88.
Isodectes copei WILLISTON, 1908, p. 399.
Eosauravus copei (Williston): WILLISTON, 1910, p. 272.

TYPE SPECIES: *Tuditanus punctulatus* Cope, 1874; designated by S. A. Miller (1889, p. 626).

TYPE: A.M.N.H. No. 6926, skull and much of postcranial skeleton, in counterpart blocks.

REFERRED SPECIMEN: U.S.N.M. No. 4457, vertebral column, manus, and hind limbs.

HORIZON: Canneloid shale underlying Upper Freeport Coal, Allegheny Group, Middle Pennsylvanian, equivalent to the latest Westphalian D of Europe.

LOCALITY: Diamond Mine, Linton, Saline Township, Jefferson County, Ohio; NE. corner, sect. 13, T. 9 N., R. 2 W.

REVISED DIAGNOSIS: Microsaur having well-developed limbs. Skull roof sculptured with shallow pits; orbits midway in length of skull, protected by palpebral cups. A single row of approximately 25 sharply pointed marginal teeth of uniform length. Postparietals occipital in position. Twenty-nine presacral vertebrae. Endochondral shoulder girdle poorly ossified, humerus with entepicondylar foramen. Four digits in manus, phalangeal count 2, 3, 4, 3. Ilium with dorsal and posterior processes. Two proximal tarsals, five digits in pes, phalangeal count 2, 3, 4, 5, 4. Ungual phalanges of manus and pes hoe-shaped.

DESCRIPTION

SKULL AND JAWS: The skull is known only from A.M.N.H. No. 6926. The dorsal surface of the skull was present prior to etching, as far forward as the posterior portion of the nasals. As prepared, the ventral surface (including the lower jaws, palate, and marginal bones of the skull roof) is preserved as a natural mold in one block, whereas the counterpart shows the right posterior half of the skull in dorsal view. A restoration of the skull is shown in figure 9.

The skull is roughly triangular in dorsal view, with the orbits midway along its length. The skull table is about twice as wide as the cheek region is deep. The slope of the cheek region appears to be quite abrupt, giving a very reptilian appearance to the skull in lateral view. The orbits are large, almost (or just barely) reaching the frontals. The posterior margin of the skull table is concave, and the entire occipital region slopes forward.

Unlike the skulls of many microsaurs, the skull of *Tuditanus* is distinctly sculptured. The posterior skull roof and cheek regions are marked by shallow, rounded depressions, rather than the ridge-and-groove pattern seen in many labyrinthodonts. Anterior to the orbits the depressions become less distinct but more elongated. The maxillae and premaxillae are marked by a series of small pits. Unsculptured portions of the postparietals, supratemporals, squamosal, and quadratojugal extend onto the occipital surface. There are no grooves for lateral-line canals.

The pattern of bones of the skull roof is typically microsaurian, with a large supratemporal in contact with both the postfrontal and post-
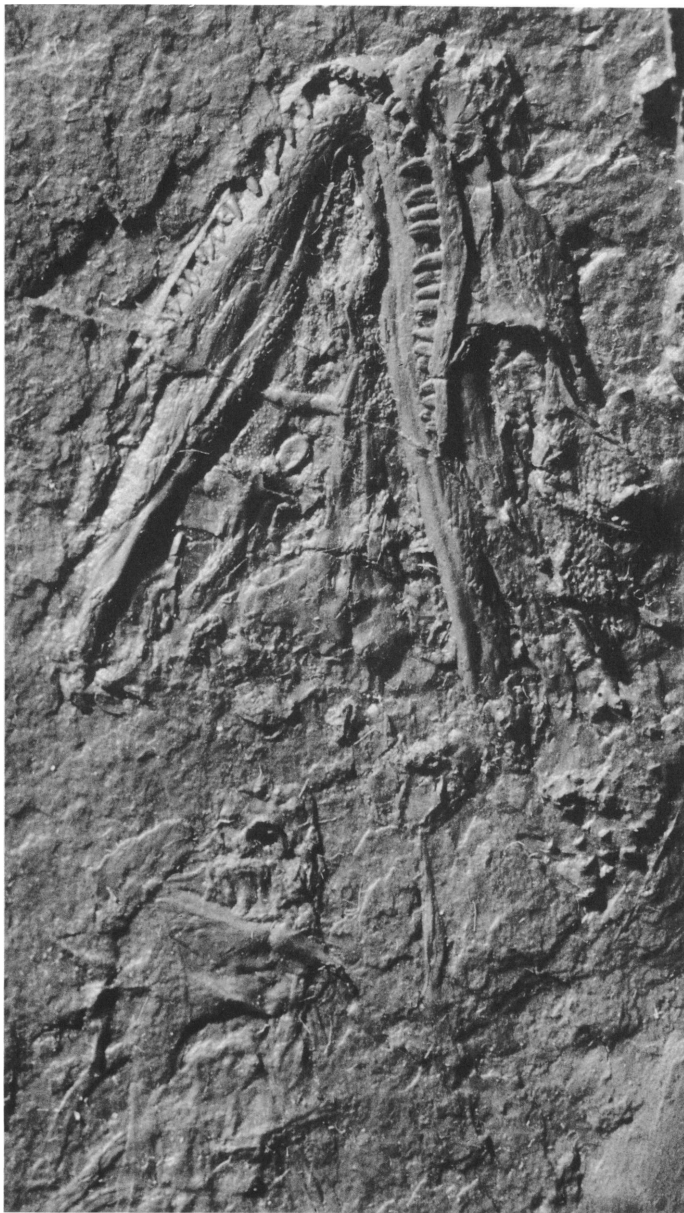
FIG. 3. *Tuditanus punctulatus,* A.M.N.H. No. 6926, type, latex cast of palate after preparation. ×4.

orbital. The postparietals are narrow, and occipital in position. The central portion of these bones and the back of the postparietals are missing but can be readily restored. There is no tabular.

The orbit is protected by a rigid palpebral cup which is sculptured like the skull roof. A similar palpebral ossification has been reported in the Nýřany microsaur *"Ricnodon" limnophyes* by Watson (1913) and Steen (1938)[1] and is clearly present in *Microbrachis pelikani* (A.M.N.H. No. 2557).

The postorbital and squamosal have separated slightly from the postfrontal and supratemporal. A similar disarticulation of the cheek region from the skull table was also encountered in the Joggins microsaur *Asaphestera* (Carroll, 1963), which in several other respects resembles *Tuditanus*. This condition is also a feature of several primitive captorhinomorphs (Watson, 1954) and labyrinthodonts. In neither group is there reason to think that this line of weakness is a result of failure to close a former otic notch. It seems much more logical to assume that this feature has some functional significance. If the cheek and skull roof were movable relative to each other in the living animal, the muscles of mastication would have had greater freedom for lateral expansion. Thus a movable cheek would have served the same function as the temporal openings in advanced reptiles. A similar explanation in functional terms is offered by Panchen (1964) for the analogous construction found in embolomeres.

The quadratojugal is large and extends below the level of the tooth row. The septomaxilla is oval and nearly as large as the external naris.

Teeth and alveoli number approximately 19 in the maxilla and six in the premaxilla. Each tooth is a simple sharp peg, slightly recurved at the tip; although it may show a longitudinal groove as a result of crushing, there is definitely no labyrinthine folding of the enamel. Tooth length increases gradually from back to front, is greatest near the anterior end of the maxilla, and decreases in the premaxillary and first few maxillary teeth.

Much of the lateral portion of the palate is obscured by the lower jaws, which completely cover the area of the ectopterygoid and palatine and much of the vomers, as well as the internal nares. The pterygoid, as in other microsaurs, has a smooth, continuous margin surrounding the subtemporal fossa and lacks a transverse flange. Its palatine ramus is covered with small denticles, extending back to the area of the basi-

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[1] *"Ricnodon" limnophyes* in all probability belongs to a different genus from that of the type species, *Ricnodon copei* (Carroll, 1966); it is nevertheless a microsaur.
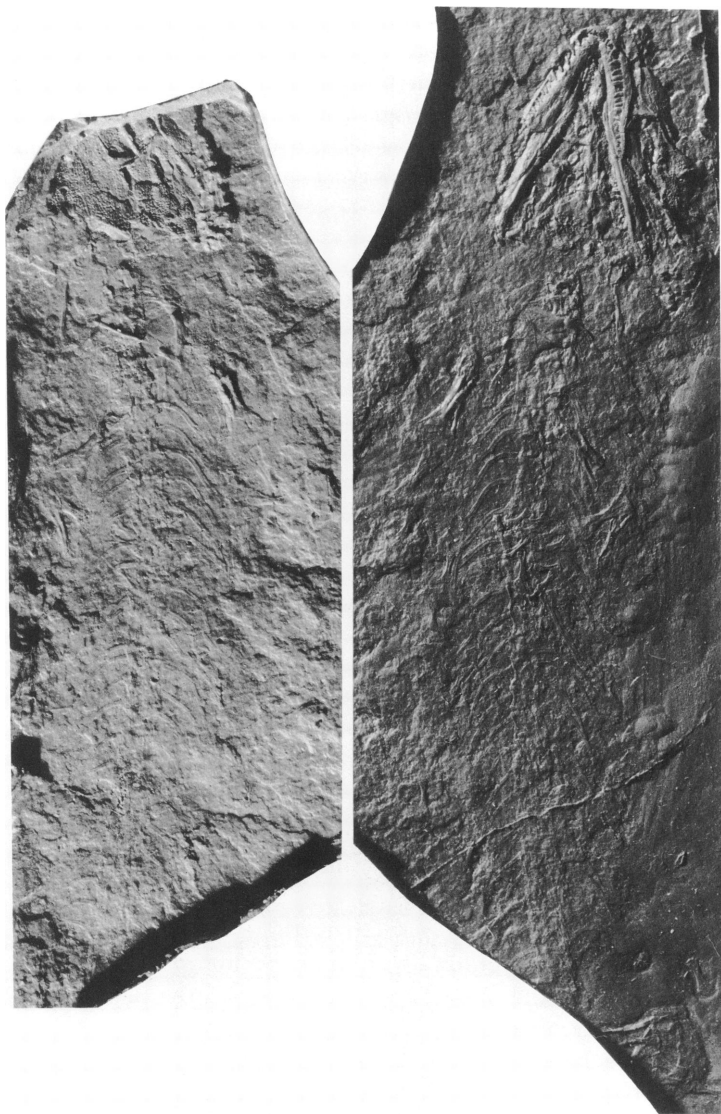
FIG. 4. *Tuditanus punctulatus,* A.M.N.H. No. 6926, type, latex casts of counterparts of skeleton. ×4/3.

cranial articulation. The interpterygoid vacuities are fairly large for a microsaur.

