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A cochleosaurid temnospondyl amphibian from the Middle Pennsylvanian of Linton, Ohio, U.S.A.

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Two temnospondyl amphibian specimens from the Middle Pennsylvanian locality of Linton, Ohio, USA are described as *Adamanterpeton ohioensis* gen. et sp. nov., a member of the family Cochleosauridae and sister-taxon to the clade comprising the genera *Cochleosaurus* + *Chenoprosopus*. *A. ohioensis* is a very rare component in the large Linton vertebrate assemblage and may have been a relatively terrestrial form, perhaps similar to *Cochleosaurus florensis* from the contemporaneous lycopsid-trunk locality at Florence, Nova Scotia. An overview of the edopoid and eryopoid adaptive radiations is presented and it is argued that they were sequential radiations, each of monophyletic origin filling the same range of niches.

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ADDITIONAL KEY WORDS:—Carboniferous – Amphibia – anatomy – phylogeny.

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INTRODUCTION

The temnospondyl amphibians are among the major elements of the Upper Carboniferous and Pennsylvanian lowland coal-swamp vertebrate assemblages. One of the characteristic families in these assemblages is the Cochleosauridae, made up of small superficially alligator-like forms probably growing to about a metre and a half in length. The best known taxon is *Cochleosaurus bohemicus* (Fritsch) from the Westphalian D of Nýřany and Třemošná, in the Czech Republic. This species is currently being restudied by the junior author. Other cochleosaurids include *Cochleosaurus florensis* Rieppel, 1980 (recently redescribed by Godfrey & Holmes, 1995) from the Westphalian D of Nova Scotia, *Procochleosaurus jarrowensis* Sequeira, 1996, from the Langsettian (= Westphalian A) of Ireland, *Chenoprosopus milleri* Mehl, 1913 from the Permo-Carboniferous boundary of New Mexico, *Chenoprosopus lewisi* Hook, 1993, from the Permo-Carboniferous of Texas, and some palatal material, indeterminate within the family, from the Langsettian (= Westphalian A) of Joggins, Nova Scotia (Milner, 1996). Most of this material has been described or reassessed in recent years, and the Cochleosauridae can now be characterized as a clearly definable family of amphibious carnivores extending from at least the Langsettian to the base of the Permian in Euramerica (Sequeira, 1996).

One rich coal-swamp assemblage from which cochleosaurids have not been formally described is that from the shale below the Upper Freeport Coal at the Diamond Mine at Linton, Ohio. The two cochleosaurid specimens which form the basis of the following account have been described briefly and discussed in the literature on several occasions. They have always been associated together and have a common systematic history. They were first reported, though not figured or described, by Moodie (1916: 184) and were referred by him to *Macrerpeton huxleyi* (Cope, 1874), the holotype of which also came from Linton, Ohio. However, the holotype of *M. huxleyi* (AMNH 6834) is a distinct form, characterized by very fine evenly pitted dermal ornament, small widely set orbits, no intertemporal bones, a stout cultriform process and pronounced peaking of the anterior maxillary dentition, all of which distinguish it from the two specimens described here. Consequently, no later author accepted this attribution. The two specimens were then described briefly and figured by Romer (1930: 126–131). Romer interpreted them as anthracosaurs of the family Cricotidae, misassociating them with the name-bearing specimens of ‘*Rhizodus*’ *lancifer* (Newberry) which were isolated labyrinthodont teeth, and *Leptophractus obsoletus* Cope, 1873 based on some anthracosaur jaw fragments, also from Linton. The resulting description and reconstruction (Romer 1930: fig.24) of the ‘cricotid anthracosaur’ *Leptophractus lancifer* was largely based on these two cochleosaurid specimens, however. In 1947, Romer reviewed the material again, this time as a temnospondyl, providing a broadly similar description, but excluded the ‘*L. lancifer*’ teeth, and combined the rest as *Leptophractus obsoletus* Cope. In that paper, he described the material as an essentially orthodox small temnospondyl of the family Edopsidae, using the two cochleosaurid specimens rather than the name-bearing types of *L. obsoletus*. Langston (1953) followed this interpretation of the systematic position of this material. In 1963, Romer reviewed the anthracosaurs