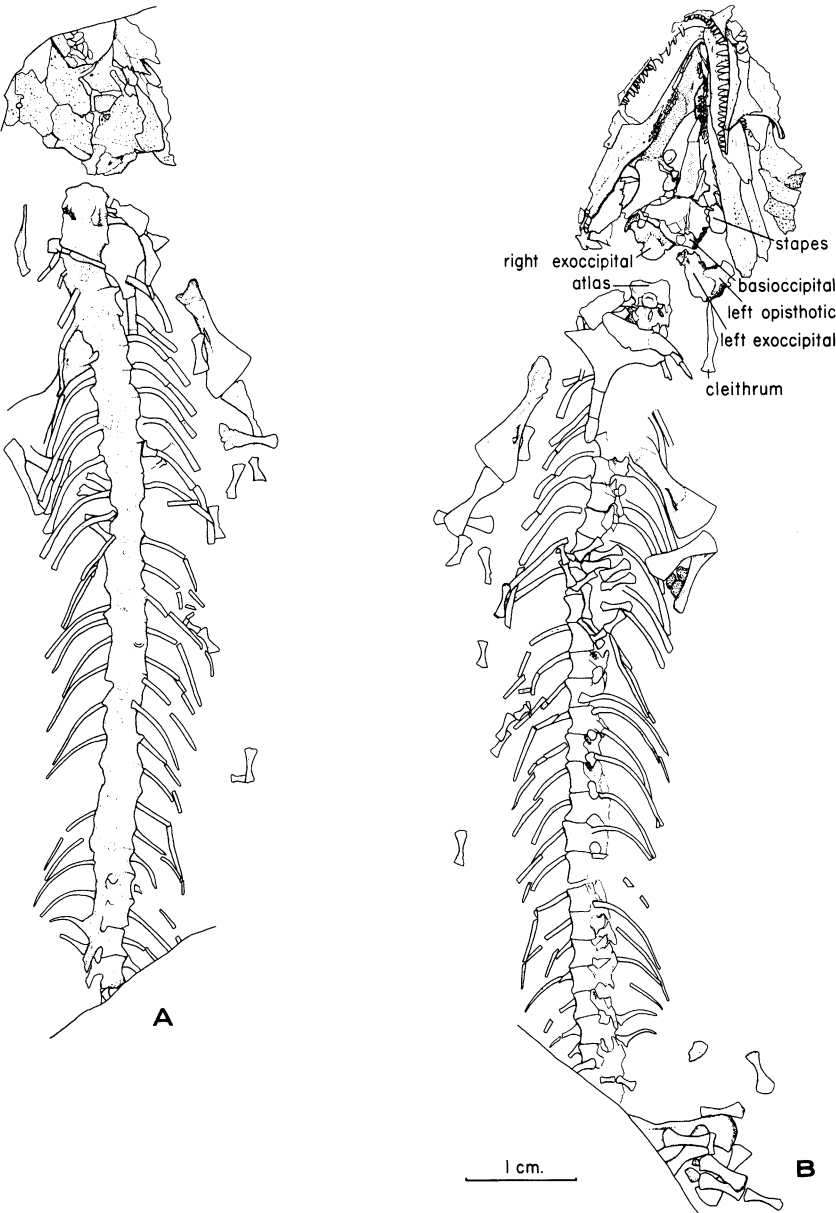The articulation between pterygoid and parasphenoid is movable, and

FIG. 5. *Tuditanus punctulatus*, A.M.N.H. No. 6926, type. A. Dorsal view. B. Ventral view. ×1½.

the parasphenoid has become disarticulated on both sides. The posterior portion of the parasphenoid is very broad, stretching to the quadrate ramus of the pterygoid; although flattened in preservation, it undoubtedly curved dorsally around the base of the braincase. The basipterygoid processes, which have broken from the body of the parasphenoid on both sides, are blunt and marked off basally by a faint groove. The broad-based cultriform process tapers gradually and apparently extends anteriorly above the pterygoids. Neither the epipterygoid nor the basisphenoid is visible. Anterior to the basicranial articulation, a portion of the left sphenethmoid extends anterodorsally above the parasphenoid. The base of the basioccipital, its posterior surface broadly concave, is visible behind the parasphenoid.

The quadrate, visible only on the right side of the specimen, extends below the level of the palate, with its articular surface facing anteriorly and ventrally. As reconstructed, the quadrates lie on a level posterior to that of the occipital condyle and otic region.

The exoccipitals and otic bones have become disarticulated and lie behind the back of the skull. It is impossible to determine the presence or extent of the posttemporal fenestra or the supraoccipital. The left exoccipital is exposed laterally, together with the dorsal portion of the opisthotic. The right exoccipital is exposed medially. Its dorsal portion appears to be broken, exposing the medial wall of the otic capsule. The rugose bases of the exoccipitals indicate the areas of articulation with the basioccipital. The surfaces that formed part of the occipital condyle cannot be seen. Just above its base each exoccipital has a series of small openings for branches of the hypoglossal nerve. The anterior margin of the bone is indented for the passage of the vagus nerve. The left opisthotic is bluntly rounded dorsally. Its anterior ventral margin is embayed with an unfinished edge, indicating either a large fenestra ovalis or an area for the attachment of the prootic (which is not preserved). The base of the opisthotic is not visible on either side.

An element that appears to be the stapes can be seen between the parasphenoid and the pterygoid on the left side. It has the form of an oval plate, similar to the footplate in *Cardiocephalus*, with a rugose ventral surface but little or no stem.

The lateral surfaces of both mandibles are exposed, though the dorsal areas of the dentaries are concealed by the skull roof and only the three most posterior teeth are visible through the left orbit. The dentary is marked by deep pits near the symphysis and by shallow longitudinal grooves over the rest of its surface. The angular, which extends more than half of the length of the jaw, is sculptured with grooves and ridges

radiating from the center of ossification. The surangular is marked with shallow pits. The splenials, exposed laterally at the base of the jaw, are unsculptured.

The posterior part of the right mandible is exposed medially, showing the point of articulation near the base of the jaw. Only a single bone, presumably the prearticular, is exposed anterior to the articular. There appear to be no openings below the masseteric fossa. On and between the ventromedial surfaces of both lower jaws lies a sheet of small, pebbly ossicles which presumably reinforced the skin between the mandibles. Similar ossicles are present in the Nýřany species *"Ricnodon" limnophyes.*

POSTCRANIAL SKELETON: In the type specimen there are 29 presacral vertebrae followed by one very poorly preserved sacral. In the United States National Museum specimen 19 presacral vertebrae and the ribs of five more are preserved. From the position of the manus Peabody estimated that the United States National Museum specimen had as few as four additional presacrals, but, judged from the type, there were probably five. The vertebral column of *Tuditanus* is thus slightly longer than that of most early reptiles (Romer, 1956, suggested 26 presacrals as a high count for primitive reptiles), yet it is considerably shorter than that of such microsaurs as *Microbrachis,* which has 38. Two vertebrae in the sacral region do not bear normal ribs, but whether the second of these is a true sacral is uncertain. The true number of caudal vertebrae cannot be determined, as only the five proximal caudals are normal; the rest of the tail appears to have been lost and regenerated.

Each of the trunk vertebrae consists of a single central element and a solidly attached neural arch. Contrary to Peabody's (1959) interpretation, intercentra or haemal arches are nowhere visible in the column. In the type specimen, the centra of all the vertebrae are in close contact, precluding the presence of even small cartilaginous intercentral elements. In the United States National Museum specimen the vertebral column is not so closely articulated, but it is better ossified, and the vertebrae are clearly visible now that the specimen has been prepared. *There are no intercentra.*

There is a single cervical vertebra which may be termed the atlas. It is poorly preserved, but apparently, as in the gymnarthrid microsaurs, it consists of a single ossification with the neural arch fused to the centrum. The anterior articulating surface is shown quite well in dorsal view, consisting of a median "odontoid" and lateral articulating facets, united into a single convex surface adapted to fit a strap-shaped, concave, occipital condyle. On the expanded anterior portion of the

centrum there is a facet for the capitulum of the first rib, but the area of attachment for the tuberculum is obscured, as are the posterior zyga-pophyses. The second cervical vertebra cannot be termed an axis, since it resembles the vertebrae in the remainder of the column.

There is no noticeable regional differentiation in the trunk vertebrae. The neurocentral suture is obliterated in almost all the vertebrae, though in the larger specimen a noticeable swelling has resulted from fusion of the suture. The situation seems to be analogous to that found in various pelycosaurs (Romer and Price, 1940, p. 101), in which neurocentral sutures are present in the young but the neural arch becomes fused to the centrum in adults.

The structure of the trunk vertebrae is best seen in the better-pre-served United States National Museum specimen. The centrum is hour-glass-shaped internally and is perforated by the notochord. Its rear margin extends laterally to accommodate the capitulum, and its lateral surface is indented beneath the point of attachment of the neural arch. The pedicles are attached to the anterior two-thirds of the centrum and bear prominent transverse processes which extend anteriorly and ven-trally. The zygapophyses are lightly built, with little of the swelling evident in *Limnoscelis, Seymouria,* or *Pantylus.* The neural spines are more prominent than those of the gymnarthrids (aside from the Joggins genus *Trachystegos*), but are comparable in development to those of *Hylonomus.* They are situated above and behind the pedicle.

The more anterior of the two vertebrae termed sacral by Peabody bears unmodified ribs and is therefore the last presacral. Behind it are two vertebrae with atypical ribs. The rib of the first, best seen in the type specimen, is thickened at the base and is evidently a sacral; the rib of the second vertebra is obscure. From the narrowness of the iliac blade it is doubtful that more than a single sacral rib could have articu-lated directly. Aside from its specialized rib, the principal sacral vertebra does not appear to differ significantly from its neighbors. The second appears to have a considerably larger transverse process.

The first three postsacral vertebrae are similar to those anterior to the sacrum, but the fourth has poorly developed transverse processes and no ribs. The fifth, the neural arch of which is broken from the centrum, is the last normal caudal. Following this is a series of 17 irregular, centrum-like blocks without neural arches, which appear to be formed of spongy bone without a perichondral layer. These blocks are of varying lengths, but most are shorter than the trunk centra. Their dorsal and ventral surfaces are grooved longitudinally, presumably for the neural and haemal canals. It seems probable that they developed as the sup-

port for a regenerated tail, although such a structure is normally un-segmental. The anterior caudals show no adaptation for intracentral autotomy, nor is such a mechanism reported in any other microsaur.

All the presacral vertebrae bear ribs. Those on the first two vertebrae are broken at the ends, but were apparently short. Those on the third and fourth are somewhat longer, though not so long as the correspond-ing ribs in early reptiles. Rib length remains more or less constant back to the twenty-second vertebra and then gradually shortens; the last two presacral ribs are very short. All the ribs are double-headed, although the heads are not separated on the two most anterior pairs. On the second and subsequent vertebrae the tuberculum articulates with the transverse process, and the capitulum with the posterior margin of the preceding centrum. The ends of the ribs on vertebrae 4 through 13 are blunt in the type specimen (this may be somewhat accentuated by crushing), indicating that they were attached to costal cartilages. Such blunt terminations are evident only back to the ninth rib in the United States National Museum specimen.

The sacral ribs are not well preserved in either specimen. The proximal end of the anterior sacral is conspicuously thickened and is apparently not fused to the sacral vertebra. If the rib of the next vertebra is func-tionally a part of the sacrum, it must be attached to the posterior sur-face of the principal sacral rib (as in *Ophiacodon*), since the blade of the ilium is too narrow for the separate attachment of two ribs. The distal ends of these ribs are not visible.

The anterior caudal ribs, which are about twice the length of the last two presacral ribs, are sharply curved to parallel the tail. Unlike the anterior caudal ribs of *Hylonomus* and other early reptiles, they are not fused to the vertebrae but appear to have two points of articula-tion. Presumably the ribs of the fourth and subsequent caudals were lost with the remainder of the tail.

The shoulder girdle lies at the level of the second through sixth ver-tebrae. The endochondral girdle is not preserved; presumably it was largely cartilaginous. This situation is surprising, since the front limb is well developed. The scapula, although only rarely preserved in *Micro-brachis,* is well ossified in the gymnarthrids.

The interclavicle is reptilian in structure, with a long stem and a smooth anterior margin. It resembles that of *Pantylus* but differs markedly from the "typical" microsaurian interclavicle of *Microbrachis* (Fritsch, 1883). The plate is flat and unsculptured, with anterior recesses to re-ceive the clavicles; the posterior end of the stem bears a small median ridge on its ventral surface. The clavicle has a broad ventral plate, also
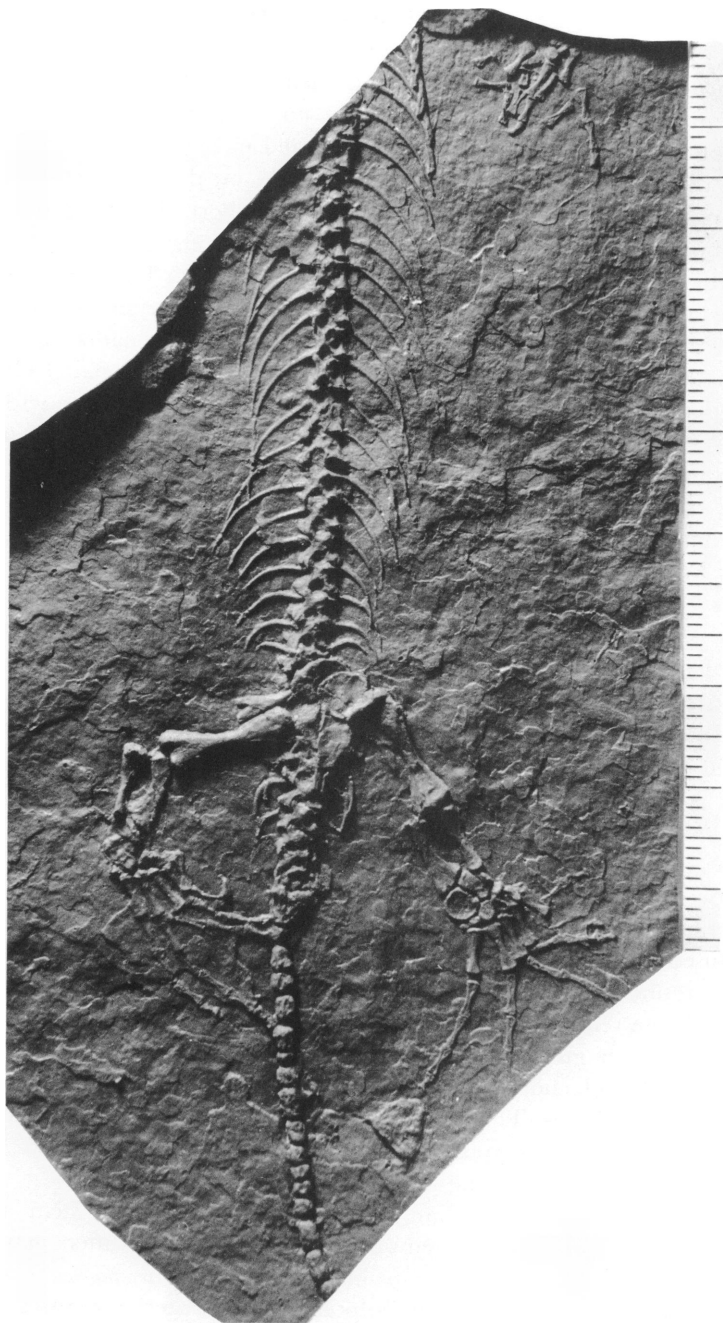
Fig. 6. *Tuditanus punctulatus,* U.S.N.M. No. 4457, latex cast of skeleton after preparation. Scale in millimeters.
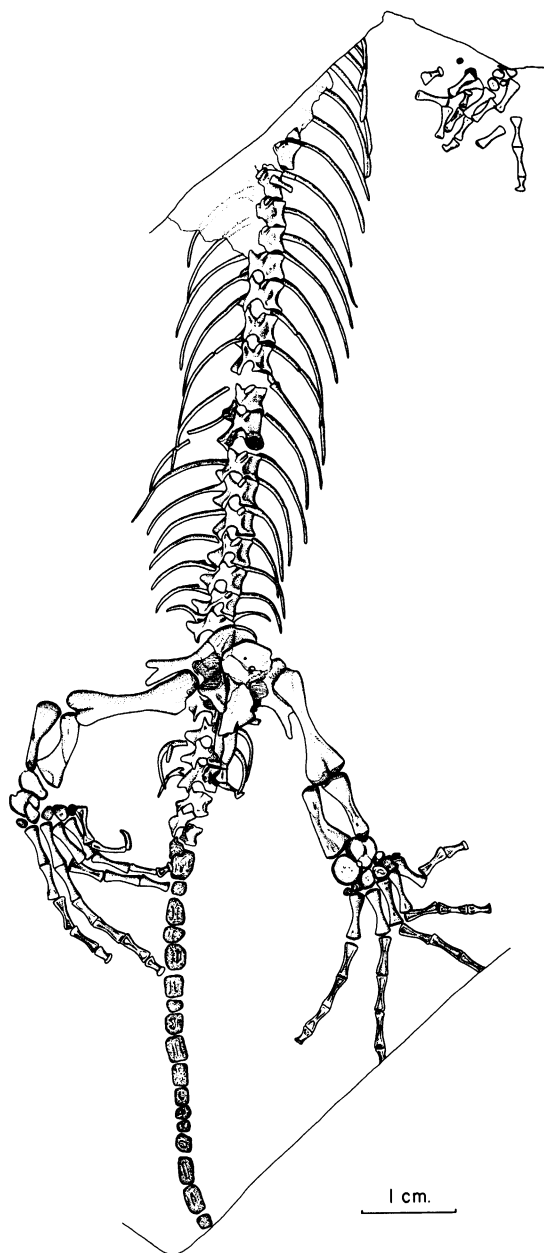
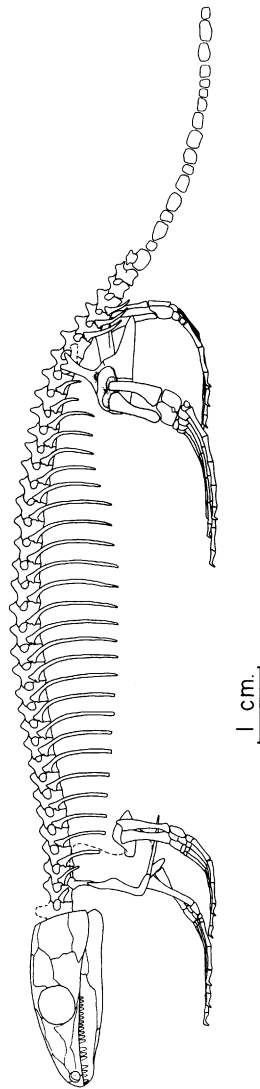FIG. 7. *Tuditanus punctulatus,* U.S.N.M. No. 4457. ×5/4.

1 cm.

Fɪɢ. 8. *Tuditanus punctulatus*, restoration of skeleton based on U.S.N.M. No. 4457. Life size.

unsculptured, and a long dorsal process which is grooved posteriorly for the reception of the cleithrum. Both cleithra are displaced, the left lying beside the first three vertebrae and the right above and across the third. Each has a narrow stem with a thin flange extending from it; the dorsal end is expanded into a small flat plate.

The front limb is large, comparable in relative size to that of early reptiles and far larger than the front limbs of such microsaurs as *Microbrachis* and *Hyloplesion*. The humerus is equal in length to about four and one-half dorsal vertebrae. Its articulating surfaces are not well defined, reflecting the juvenile nature of the type specimen. As in other Paleozoic tetrapods, the ends of the humerus are rotated relative to each other, but the extent of twisting is difficult to judge because of crushing. The entepicondylar foramen is a large, elongate opening in the distal portion of the shaft, partially covered ventrally by a bony extension from its margin.

The ulna and radius are a little more than one-half of the length of the humerus. Both ends of the radius are expanded to about the same extent. The ulna has a narrower shaft than the radius, and its distal end is only slightly expanded. The olecranon extends above the shaft as a triangular process.

The arrangement of the carpals cannot be reconstructed. The proximal carpals are represented by three cartilaginous patches in the American Museum specimen, and in the United States National Museum skeleton there are several scattered distal carpals.

In the left manus of the type specimen a total of 15 metacarpals and phalanges (including three unguals) are exposed in ventral view. An additional ungual phalanx, apparently also from the left hand, is visible on the counterpart slab. A scattering of metacarpals and phalanges from the right manus are also present. In the United States National Museum specimen there are 16 metacarpals and phalanges (including four unguals) in the area of the left manus. When the two specimens are collated, the manus of *Tuditanus* can be reconstructed with confidence as having four digits and a phalangeal count of 2, 3, 4, 3. The metacarpals are a little longer than the trunk vertebrae, and the phalanges are progressively shorter. The dorsal surface of the phalanges is rounded in cross section, and the ventral surface has a median longitudinal groove. The ungual phalanges are uniquely hoe-shaped, with their tips expanded laterally and bent ventrally (fig. 10A).

Three manus digits, the number present in *Microbrachis* and *Hyloplesion*, has been assumed to be the typical count in microsaurs (Romer, 1950), but *Pantylus* is now known to have four. Probably the tetradactyl

condition of *Tuditanus* and *Pantylus* is primitive for the microsaurs, and the reduced digital count in other genera is a specialized rather than a primitive feature of the group.

The structure of the hand, more than any other single feature, proves that the two specimens are conspecific. The digital and phalangeal counts, particularly when compared with those of the pes (which is essentially reptilian) are unique, and hoe-shaped unguals are otherwise unreported in Carboniferous tetrapods.

No part of the pelvic girdle is preserved in the type specimen. Before preparation the sacral region of the United States National Museum skeleton was exposed dorsally but with little of the girdle actually visible; since preparation the entire girdle is displayed in ventral and lateral views. The three pelvic elements are firmly united, although dividing sutures are visible, and all three contribute to the large acetabulum. The ilium has a narrow shaft, apparently directed almost vertically, with separate dorsal and posterior processes. Similar ilia occur in *Ricnodon* sp., *Asaphestera intermedium*, and *Leiocephalikon problematicum* from Joggins, and *Ricnodon copei* from Nýřany (Carroll, 1966). The pubis is roughly circular in outline and is pierced by an obturator foramen. The ischium extends posteriorly to the level of the third postsacral vertebra.

The hind limbs are large, well ossified, and generally reptilian in proportions. The left femur is exposed ventrally and the right dorsally in the United States National Museum specimen. Its head is terminal and roughly hemispherical. The internal trochanter projects ventrally a distance equal to the thickness of the shaft. It originates beyond the head of the femur and extends distally as an adductor ridge to the anterior margin of the distal end, without crossing over to the posterior side of the shaft as is normally the case. A prominent ventral process extends proximally from the tibial condyle but does not meet the adductor ridge.

The tibia and fibula of both limbs are exposed in flexor aspect. Each is about three-fifths of the length of the femur. The proximal end of the tibia is expanded to about two-thirds of the width of the distal end of the femur. The distal end is little expanded laterally but probably broadens anteroposteriorly to a greater (though undetermined) extent. The flexor surface is slightly concave when viewed laterally, with longitudinal ridges at the margins of the shaft. The fibula is quite strongly built, with a broad expansion distally and a smaller one proximally. Its distal end is compressed anteroposteriorly, except for an expanded area where it articulates with the astragalus. There are grooves for at-
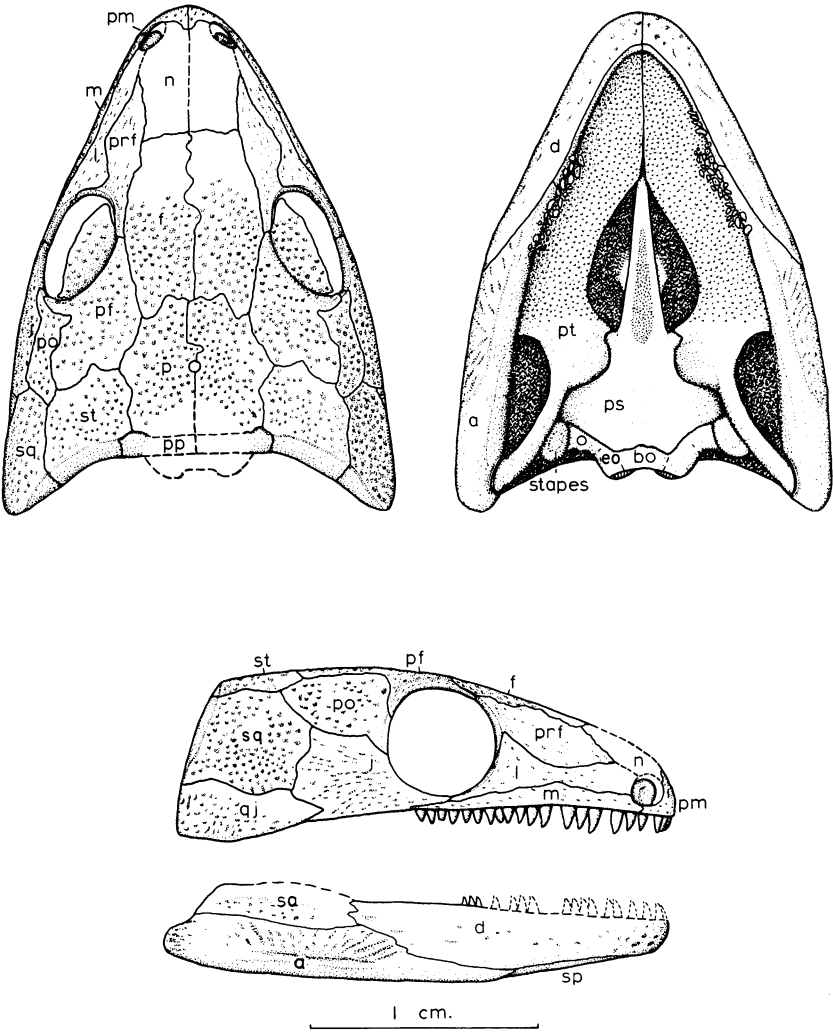
FIG. 9. *Tuditanus punctulatus*, restoration of skull in dorsal, ventral, and lateral views. ×3.