from the Carboniferous of North America and concluded that the Linton anthracosaur material comprised an anthracosaurid, *Anthracosaurus lancifer* (Newberry) and an eogyrinid, *Leptophractus obsoletus* Cope. This left the two cochleosaurid specimens without any valid name, systematic status or coherent description, and they have subsequently remained in this unsatisfactory state. Hook & Baird (1986) suggested that they be referred to the Nýřany taxon *Gaudrya latistoma* Fritsch, and identified them as *Gaudrya* cf. *latistoma*. Milner (1987) followed Hook and Baird in referring the specimens to *Gaudrya*, but Sequeira & Milner (1993) have demonstrated that the type of *Gaudrya latistoma* from Nýřany is merely a large snout of *Cochleosaurus bohemicus*, while other specimens referred to *Gaudrya* were attributable to *Capetus palustris*, a primitive temnospondyl which is not an edopoid and hence not a cochleosaurid. The Linton cochleosaurids are clearly not *Capetus*, nor are they identical to *Cochleosaurus bohemicus*, and Milner & Sequeira (1994b) have referred to the material as the 'Linton cochleosaur'. Most recently, Godfrey & Holmes (1995: 19) have cited a suggestion from Dr D. Baird that the two specimens be reassigned to the genus *Cochleosaurus*. The purpose of this work is to describe these two specimens and determine their relationship to other cochleosaurids. The specimens were studied from silicone-rubber casts.

Institutional abbreviations

AMNH: American Museum of Natural History, New York, USA.

MB: Museum für Naturkunde, Humboldt Universität, Berlin, Germany.

ABBREVIATIONS

a	angular	pmx	premaxilla
ch	choana	po	postorbital
cor	coronoid	pp	postparietal
d	dentary	pra	prearticular
ect	ectopterygoid	prf	prefrontal
eo	exoccipital	pt	pterygoid
f	frontal	q	quadrate
ins. j.	insula jugalis	qj	quadratojugal
it	intertemporal	sa	surangular
j	jugal	se	sphenethmoid
l	lacrimal	smx	septomaxilla
m	maxilla	spl	splenial
n	nasal	spp	postsplenial
p	parietal	sq	squamosal
pal	palatine	st	supratemporal
pas	parasphenoid	t	tabular
pf	postfrontal	v	vomer

SYSTEMATIC PALAEONTOLOGY

Class Amphibia Linnaeus, 1758

Temnospondyli Zittel, 1888

Superfamily Edopoidea Romer, 1945 (as Edopsoidea) emended Langston, 1953

Family Cochleosauridae Broili in Zittel, 1923

Diagnosis. Edopoid temnospondyls with the following derived character-states: depressed areas with subdued sculpture between parallel anteroposterior sculpture ridges on either side of the skull table; elongate vomers with both elongate prechoanal region, and elongate interchoanal region associated with long choanae, interpterygoid vacuities set back in posterior half of skull; choanae wider anteriorly than posteriorly; extensive contact between insula jugalis and lateral extension of pterygoid, separating the maxilla from the jugal, and the ectopterygoid from the subtemporal fossa. Retained primitive character-states include: presence of intertemporals; pterygoids extending anteriorly to meet anterior of cultriform process, thus excluding vomers from margin of interpterygoid vacuities.

***Adamanterpeton* gen. nov.**

Diagnosis. As for the type and only species.

Derivation of name. *Adamantas* (Greek)=Diamond, after the Diamond Coal Mine at Linton; *erpeton* (Greek)=a creeping animal.