Abbreviations: a, angular; bo, basioccipital; d, dentary; eo, exoccipital; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; o, otic; p, parietal; pf, postfrontal; pm, premaxilla; po, postorbital; pp, postparietal; prf, prefrontal; ps, parasphenoid; pt, pterygoid; qj, quadratojugal; sa, surangular; sp, splenial; sq, squamosal; st, supratemporal.

tachment of ligaments near the distal end of the tibia and near both ends of the fibula.
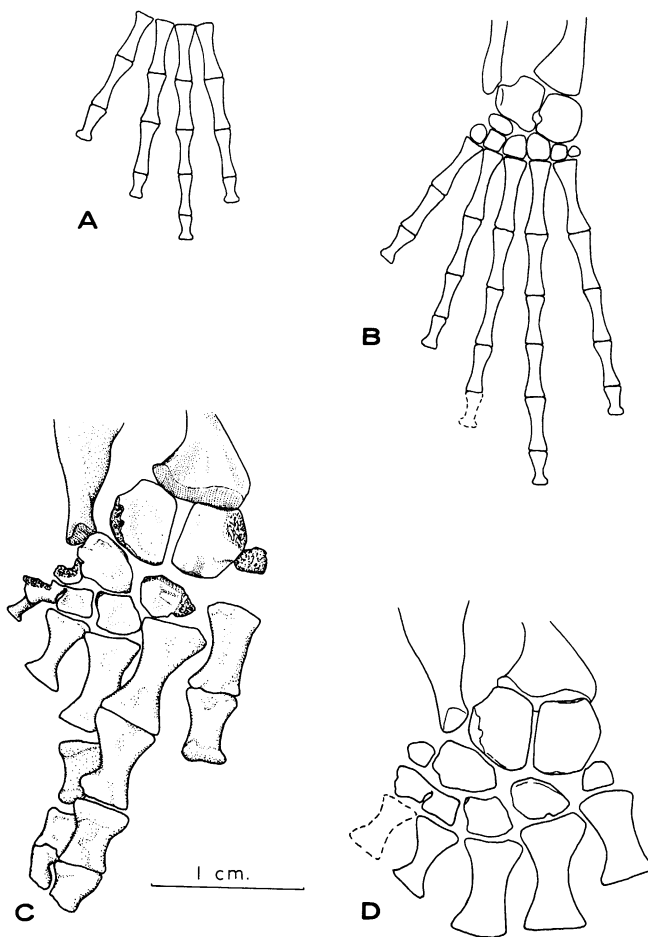
FIG. 10. A, B. *Tuditanus punctulatus,* restorations of left manus and pes, based on U.S.N.M. No. 4457. C, D. *Pantylus,* U.T. No. 40001-1, pes as preserved and as restored, showing astragalus and calcaneum. Both ×2.

The tarsals are very well preserved and have a generally reptilian configuration. Two proximal elements may be referred to as the astragalus and calcaneum. In ventral view the astragalus is seen to be formed from three distinct centers of ossification, incompletely fused, which correspond exactly to the ankylosed tibiale, intermedium, and centrale in the astragalus of *Captorhinus* (Peabody, 1951). Evidently the astragalus of *Tuditanus* has evolved from the same elements. Peabody assumed from the reptilian appearance of the tarsus that *Tuditanus* must be a reptile,

but a similar tarsus is present in *Pantylus* (fig. 10C), which in other respects is certainly a microsaur, and apparently also in *Ricnodon copei* from Nýřany (Carroll, 1966). There is only a single distal centrale, rather than two as suggested by Peabody. Six distal tarsals are present, the second and fourth larger than the rest, the fifth and sixth supporting the fifth toe. There are five digits, with a phalangeal count of 2, 3, 4, 5, 4. Five digits are also present in the pes of *Pantylus,* but the phalangeal count is not known.

The metatarsals are about two-thirds of the length of the tibia and fibula. Their dorsal and ventral surfaces are rounded in cross section, except for the first which shows a longitudinal groove on the ventral side. The phalanges are progressively shorter than the metatarsals. The dorsal surface of each is rounded in cross section, and the ventral surface is marked by a longitudinal groove. Like those of the manus, the terminal phalanges are hoe-shaped, unlike those of any other microsaur or primitive reptile.

The metatarsals and phalanges of the foot are about one-third again as long as those of the hand. With the additional phalanges this makes the foot much larger, as can be seen in figure 10B.

SQUAMATION: Extremely delicate dorsal scales of elongate-oval shape are present between (and occasionally overlapping) the ribs of the better-ossified United States National Museum specimen. These were reported by Peabody, but his illustration, in our opinion, exaggerates the linear striation of the scale surface. As preserved, the surface of each scale shows a minutely crumpled appearance, with the more prominent wrinkles aligned anteroposteriorly. If allowance is made for their insubstantial nature, the scales of *Tuditanus* are essentially similar to those of other Carboniferous microsaurs (Carroll, 1966). There is no evidence of rodlike ventral scales such as occur in other lepospondyls (Baird, 1965), or wheat-shaped gastralia like those of primitive reptiles.

DISCUSSION

As has been evident to earlier workers, *Tuditanus* has a number of reptilian features, most obviously the general proportions of the skeleton (restoration, fig. 8). *Tuditanus* has a relatively short vertebral column and well-developed limbs, in contrast to the elongate body and small limbs of such microsaurs as *Microbrachis, Hyloplesion,* and *Cardiocephalus.* The head is also of normal reptilian proportions, with large orbits about midway in the length of the skull, unlike such microsaurs as *Adelogyrinus* and *Microbrachis* which have anteriorly situated orbits. The individual

vertebrae appear similar to those of captorhinids, with large centra and relatively short neural spines. The interclavicle of *Tuditanus* is reptilian in form, with a long stem and smooth anterior margin. The humerus is large and has an entepicondylar foramen. There are at least four digits in the manus, rather than three as in *Hyloplesion* and *Microbrachis*. The construction of the hind foot in *Tuditanus* was accepted by Peabody as the prime indicator of affinity with reptiles, since no Paleozoic amphibians had been described as possessing an astragalus and calcaneum, and the phalangeal count is a typically reptilian 2, 3, 4, 5, 4.
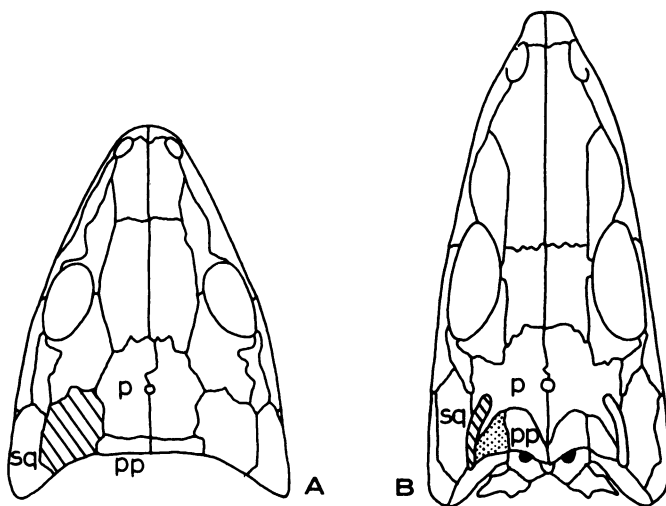
FIG. 11. Skull roof, to show comparison of temporal region. A. *Tuditanus.* B. *Protorothyris* (from Watson, 1954, fig. 13b). Supratemporal is cross-hatched; tabular is coarsely stippled. *Ca.* ×2.

Abbreviations: p, parietal; pp, postparietal; sq, squamosal.

Despite these reptilian features, other morphological characters are shared only with other microsaurs and are not present in any early reptiles.

The structure of the skull is the most diagnostic. In *Tuditanus,* as in typical microsaurs, there is only a single, large bone in the temporal series, the supratemporal, whereas in reptiles there are primitively two small bones, the supratemporal and tabular (fig. 11). As in many other microsaurs, the supratemporal of *Tudinatus* is in contact anteriorly with both the postorbital and postfrontal, a position that neither the supratemporal nor the tabular ever has in reptiles. The pterygoid in *Tudi-*

tanus, as in all other microsaurs, lacks a transverse flange. The latter structure is present in all primitive reptiles (fig. 12).

The stapes (if this element has been correctly identified) has a very broad footplate and little or no stem. In early reptiles there is a relatively long stem, which is perforated for the stapedial artery, and a dorsal process (fig. 13).

Although the occipital area of the skull is not well preserved, it is evident from the configuration of the atlas that the occipital condyle has a broad, strap-shaped, *concave* articulating surface rather than a blunt *convex* knob as in all reptiles (figs. 14 and 15).

The atlas of *Tuditanus,* similar to atlases that have been described in the microsaurs *Cardiocephalus, Euryodus,* and *Leiocephalikon,* consists of a single ossification and has a broad, strap-shaped, anterior articulating surface which is convex and fits into the occipital condyle. In all primitive reptiles, the atlas is composed of a number of separate ossifications (intercentrum, pleurocentrum, and neural arch) and has a concave surface of articulation with the occipital condyle. The second cervical vertebra of *Tuditanus* resembles the vertebrae posterior to it, rather than being specialized as an axis. All reptiles have a distinct axis (figs. 16–19).

The remaining dorsal vertebrae resemble in general those of primitive captorhinomorphs, but lack intercentra. The reports of trunk intercentra in microsaurs have never been verified, but intercentra are present in all early reptiles (with the exception of *Bolosaurus*).

Although the skeleton as a whole is well ossified in *Tuditanus,* the endochondral shoulder girdle is completely unossified. The endochondral girdle is invariably well ossified in early reptiles but is poorly ossified in such microsaurs as *Microbrachis.*

The ilium differs from the pattern in early reptiles in having both a dorsal and a posterior process, as in the microsaur genera *Leiocephalikon, Asaphestera,* and *Ricnodon.*

Both specimens of *Tuditanus* show that the manus has only four digits. All primitive reptiles have five anterior digits, but microsaurs tend to have fewer. *Microbrachis, Hyloplesion,* and *Odonterpeton* have only three, whereas *Pantylus* has four.

The dorsal scales present in the United States National Museum specimen are oval and show a pattern of fine parallel ridges on the inside surface. Similar scales have been found with most microsaur genera, whereas reptiles lack ossified dorsal scales.

The combination of reptilian and microsaurian features in *Tuditanus* indicates that the morphological characters that have been accepted as typifying the Microsauria do not pertain to all members of the group.
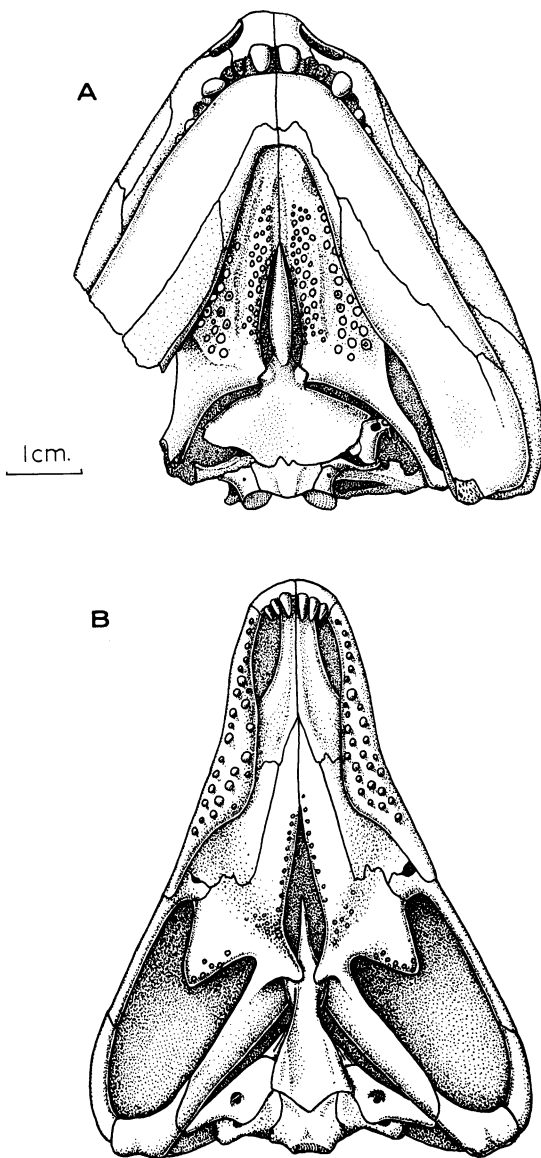
FIG. 12. Palate, to show comparison of pterygoid. A. *Pantylus*, M.C.Z. No. 2040. ×1. B. *Captorhinus* (from Romer, 1956, fig. 36b). *Ca.* ×1.

If they do not, then the microsaurs may not conform to a single morphological pattern, and the possibility arises that some may be related to

reptiles. Hence the various features by which microsaurs are character-
ized and differentiated from reptiles must be evaluated. Similar appraisals
were made by Romer in 1950 and Gregory in 1965, but additional work,
particularly on other Carboniferous microsaurs (Carroll, 1963, 1966,
1967, as well as other work in progress), makes it necessary to reconsider
several of these features.

Before a detailed discussion of the morphological differences between
microsaurs and primitive reptiles is given, however, it will be useful to
mention briefly the genera included in both groups, and their presumed
phylogeny.

The general phylogeny of Paleozoic reptiles is fairly well known,
although there is not universal agreement as to its details. The most
primitive and generalized of all undoubted reptiles is the recently de-
scribed limnoscelid *Romeriscus* (Baird and Carroll, 1967) from the Early
Pennsylvanian (Westphalian A) of Cape Breton Island, Nova Scotia.
This genus makes a plausible ancestor for later limnoscelids and is not
far removed from the ancestry of the more advanced captorhinomorph
groups and the pelycosaurs. Next in level of organization are the ro-
meriid captorhinomorphs, of which the earliest record appears in the
genera *Hylonomus* and *Archerpeton* from the Westphalian B of Joggins,
Nova Scotia. Subsequent romeriids include *Cephalerpeton* from the Mid-
dle Pennsylvanian (Westphalian D) of Mazon Creek (Baird, 1965) and
Romeria and *Protorothyris* from the Early Permian of Texas. From the
romeriids have evolved the captorhinids (discussed recently by Seltin,
1959, and by Fox and Bowman, 1966), which diversified in the early
Permian but apparently left no descendants. The synapsids, which had
separated from the romeriids by early Pennsylvanian time, are repre-
sented at Joggins by the generalized genus *Protoclepsydrops* (Carroll,
1964b). *Protoclepsydrops* or a closely allied genus could have given rise
to all the major lines of pelycosaurs that had differentiated by the end
of the Pennsylvanian. From the same romeriid ancestry come the "saur-
opsids" (archosaurs and lepidosaurs), of which *Petrolacosaurus* (Peabody,
1952) from the late Pennsylvanian of Garnett, Kansas, may represent
an early offshoot. The mesosaurs probably also have their ancestry
among the romeriids or captorhinids.

The romeriids themselves apparently evolved from the anthracosaurian
labyrinthodonts. Their antecedents were probably very similar in mor-
phology to the genus *Solenodonsaurus* (Broili, 1905, 1924) which is known
from the Middle Pennsylvanian and possibly earlier. This genus, re-
cently redescribed by Brough and Brough (1967c) and Carroll (1968),
has been classified among the seymouriamorphs, but it should not be

TABLE 1

COMPARISON OF MICROSAURIAN AND REPTILIAN FEATURES IN ALL DESCRIBED GENERA
OF THE MAIN MICROSAUR STOCK AND IN CHARACTERISTIC PALEOZOIC REPTILES

	Temporal Region	Transverse Flange on Pterygoid	Occipital Condyle	Atlas-Axis Complex	Trunk Intercentra	Scales
MICROSAURS						
Gymnarthridae						
Cardiocephalus	—[a]	—	—	—	0[b]	0
Euryodus	—	—	—	—	0	0
Hylerpeton	0	0	0	0	0	—
Leiocephalikon	—	—	—	—	—	0
Parioticus	—	—	—	0	0	0
Sparodus	0	0	0	0	0	—
Trachystegos	0	—	0	0	0	—
Pantylus	—	—	—	—	—	—
Tuditanidae						
Asaphestera	0	0	0	0	—	—
Boii	0	0	0	0	0	—
Ricnodon copei	—	—	—	0	—	—
Tuditanus					—	—
Hyloplesionidae						
Hyloplesion	—	—	—	—	—	—
Odonterpeton	—	—	0	—	—	—

TABLE 1—(Continued)

	Temporal Region	Transverse Flange on Pterygoid	Occipital Condyle	Atlas-Axis Complex	Trunk Intercentra	Scales
Microbrachidae						
Microbrachis	—	—	—	—	—	—
Undesignated families						
Novascoticus	0	0	—	0	—	—
"Ostodolepis"	—	—	—	—	—	—
"Ricnodon" limnophyes	—	—	0	0	0	—
"Hylonomus" geinitzi	—	—	—	—	—	—
REPTILES						
Pelycosauria						
Ophiacodon	+[c]	+	+	+	+	+
Captorhinidae						
Captorhinus	+	+	+	+	+	+
Romeriidae						
Protorothyris	+	+	+	+	+	+
Limnoscelidae						
Limnoscelis	+	+	+	+	+	+
Solenodonsauridae						
Solenodonsaurus	x[d]	+	+	0	+	+

[a] —, Microsaurian configuration.
[b] 0, Indeterminate, unprepared, or not preserved.
[c] +, Reptilian configuration.
[d] x, Anthracosaurian configuration.

thought of as closely related to the seymouriids. The solenodonsaurids represent an independent stock, characterized by the loss of labyrintho- dont infolding of the enamel, the absence of palatine fangs, and the development of a transverse flange on the pterygoid.

The captorhinomorphs and their immediate ancestors constitute the main reptilian stock that is compared with microsaurs. The position of other early reptiles is subject to considerable controversy, which lies outside the scope of this discussion. The diadectids, *Bolosaurus,* pareia- saurs, procolophonids, and turtles may or may not be related to one another or to the main reptilian stock (see Olson, 1965, 1966). In any case, they show no similarities to microsaurs and have never been seri- ously considered to be related to them.

A detailed classification of the Microsauria as a whole has never been attempted. At least an informal classification of the order will be help- ful for an understanding of the patterns of morphological variation, hence is included here, although subject to considerable refinement in the future.

Romer, in 1950, distinguished a large group of "typical" microsaurs (see table 1) which have solidly roofed skulls and correspond more or less to the pattern of *Microbrachis.* No members of this group are known earlier than the Westphalian B, although several lineages had already differentiated by that time. Family groupings of these genera are un- settled, except for the gymnarthrids (described by Gregory, Peabody, and Price, 1956) and clearly related antecedent forms from Joggins and Nýřany (Carroll, 1966). The genus *Pantylus* may provisionally be in- cluded in the same family. *Tuditanus* and other genera with simple piercing teeth and well-developed limbs, such as *Asaphestera* from Jog- gins, *Boii* from Nýřany, and *Ricnodon* from both areas, may constitute another family. *Hyloplesion* from Nýřany and *Odonterpeton* from Linton apparently are closely related to each other. Other genera such as *Microbrachis* and *"Ostodolepis"*[1] appear to belong to monotypic families. All these "typical" microsaurian genera share a common morphological pattern and presumably have a common ancestry in the early Carbonif- erous.

Other genera termed microsaurs clearly come from separate stocks

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[1] The genus *Ostodolepis* is currently under study by the senior author. The specimen assigned to that genus by Case (1929) is a typical microsaur. The vertebrae designated as the type of the type species (Williston, 1913), however, are quite unlike those of Case's specimen, and are typically reptilian in having well-developed intercentra. The specimen described by Case is here cited as *"Ostodolepis,"* since it belongs to a different genus and must be renamed.
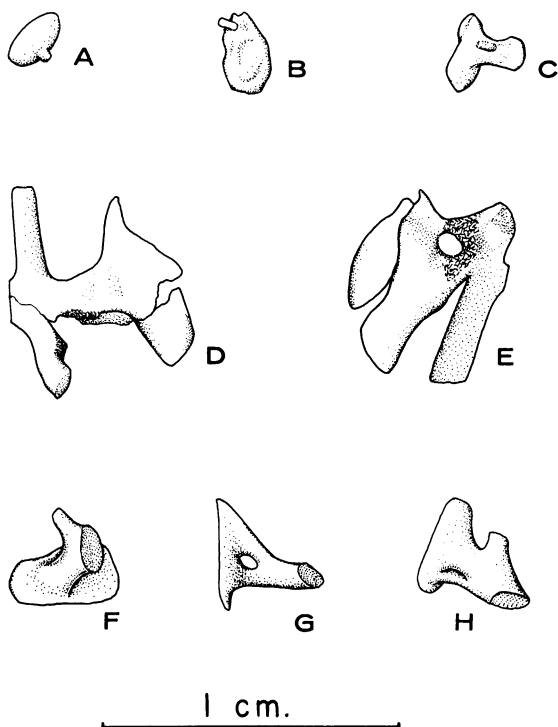
FIG. 13. Stapes. A. *Cardiocephalus* in posterior view (from Gregory, Peabody, and Price, 1956, fig. 13b). B. *Tuditanus* in ventral view. C. *Microbrachis,* H.M. No. V.2012/1, in ventral view. D, E. *Pantylus,* M.C.Z. No. 2040, in posterior and dorsal views. F–H. The reptile *Hylonomus lyelli,* N.M.C. No. 10047, in obliquely lateral, ventral, and obliquely posterior views. All ×4.

and are characterized particularly by having a reduced number of skull bones. The lysorophids are known from *Lysorophus* (Sollas, 1920) and *Megamolgophis* (Romer, 1952) in the Permo-Carboniferous and *Molgophis* and *Cocytinus* in the Pennsylvanian (Romer, 1930). All have elongate bodies, and the bones of the cheek region are much reduced.

The adelogyrinids (considered here as a family rather than an order) are known from only four described specimens, allocated to three genera. *Adelogyrinus* and *Dolichopareias* (Watson, 1929) from the Missis-sippian of Scotland were recently restudied by Brough and Brough (1967a). A third genus, *Adelospondylus,* from a slightly higher horizon, has also been described recently (Carroll, 1967). The cheek region is fully roofed in adelogyrinids, but there are only three pairs of bones across the back of the skull. The postorbital is greatly reduced and

does not enter the margin of the orbit. The orbits are situated far forward. An early Mississippian lepospondyl, *Palaeomolgophis,* has been described by Brough and Brough (1967a) as a possible forerunner of the *Molgophis-Lysorophus* assemblage. What is known of the skull of *Palaeomolgophis,* however, resembles that of *Adelogyrinus* and *Adelospondylus* in having a fully roofed cheek region and small columnar teeth and shows no significant similarities to the skulls of known lysorophids. Although *Palaeomolgophis* may conceivably be related to the ancestry of lysorophids, it is not sufficiently similar to the known Pennsylvanian and Permian genera to be included within that group as it is currently understood.

The lysorophids and adelogyrinids are usually thought to be fairly closely related to each other (Baird, 1965; Brough and Brough, 1967a), but none of the known genera could have given rise to any of the "typical" microsaurs.

It is the central stock of microsaurs which is usually compared with reptiles, and from which most of our general conceptions of the group are formed.

Romer (1950, pp. 632–636) listed 10 features as being characteristic of microsaurs. We consider here whether these are characteristic of all microsaurs, and which (if any) of them differentiate microsaurs from reptiles.