Adamanterpeton ohioensis* sp. nov.Synonymy*

- 1916 *Macrerpeton huxleyi* (Cope); Moodie p.184 (*partim*), *non* Cope 1874 p. 274.
- 1930 *Leptophractus lancifer* (Newberry); Romer pp. 126–131, fig.23 (*partim*), *non* Newberry 1856 p. 99.
- 1947 *Leptophractus obsoletus* (Cope); Romer pp. 107–108, fig.20 (*partim*), *non* Cope 1873 p.341.
- 1970 'edopoid temnospondyls' Panchen p. 56.
- 1986 *Gaudrya* cf. *latistoma* Fritsch; Hook & Baird pp. 180–182, *non* Fritsch 1885.
- 1987 *Gaudrya* Fritsch; Milner p. 505, *non* Fritsch 1885.
- 1994 Linton cochleosaur; Milner & Sequeira pp. 196–198.
- 1995 *Cochleosaurus* Fritsch; Godfrey & Holmes p. 19, *non* Fritsch 1885.
- 1996 Undescribed cochleosaurid; Sequeira p. 76, table 2.

Holotype. AMNH 2933, a skull in partial counterpart on two slabs of coal. Figured by Romer (1930: fig. 23 left) at which time most of the large slab bearing the skull visible in dorsal aspect was unprepared, but the block bearing the snout-tip had been acid-etched. After further acid-etching by Dr D. Baird in the 1950s, the larger slab bears a mould of most of the palate and mandibles (Figs 1, 2), and the smaller slab bears a mould of the anterior region of the snout (Figs 3, 4).

Locality and horizon. The Ohio 'Diamond' Coal Mine, Linton, Jefferson County, Ohio, U.S.A. Canneloid shale below the Upper Freeport Coal, Allegheny Series,

Middle Pennsylvanian, equivalent to late Westphalian D of the Upper Carboniferous.

Derivation of name: *ohioensis* = from Ohio.

Diagnosis. Cochleosaurids with the above-listed family characteristics but plesiomorphic in relation to both *Cochleosaurus* and *Chenoprosopus* in the following features: snout less elongate at 120 mm skull length, particularly the premaxillae, which have a lateral length: medial suture length ratio of 1.4; pineal foramen present in skull of 120 mm length; palatine fangs massive, significantly larger than vomerine fangs or marginal teeth; mandible with space for about 45 teeth; premaxilla with space for 14 teeth.

Primitive character-state *contra Cochleosaurus* is as follows: amorphous patch of denticles on basal plate of parasphenoid.

Primitive character-states *contra C. bohemicus* skulls of similar size are as follows: postorbital with no ornament pattern on ventral surface; sculpture of dermal roof very rugose and deeply pitted with prominent ridge patterns.

Primitive character-states *contra C. florensis* skulls of similar size are as follows: anterior region of vomer flat and denticle-covered with anteromedial strut extending from site of fangs; prefang length of vomer shorter or equal to length of postfang vomer; ossified sphenethmoid broadens anteriorly.

Primitive character-states *contra Chenoprosopus* are as follows: broad lacrimal-septomaxilla contact, clearly separating the nasal from the maxillary; broadly rounded anterior snout; choana with straight anterior edge and sharply angled anteromedial corner; jugal broad anteriorly with broad suture with lacrimal; dorsal face of postorbital in large specimens not triangular but with a long finger-like process extending back between the supratemporal and squamosal; posterior region of vomer covered with small denticles, no localization to a few ridges; splenial separated from symphysial region by downgrowth of dentary.

Referred specimen. AMNH 6954, a skull in partial counterpart on two slabs of coal. This specimen appears to have been acid-etched before 1930, as Romer (1930: fig. 23 right) depicted it in this condition. The larger counterpart bears the mould of most of the skull roof (Figs 5, 6), and the smaller slab bears the mould of the anterior region of the palate and mandibles (Figs 7, 8). These counterparts were referred to by Moodie (1916) by their Newberry collection numbers 8532G and 8572G, and by Romer (1930) by the completely erroneous numbers AMNH 6939 and AMNH 6951.