1. "Small size. . . ." None of the animals that have been described as microsaurs are large. *Pantylus,* with skulls up to 3 or 4 inches in length, is the largest genus known; other genera are much smaller. Their size, however, does not differentiate them from early reptiles. *Trachystegos,* a gymnarthrid microsaur in the Joggins fauna, is known from specimens that are larger than those of any of the reptiles from that deposit, and *Asaphestera* and *Hylerpeton* are nearly as large. *Cephalerpeton* is no larger than the contemporary microsaur *Tuditanus. Pantylus* and *"Ostodolepis"* are larger than many of the early Permian captorhinomorphs. It is only after Middle Pennsylvanian time that any reptiles become significantly larger than microsaurs, and there are still many Permian reptiles which are no larger than contemporary microsaurs.

2. "Body moderately long and slender. . . ." There are relatively few microsaurs in which the actual vertebral count is known. *Microbrachis* has 38 presacrals; *Hyloplesion,* 30; *"Hylonomus" geinitzi,* 28 + ; *"Ostodolepis,"* 26; and *Tuditanus,* 29. Snakelike genera such as *Cocytinus, Lysorophus,* and *Molgophis* have considerably longer vertebral columns. Except for *"Ostodolepis,"* which has a reptilian vertebral count, microsaurs tend to
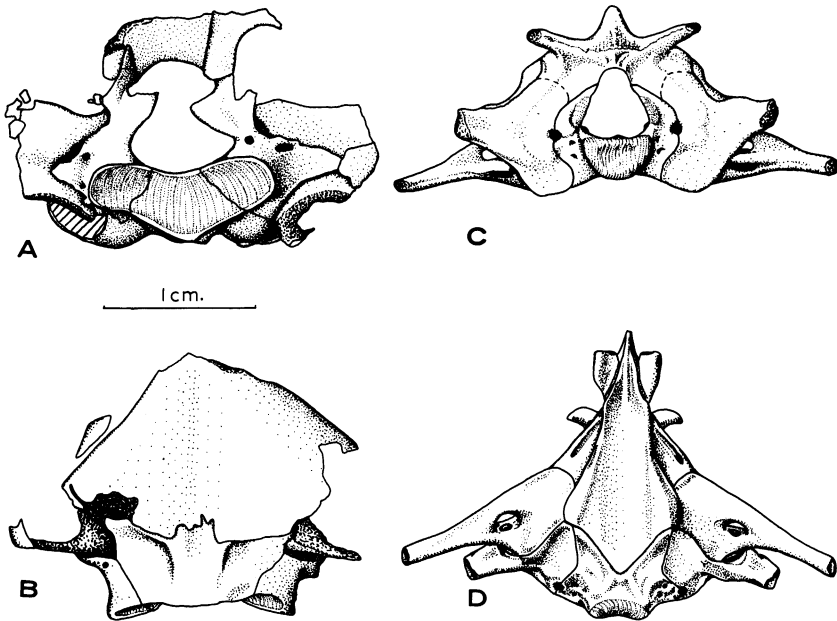
Fɪɢ. 14. Occiputs in posterior and ventral views. A, B. *Pantylus,* M.C.Z. No. 3302. ×2. C, D. *Captorhinus* (from Price, 1935, pls. 9A, 7B). *Ca.* ×1.

have longer trunk regions than do early reptiles. The length of the pre-sacral column is so variable among microsaurs, however, that it is a poor criterion for distinguishing them from reptiles.

3. "Spool-shaped vertebral centra; no trunk intercentra; caudal chevrons?; neural arch pedicel relatively high and narrow anteroposteriorly; neural arch not expanded transversely nor swollen; neural spine little developed. . . ." The individual vertebrae of microsaurs are difficult to differentiate from those of captorhinomorphs. Generally the neural spine is short, as in *Captorhinus. Trachystegos,* however, has relatively long spines. The neural arches may be swollen, as in *Pantylus,* in a manner resembling that of some captorhinids, but such cases are exceptional. Because swollen neural arches have developed separately in several lines of reptiles and anthracosaurs, they are evidently a structural adaptation for greater vertebral support in larger animals and therefore have little taxonomic significance. The neural arch may be either suturally attached or fused to the centrum in the central microsaur stock, but such attachment is primarily a function of the size or age of the animal and has no taxonomic significance.

All described microsaurs have a single ossification of the vertebral centra in the trunk region. The homology of this element has been variously interpreted. If the centrum of microsaurs is homologous to the pleurocentrum of reptiles, it is probable that trunk intercentra and typical haemal arches will eventually be described in some genera. Trunk intercentra are, however, quite definitely missing from most genera. This general absence suggests that intercentra may not be present in any members of the group. If microsaurs, as a group, lack intercentral ossifications, doubt is cast on the identification of the definitive centrum as the homologue of the pleurocentrum of other early tetrapods.

In general, the absence of trunk intercentra may be accepted as differentiating microsaurs from reptiles. The small size of intercentra in early reptiles makes them difficult to recognize (intercentra have never been reported in *Bolosaurus*), so that their apparent absence cannot alone be accepted as proof that a particular animal is a microsaur.

Haemal arches have been reported in several microsaurs, including a specimen of *Pantylus* now under study. Even if this structure were proved to be present in microsaurs in general, this occurrence would not, of itself, necessarily indicate the proper homology of the major central elements or imply the presence of trunk intercentra. Among other lepospondyls, structures at least analogous to typical haemal arches are present in nectrideans. They are not intercentral in position, however, but fused midway in the length of the definitive central elements. No trunk intercentra are reported in that group. Aïstopods also lack trunk intercentra and have longitudinal grooves on the ventral surface of the caudal centra serving the function of haemal arches.

The question of the homology of the microsaur centrum has most recently been discussed by Brough and Brough (1967a, 1967b, 1967c), who maintained that it is directly comparable to the reptilian pleurocentrum. They cited the presence of caudal intercentra in the genera *Palaeomolgophis* and *Microbrachis* and trunk intercentra in *Microbrachis mollis* and *Microbrachis obtusatum*. The evidence for trunk intercentra in the latter two species is very questionable, since the Broughs' observations were based only on metal casts, rather than on the specimens themselves. Although the casts are of fairly high fidelity, they do not preserve the original texture of the bone; it is therefore possible to confuse sutures with cracks. The objects noted by Brough and Brough are visible on other casts of the same specimens, but it is not possible to confirm the identity of these bones as intercentral elements. They could also be interpreted as pieces broken from the ends of the centra.

The absence of trunk intercentra in the numerous specimens of the very closely related (if not identical) species, *Microbrachis pelikani,* suggests that they are probably absent from all members of this genus.

Even if microsaur central elements are pleurocentra (in the sense of primitively alternating with intercentra), this fact does not in itself indicate that they are truly comparable to reptilian centra. Špinar (1952) has shown that the pleurocentra in discosauriscids (close relatives of the seymouriids and thus related to the ancestry of reptiles) develop during ontogeny from paired crescentic elements, comparable to the pleurocentra in rhachitomous amphibians. Romer (1964) has demonstrated that the anthracosaurian pleurocentra also developed phylogenetically from paired crescentic elements. Even in the earliest reptiles and solenodonsaurids, however, the pleurocentra reach their definitive configuration too early in ontogeny for any evidence of their paired origin to remain. The persistence of paired pleurocentra in larval seymouriamorphs and in the adults of primitive anthracosaurs demonstrates the method of development of the reptilian centrum and suggests that this structure reached its definitive stage only late in the Mississippian. The centrum in lepospondyls, in contrast, is already fully developed in Lower Carboniferous adelogyrinids and aïstopods and shows no evidence in either ontogeny or phylogeny of having originated from paired structures (Baird, 1965), which has led Carroll (1967) and Thomson (1967) to suggest that the lepospondyl centrum was inherited directly from a rhipidistian ring centrum. Holospondylous centra are known in the genera *Megalichthys, Ectosteorhachis,* and *Rhizodus.* In these genera the centra are homologous with the intercentra of labyrinthodonts, and the pleurocentra do not ossify, suggesting that the ring centra in lepospondyls might also be intercentra. These particular rhipidistians have no other important lepospondyl features, however, and it is conceivable that some other rhipidistians may have had ring pleurocentra.

Whatever the origin and homology of lepospondyl centra, it is certain that the holospondylous condition is primitive in the group, whereas it is a derived condition in the anthracosaurian ancestors of reptiles (Baird, 1964). Despite their general similarities, lepospondyl centra hence are not truly comparable to those of reptiles.

4. "Ribs two-headed, capitulum often articulating with facet or low process on the centrum, tuberculum articulating with transverse process. . . ." These characteristics are consistent throughout the group but are of no value for differentiating microsaurs from reptiles. The capitulum may articulate with the posterior margin of the centrum as in *Trachystegos, Microbrachis,* and *Tuditanus,* or with the anterior margin

as in *Ricnodon copei.*

5. "Interclavicle with very broad but short fan-shaped head and short, slender stem. . . ." As is pointed out above, the type of interclavicle possessed by *Microbrachis* is not present in all members of the group. The interclavicle of *Tuditanus,* as well as that of *Pantylus,* resembles that of early reptiles. The genus *Boii* has a roughly diamond-shaped interclavicle, and *Molgophis* has a star-shaped plate which is forked anteriorly. This variation in configuration makes the interclavicle an unsuitable feature for differentiating microsaurs from reptiles.
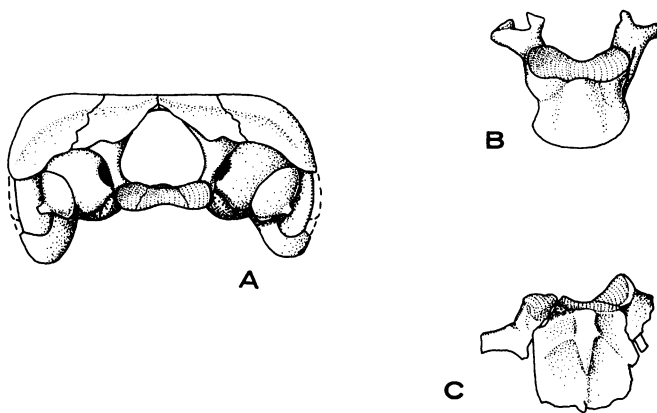

FIG. 15. Occiputs. A. *Cardiocephalus* (from Gregory, Peabody, and Price, 1956, fig. 13b). ×4. B. *Asaphestera,* N.M.C. No. 10041. ×2. C. *Microbrachis,* Č.G.H. No. 3018. × 6.

6. "Limbs relatively short and feeble; manus three-toed. . . ." The limbs of some microsaurs, for example *Tuditanus,* may be of the same relative proportions as those of reptiles. *Pantylus* and *"Ostodolepis"* also have fairly large limbs, as does *Trachystegos.* Although *Microbrachis, Hyloplesion, Cocytinus,* and *Odonterpeton* all have only three front toes, *Pantylus, Molgophis,* and *Tuditanus* have four digits in the manus. No microsaur is known to have five manus digits, but the variability within the group would not preclude it.

7. "Scales with a characteristic radiate striation; ventral scales suboblong, with a pronounced posterior ridge; dorsal scales rounded. . . ." Microsaur scales are indeed a feature by which members of the group can be easily distinguished. Except in the adelogyrinids and lysorophids (discussed below), microsaur dorsal scales (fig. 20) are roundish, and the ventral scales are transversely elongate, rather like the dorsal and

ventral scales in labyrinthodonts such as *Trimerorhachis* (Colbert, 1955). Both dorsal and ventral scales are ridged on the posterior edge. In well-preserved specimens concentric growth rings can be seen on both dorsal and ventral scales. Although scale structure, when well preserved, resembles that of labyrinthodonts, the radial pattern is more pronounced, particularly if the scales are somewhat weathered. Integument with scales of this nature is preserved in place in *Tuditanus, Microbrachis, Odonterpeton, Hyloplesion, Boii,* and *"Hylonomus" geinitzi.* Other species, such as *Ricnodon copei* and *"Ricnodon" limnophyes,* show disarticulated scales typical
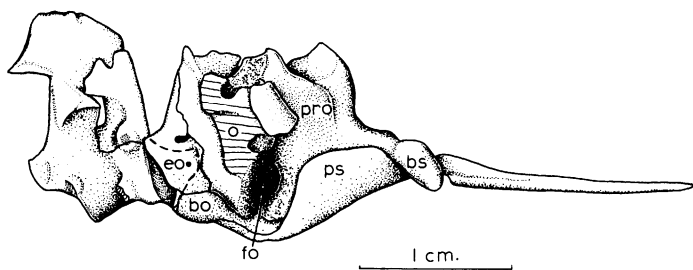

Fig. 16. *Pantylus,* atlas of M.C.Z. No. 3302 shown in articulation with occipital condyle of M.C.Z. No. 2040. ×2.

Abbreviations: bo, basioccipital; bs, basisphenoid; eo, exoccipital; fo, fenestra ovalis; o, otic; pro, prootic; ps, parasphenoid.

of both dorsal and ventral patterns. All the Joggins microsaurs show scales of either dorsal or ventral patterns, both being clearly evident in *Asaphestera.*

Pantylus was protected by small, contiguous, polygonal plates in the pectoral region. Otherwise scales are not known in this genus or in the Permian gymnarthrids described by Gregory, Peabody, and Price (1956), owing certainly to the mode of preservation in the Permian redbeds and fissure fillings (as contrasted with that of the Pennsylvanian deposits) rather than to the absence of scales from the living animals.

As might be expected on the basis of other characteristics, the adelogyrinids differ from other microsaurs in the nature of the integument. In the pectoral region of *Adelospondylus* are numerous ventral scales. Each has the form of a short cylindrical rod, which is sculptured, pointed at both ends, and much heavier than the scales in reptiles. Dorsal scales are unreported in adelogyrinids. Lysorophids lack ventral armor, and the evidence for dorsal scales is equivocal.

Clearly there is little possibility of confusing microsaur scales with

those of early reptiles. In reptiles only the ventral scales are bony, and these take the form of small rods, recessed at one end to accommodate the next in the series. Except for their narrower shape, the ventral scales in early reptiles are similar to those of anthracosaurs and were evidently derived from them. These scales bear no real resemblance to the ventral scales in microsaurs. Apparently early reptiles lacked bony dorsal scales such as are retained in microsaurs.

8. "Skull greatly elongated postorbitally; otic notch absent. . . ." Several microsaurs are now known that have skulls of normal proportions, with the orbits midway along the length. In addition to *Tuditanus*, these include *Asaphestera*, *Trachystegos*, *"Ricnodon" limnophyes*, and *Hyloplesion*. Among the microsaurs, only the adelogyrinids have a structure that may be termed an otic notch (Carroll, 1967). Because these genera have a reduced complement of roofing bones, it is difficult to homologize this notch with that in labyrinthodonts, or with the "zone of weakness" between skull table and cheek in the skulls of early reptiles. The position and configuration of the stapes in the main line of microsaurs appear to be incompatible with an external tympanic membrane. Primitive reptiles, in contrast, almost certainly did have a tympanum (Fox and Bowman, 1966). The skull roof is firmly attached to the cheek region in most microsaurs, but there was apparently some degree of mobility in *Tuditanus* and *Asaphestera*, as in the early captorhinomorphs. Such mobility would facilitate the expansion of the temporal musculature in forms that lack a temporal opening. It does not indicate a close degree of relationship.

9. "Skull roofing pattern generally primitive, but tabular absent from roof and a very large supratemporal interposed between parietal and squamosal. . . ." Although the cheek region of the lysorophids is greatly reduced, and the back of the skull table is considerably modified in the adelogyrinids, the "typical" microsaurs show little variation in the configuration of the temporal series. No genus has more than a single bone in this area. As was noted by Romer, this bone may be called either a "tabular," the term employed by Steen (1934, 1938), or a "supratemporal," as most authors designate it. The supratemporal is invariably large and separates the parietal from the squamosal. In several genera (*Tuditanus*, *Asaphestera*, the gymnarthrids, and *"Ostodolepis"*), the supratemporal makes contact with both the postorbital and postfrontal. In *Microbrachis*, which has a very long skull table, the supratemporal reaches only the postorbital.

In reptiles there is a progressive reduction of the temporal bones. There are three, including the intertemporal, in the solenodonsaurid

anthracosaurs. All true reptiles have two or fewer, the most primitive configuration being represented by *Limnoscelis*. As was pointed out by Vaughn, the supratemporal may be large in some early reptiles such as limnoscelids and *Paracaptorhinus* (Watson, 1954) among the captorhinomorphs, and *Eothyris* and *Oedaleops* (Langston, 1965) among the pelycosaurs. In no reptile does the supratemporal meet the postorbital and postfrontal as it does in microsaurs. In most captorhinids, the supratemporal is greatly reduced and the tabular is eliminated. In the ro-
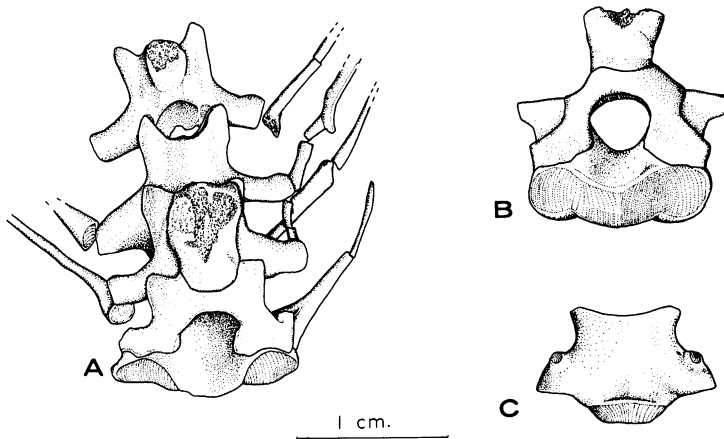

FIG. 17. Cervical vertebrae of *Pantylus,* M.C.Z. No. 3302. A. Dorsal view. B. Anterior view. C. Ventral view. All ×2.

meriids and pelycosaurs, both bones are reduced but vestiges remain. Thus, as was pointed out by Romer, the microsaurian pattern of reduction in the temporal series is not comparable to that of reptiles.

10. "Palate essentially primitive in nature, with slender cultriform process of parasphenoid; movable basal articulation of braincase and palate, narrow interpterygoid vacuities. . . ." These palatal features are, in general, typical of microsaurs but do not serve to distinguish them from reptiles. Microsaurs indeed resemble reptiles in lacking the fixed basicranial articulation and wide palatal vacuities such as are seen in advanced rhachitomes and stereospondyls. The palate is closed in gymnarthrids such as *Euryodus,* but conspicuous palatal vacuities occur in members of other groups, for example, *Microbrachis, Hyloplesion,* and *Tuditanus.* The lysorophids have very wide parasphenoid plates separating the pterygoids but still do not have large vacuities. A more distinctive feature of the palate is that mentioned by Gregory (point 11).

The structure of the occipital condyle is also elaborated below. The braincase is very poorly known in most genera; that of *Pantylus* is currently being described by Romer.

Gregory (1965) listed additional features distinctive of microsaurs:

11. Lack of transverse flange on pterygoid. As is pointed out above, no microsaur has ever been described as possessing a transverse flange on the pterygoid. This structure is present in all primitive reptiles. The presence of the transverse flange in the Joggins reptiles, and even in the technically amphibian solenodonsaurids, indicates the early origin of this structure in reptilian phylogeny. Its retention in all the major
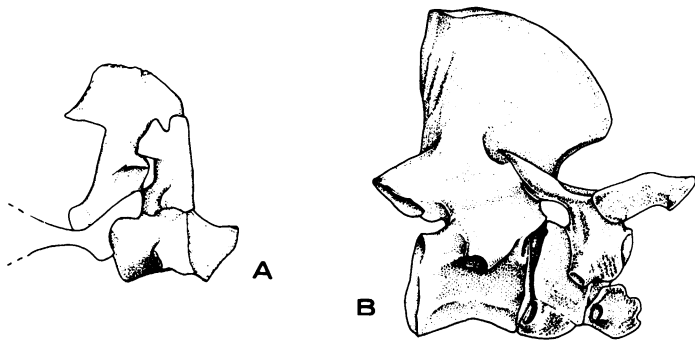

FIG. 18. Cervical vertebrae. A. *Pantylus*, M.C.Z. No. 3302. ×2. B. *Ophiacodon* (from Romer and Price, 1940, fig. 44a). ×½.

lines of early reptiles, as well as in the living tuatara, indicates its adaptive significance. Because the transverse flange of the pterygoid is a readily recognizable feature, it is a convenient characteristic for distinguishing members of the two groups.

12. Stapes with a short, imperforate stem and lacking a dorsal process. Our knowledge of the microsaur stapes has been based on that of *Cardiocephalus*, which has a large footplate and very short stem but lacks the dorsal process and stapedial foramen which are present in all early reptiles. The stapes in *Tuditanus*, if this element is correctly identified, consists simply of a large footplate with little or no stem. That of *Microbrachis* (fig. 13C) has a fairly large stem, which is indented or possibly pierced by a stapedial foramen.

The stapes of *Pantylus*, shown in M.C.Z. No. 2040 (figs. 12A, 13E), has a quite different configuration. The footplate is again large, but there is a long stem, which is pierced by the stapedial foramen, and a long dorsal process. The stapes is wedged against the quadrate ramus of the

pterygoid, with which it articulates by a special process. It is difficult to see where a tympanum might be placed which would activate a stapes in this position. Presumably it responded to vibrations transmitted through the bones of the skull, as may be the case with other microsaurs. The initial lack of an otic notch, and the apparent method of sound transmission, remain valid criteria for differentiating the otic region of microsaurs from that of reptiles, but the structure of the stapes itself appears, from the condition in *Pantylus,* to have originated from the same basic pattern in both groups.

13. A double occipital condyle and the atlas correspondingly modified. On the basis of the gymnarthrids, Gregory (1965) described the occipital condyle of microsaurs as being double and the atlas as articulating with it in much the same way as in urodeles. Simply referring to the condyle as double, however, is not sufficient to define it, since the condyle in mammals is also termed "double" but is entirely different from that of microsaurs. The occipital condyle in the gymnarthrids and *Pantylus* (M.C.Z. No. 3302; fig. 14) is a broad, concave, strap-shaped structure made up of both the exoccipitals and the basioccipital. The most important feature of the configuration of the occipital condyle in microsaurs, in contrast to that of reptiles, birds, mammals, and labyrinthodont amphibians, is that it is *concave,* rather than convex, and receives the articulating surface of the anterior cervical as the socket of a ball-and-socket joint, rather than acting as the ball. An occipital condyle of this type is also known in *Asaphestera, Microbrachis,* and *Cardiocephalus* (fig. 15), as well as in *"Ostodolepis," "Hylonomus" geinitzi, Lysorophus,* and *Cocytinus.*

The distinctive relationship of the occipital condyle to the cervical vertebra in microsaurs (and other lepospondyls), as compared with that in reptiles and other Paleozoic tetrapods, indicates separate development from the primitive level of organization represented by the ichthyostegids, in which no specialized articulating surface had developed between the skull and the anterior vertebrae. The development of a ball-and-socket joint could occur either by giving the function of the ball to the occipital condyle, as in reptiles, or to the first cervical vertebra, as in microsaurs. Functionally there is little difference, and there would be no advantage in the evolution of either pattern into the other. This feature is, therefore, an excellent one for differentiating microsaurs from reptiles.

The atlas-axis complex is best known in the genus *Pantylus.* It is most clearly shown in M.C.Z. No. 3302 (figs. 16, 17) but can also be seen in U.T. No. 40001–1. Directly articulating with the skull is a large element

which is comparable to the vertebra termed "atlas" in the gymnar-
thrids by Gregory, Peabody, and Price (1956). The centrum has a con-
vex anterior surface which fits into the occipital condyle. The neural
arch is large, comparable to that of the axis in reptiles and mammals.
Anterior to the neural arch is a separate unpaired element which wraps
around the anterior face of the neural arch but has no surface for articu-
lation with the back of the skull. It is essentially an accessory to the
first vertebra. In the Museum of Comparative Zoology specimen, in
which the ribs are in place, the tuberculum of the first rib articulates
with a facet formed jointly by the first vertebra and its accessory. The
capitulum articulates with the centrum of the first vertebra. A second rib
articulates with the transverse process and the posterior margin of the
centrum of this same vertebra.