DESCRIPTION

General features

Both AMNH 2933 and AMNH 6954 are represented entirely by skulls of similar size with no associated postcranial material. The two specimens represent the typical primitive temnospondyl condition in most of their cranial features. The full complement of cranial bones is present including the intertemporals. Neither skull is so completely preserved that the length can be measured exactly but AMNH 2933 has a midline length of about 130 mm whereas AMNH 6954 is about 120 mm long. Many of the sutures are only slightly undulating and bones have slipped

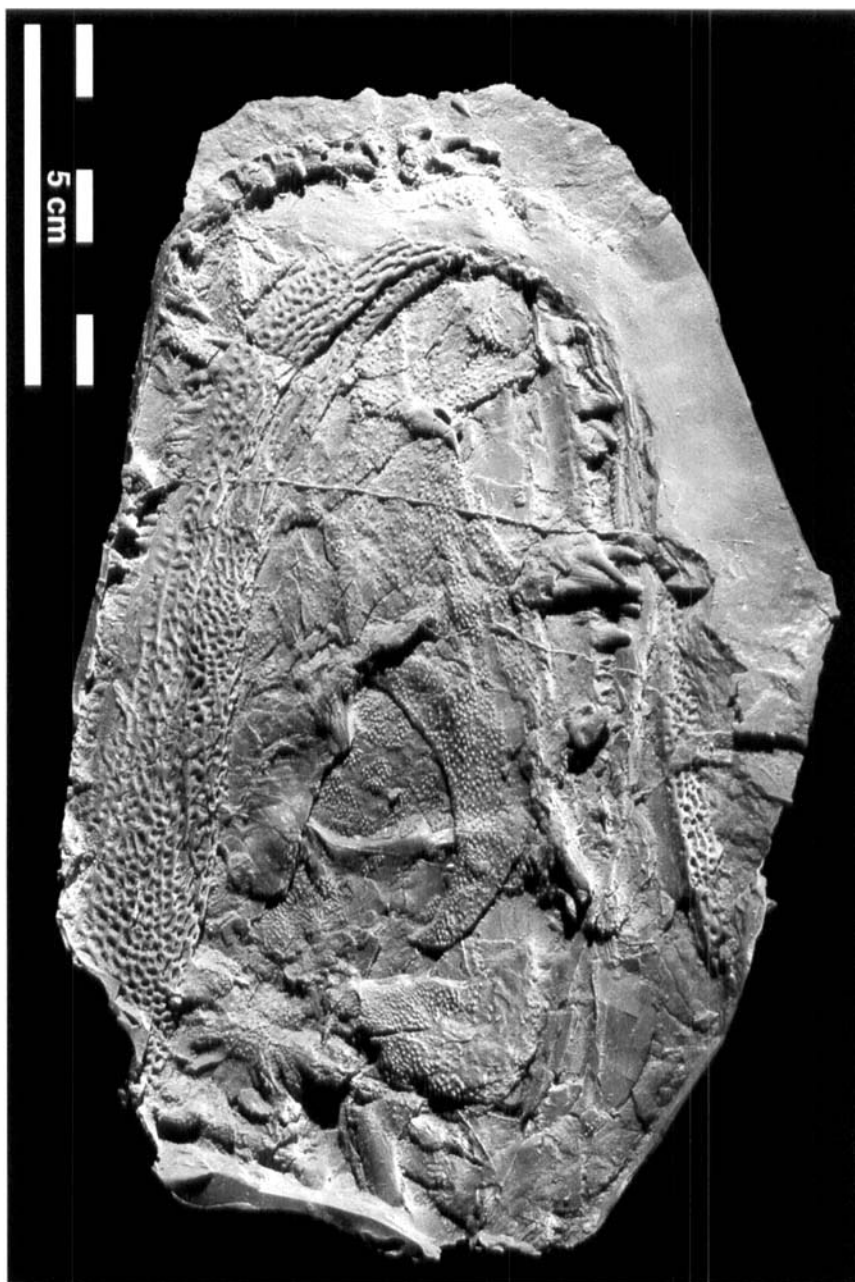


Figure 1. *Adamanterpeton ohioensis* gen. et sp. nov., Middle Pennsylvanian; Linton, Ohio. Silastomer cast of holotype AMNH 2933. Palate.

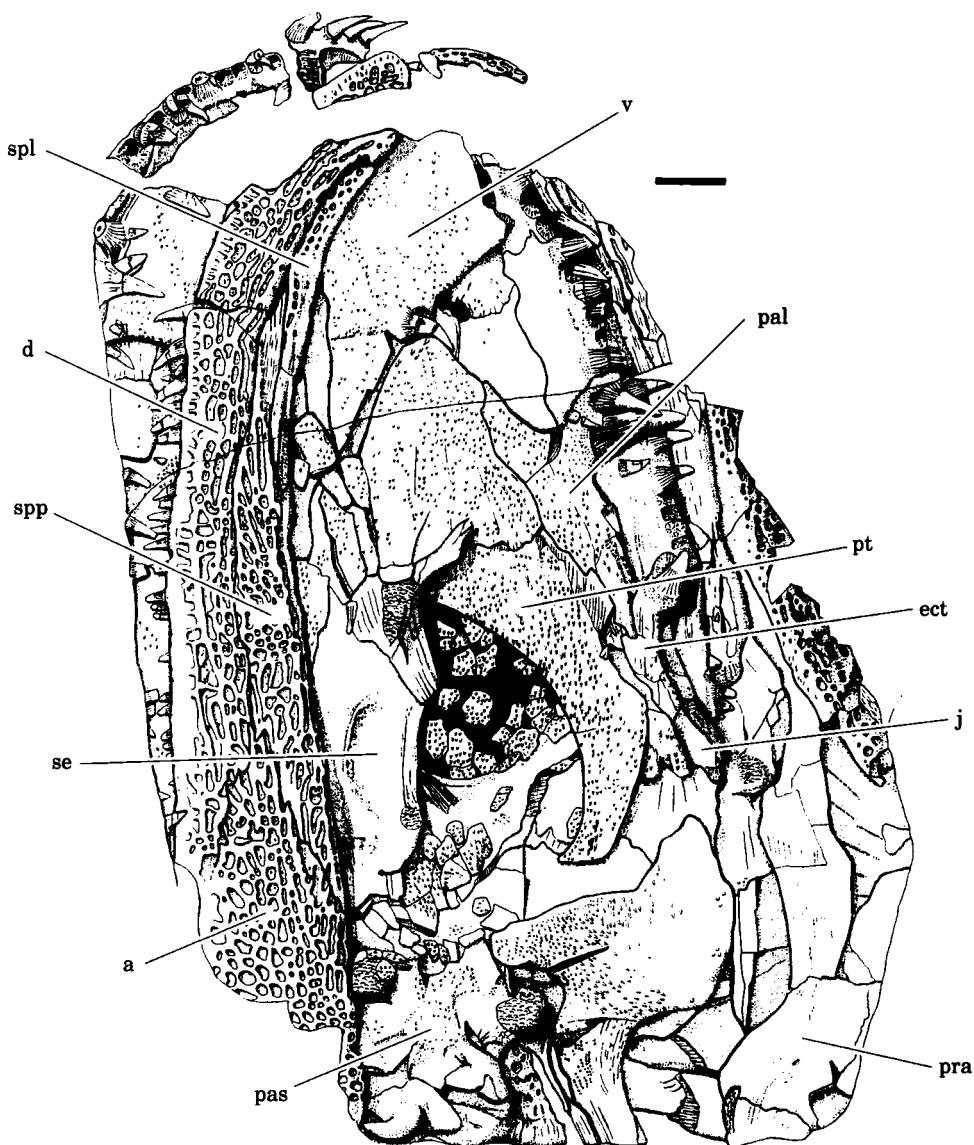


Figure 2. *Adamanterpeton ohioensis* gen. et sp. nov., Middle Pennsylvanian; Linton, Ohio. Holotype AMNH 2933. Palate. For list of abbreviations, see page 263.

relative to each other in both specimens, suggesting that the specimens were not necessarily adults and that *A. ohioensis* may have grown to a significantly larger size.