The configuration of the cervical vertebrae in *Microbrachis* (fig. 19)
agrees with that of *Pantylus*. Although poorly preserved, the first ver-
tebra of *Tuditanus* shows the same pattern, except for the absence of the
accessory. The atlas-axis complex is also known in the lysorophids
Cocytinus and *Lysorophus*. In *Lysorophus*, as was noted by Sollas (1920),
the ball-and-socket relationship of the first cervical and the occipital
condyle is the reverse of that evident in reptiles. The accessory unit,
termed "proatlas" by Sollas, appears to articulate with the back of the
skull.

A very similar configuration of the occipital region is evident in the
Lower Mississippian genus *Palaeomolgophis*, recently described by Brough
and Brough (1967a). Although they ally this genus with *Molgophis* and
other lysorophids on the basis of the vertebral structure, the configura-
tions of the dermal skull roof and dentition follow the pattern of the
adelogyrinids and show no important similarities to *Lysorophus*. If *Pal-
aeomolgophis* can be placed in the Adelogyrinidae, the distinctive pattern
of the occipital condyle-atlas-axis complex found in the central micro-
saur stock is shared by all the groups included within the Microsauria.
More important, and regardless of the specific affinities of this genus,
it demonstrates that this type of occipital condyle-atlas-axis relationship
was already fully developed far down in the Mississippian.

In primitive reptiles, such as the captorhinomorphs and synapsids
(i.e., *Ophiacodon;* fig. 18B), the atlas is composed of a paired neural arch
which bears the tuberculum of the first rib, an intercentrum which bears
the capitulum, and a pleurocentrum. The axis consists of a small inter-
centrum and a large pleurocentrum, fused to a high neural arch. The
capitulum of the second rib is supported by the axis intercentrum; the
tuberculum, by the transverse process of this vertebra.

In microsaurs it is evident from the configuration of the first vertebra and its accessory, as well as the position of the anterior ribs, that the first cervical is roughly homologous to both the atlas and axis of reptiles, mammals, and labyrinthodonts. Apparently, in *Pantylus* and other microsaurs, the central elements of the original atlas and axis have be-
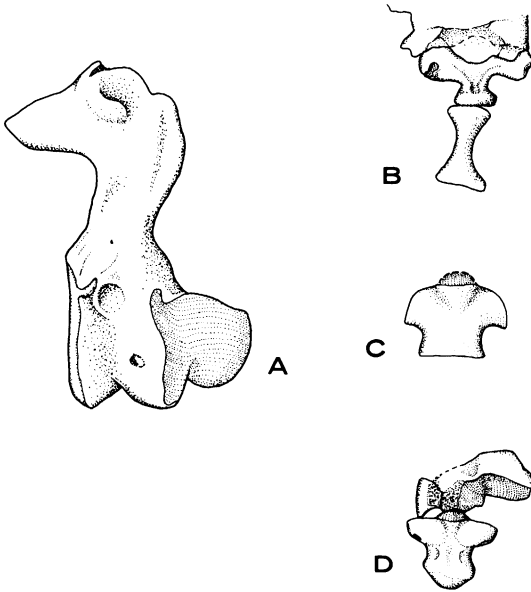

Fig. 19. Atlas vertebrae. A. *Euryodus* in lateral view (from Gregory, Peabody, and Price, 1956, fig. 16a). ×5. B. *Hyloplesion* in ventral view, R.S.M. No. 1899.32.3. ×6. C. *Microbrachis* in ventral view, C.G.H. No. 727. ×6. D. *"Hylonomus" geinitzi* in ventral view, D.M.S.W. No. B.93. ×6.

come fused without a trace of suture. The original atlas arch remains as an accessory element in *Pantylus, Microbrachis,* and *Lysorophus,* but is apparently lost in the genera *Cardiocephalus* and *Tuditanus.*

The configuration and probable origin of the cervical vertebrae in the microsaurs pose a problem in terminology. If the units are to be named according to their homologues in other tetrapods, the neural arch of the vertebra which articulates with the skull could be considered part of the axis, rather than the atlas, whereas the accessory unit found in *Pantylus, Microbrachis,* and *Lysorophus* is the remnant of the atlas, rather than a proatlas. Whatever the origin of the Lissamphibia,

the structure and relationship of the condyle and cervicals are the same in this group as in the microsaurs. Because the first cervical of the Lissamphibia has always been termed the "atlas," it is probably well to retain that terminology for the compound element in microsaurs.

Although the microsaurian cervical structure might conceivably have evolved from a configuration similar to that of early reptiles, the reptilian condition could not have been derived from that of microsaurs.
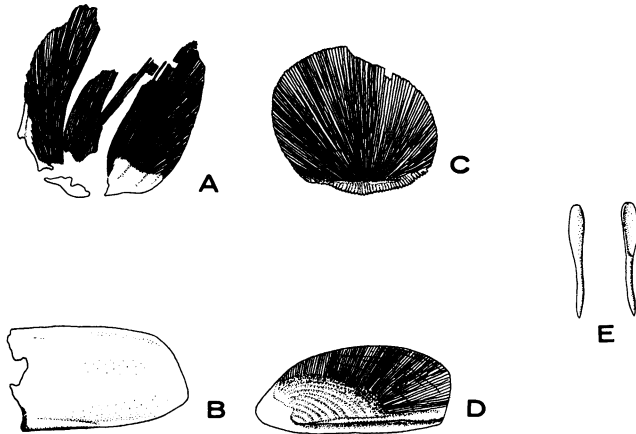

FIG. 20. A, B. Dorsal and ventral scales of *Asaphestera* in external view, R.M. No. 2.1131. ×5. C, D. Dorsal and ventral scales of *"Ricnodon" limnophyes* in medial view, B.M.(N.H.) No. R.2818. ×5. E. Ventral scales of the reptile *Hylonomus lyelli* in external and medial views, R.M. No. 2.1126. ×4.

There are hence two major differences between microsaurs and reptiles in the structure of the occipital condyle-atlas-axis complex. One is the nature of the articulating surface between the skull and the first cervical, and the second is the modification, primarily by fusion, of the atlas-axis complex in microsaurs. No microsaur with a different pattern of articulation from that described here is known.

CONCLUSIONS

Although several of the characters that have been used to distinguish microsaurs are not consistent throughout the group, at least five are: (1) the presence of a single large bone in the temporal series (number 9 in the above discussion); (2) the absence of a transverse flange from the pterygoid (number 11); (3) the structure and relationship of the occipital condyle and the atlas-axis complex (number 13); (4) the ab-

sence of trunk intercentra (number 3); and (5) the structure of the
scales (number 7).

Not only do these features characterize all members of the central
microsaur stock (see table 1) but they indicate that the microsaurs, as
so characterized, cannot be considered ancestral to reptiles. Although
some of their characteristics could have resulted from modification of a
reptile-like pattern, there is no evidence that microsaurs have evolved
from any reptilian stock. The pattern of the occipital condyle-atlas-
axis complex and the structure of the scales and temporal region sug-
gest that the two groups have had a long period of independent evo-
lution.

The known members of the central microsaur stock are, of course,
simply too late in time to be ancestral to captorhinomorphs or pelyco-
saurs. This circumstance has led to the suggestion that, whereas these
particular genera are not reptilian ancestors, the two groups may have
evolved from a common ancestor. The diversity of microsaurs in the
Early Pennsylvanian (considerably greater than that of contemporary
reptiles) suggests a long period of prior evolution. All members of this
central microsaur stock exhibit the same non-reptilian features in the
palate, skull roof, occipital condyle, and vertebrae. Although these
features may have developed separately in each of the half dozen
families, it seems more logical to assume that they were inherited from
a common ancestor that was already microsaurian in these features.
Such an ancestral stock was apparently present at the beginning of the
Carboniferous, because the other lepospondyl groups with which typical
microsaurs share their definitive vertebral characteristics (lysorophids,
adelogyrinids, aïstopods, and nectrideans) were all distinct at a very
early date (Baird, 1965). Presumably microsaurs (and other lepospon-
dyls) share a common ancestry with the labyrinthodont ancestors of
reptiles, but only in pre-Carboniferous time and only at (or close to)
the level of the rhipidistian fish.

Because we have no fossil record of the central stock of microsaurs
prior to the Westphalian B, we cannot say for certain which of the
similarities observed between certain microsaurs and reptiles result from
the retention of primitive features and which are a result of convergence.

The generally reptilian appearance of the microsaur vertebra is ap-
parently a result of the retention of the primitively holospondylous
pattern observed in all lepospondyls. Reptiles have approached this
condition by the gradual reduction of the intercentra from an originally
proto-rhachitomous pattern (Romer, 1964).

The lack of palatine teeth and of labyrinthodont infolding of the en-

amel in microsaurs is also a primitive lepospondyl trait, as is, apparently, the absence of an otic notch. Early reptiles, on the other hand, although they have reduced the conspicuous notch of the anthracosaurs, have retained a vestigial notch which is evident in *Limnoscelis* and certain pelycosaurs (Langston, 1965; Fox and Bowman, 1966). *Limnoscelis* has also retained the labyrinthine infolding but has lost the palatine fangs.

Because the ichthyostegids possess a long-stemmed interclavicle, this feature, shared by anthracosaurs, reptiles, and certain microsaurs, may be a primitive tetrapod character. The well-developed limbs and girdles of *Tuditanus* and other terrestrial microsaurs may have evolved parallel with those of reptiles, but it is more probable that sturdy limbs were characteristic of primitive tetrapods in general and that the feeble limbs of the so-called "typical" aquatic microsaurs represent a secondary adaptation. The development of an astragalus and a calcaneum certainly occurred independently in the two groups, as *Limnoscelis* among the reptiles and *Hyloplesion* among the microsaurs primitively retain four proximal tarsals.

From our knowledge of the reptilian-mammalian transition, it would not be surprising to learn of equally extensive parallelism and convergence in the amphibian-reptilian transition. Even among the rhachitomous amphibians, forms such as *Parioxys* show terrestrial adaptations in the limbs and girdles, multiple sacral ribs, and holospondylous centra (Carroll, 1964a). The reptilian features of *Seymouria* (White, 1939), which, although an anthracosaur, is not close to the ancestry of captorhinomorph reptiles (Olson, 1965), are too well known to need repeating. The microsaurs, with their holospondylous centra and non-labyrinthine teeth, have paralleled the reptiles much more closely. The structure of the temporal region, the pterygoid, and the occipital condyle-atlas-axis complex nevertheless enables us to differentiate microsaurs from reptiles and assert their separate origin.

SUMMARY

The genus *Tuditanus* [*Eosauravus*] from the Middle Pennsylvanian of Linton, Ohio, is redescribed on the basis of the two type specimens, neither of which had previously been prepared. This animal, which has been considered alternatively a microsaurian amphibian and a primitive reptile, proves to be a microsaur having these characteristics: sculptured skull roof with orbits lying at mid-length and palpebral cups; about 25 isodont marginal teeth; postparietals occipital in position; 29 pre-

sacral vertebrae; ilium with dorsal and posterior processes; stout limbs with entepicondylar foramen in humerus; tetradactyl manus with phalangeal count of 2, 3, 4, 3; pentadactyl pes with astragalus and calcaneum and a phalangeal count of 2, 3, 4, 5, 4; and hoe-shaped ungual phalanges. *Tuditanus* is clearly a member of the central group of microsaurs, although it shows a number of terrestrial adaptations similar to those observed in captorhinomorph reptiles.

The anatomy of all microsaur genera is reviewed in order to determine whether any members of this group might be related to the ancestry of reptiles. The following features are found to be characteristic of all microsaurs, and to distinguish them from reptiles: (1) the presence of no more than a single bone in the temporal series; (2) the absence of a transverse flange from the pterygoid; (3) the concave occipital condyle articulating with a single specialized cervical vertebra; (4) the absence of trunk intercentra; and (5) the oval dorsal scales with radial striations superimposed on a concentric growth pattern.

These features indicate that microsaurs could share a common ancestry with reptiles only at, or near, the level of the rhipidistian fish and only in pre-Carboniferous time.

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