Dermal ornament

Much of the skull roof is covered by a variant of the typical temnospondyl pit-and-ridge system, in which almost all the pits are deep and discrete, and separated by narrow ridges of bone. Only occasionally are pits combined to give more complex

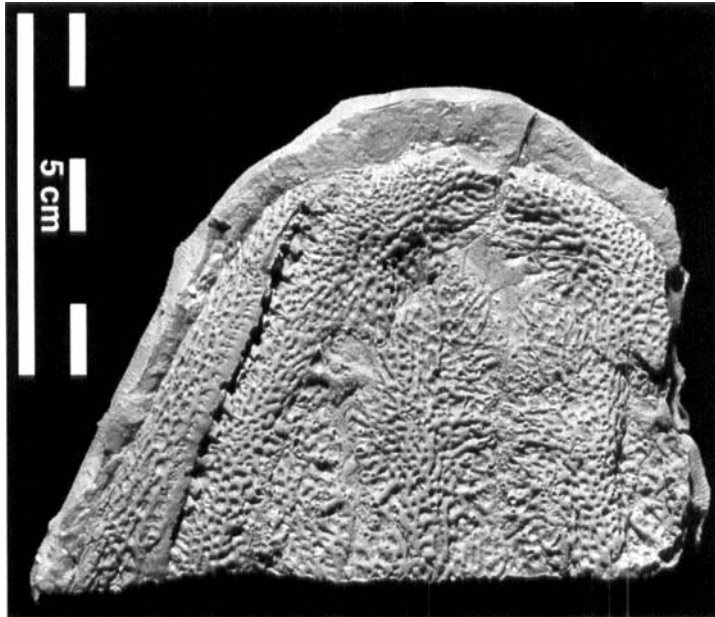


Figure 3. *Adamanterpeton ohioensis* gen. et sp. nov., Middle Pennsylvanian; Linton, Ohio. Silastomer cast of holotype AMNH 2933. Snout tip.

structures, and there are no recognizable lateral-line sulci on either specimen. Where preservation is good, small foramina are present in the bases of the pits on the skull roof surface as described by Bystrow (1935) in *Benthosuchus*. Similar foramina are more frequent on the mandibles, particularly the anterior region of the dentaries (Fig. 2).

Like other cochleosaurids, *A. ohioensis* shows a characteristic pattern of heavily ossified and deeply sculptured struts on either side of the lightly sculptured midline. Each anteroposterior strut extends back from the midline of the premaxilla, where it emerges from the centre of ossification, through the midline of each nasal, then incorporated in the lateral edge of each frontal together with the pre- and postfrontal, and finally running along the lateral edge of each parietal. Similar struts occur in both of species of *Cochleosaurus* in which they extend back through the postparietal lappets as well. A further strut extends anterolaterally from the posterior end of the lacrimal to the jaw margin. This was noted by Godfrey and Holmes (1995) in *C. florensis* and appears to characterize most of the Cochleosauridae, although it is not visible in the large specimens of *Chenoprosopus milleri* figured by Langston (1953).

Some very local zones of elongate ornament are present on the skull roof and mandibles. As in species of *Cochleosaurus*, there is a major zone of depressed elongate ornament along the midline of the skull extending over the nasals, frontals and parietals. The lateral region of the lacrimals is covered by depressed but not elongate pits. Elongate dermal pitting occurs on the splenials.

Skull roof
(Figs 3–6, 9)

All elements of a typical primitive temnospondyl skull roof were either present or can reasonably be presumed to have been so in *A. ohioensis* although the postparietals

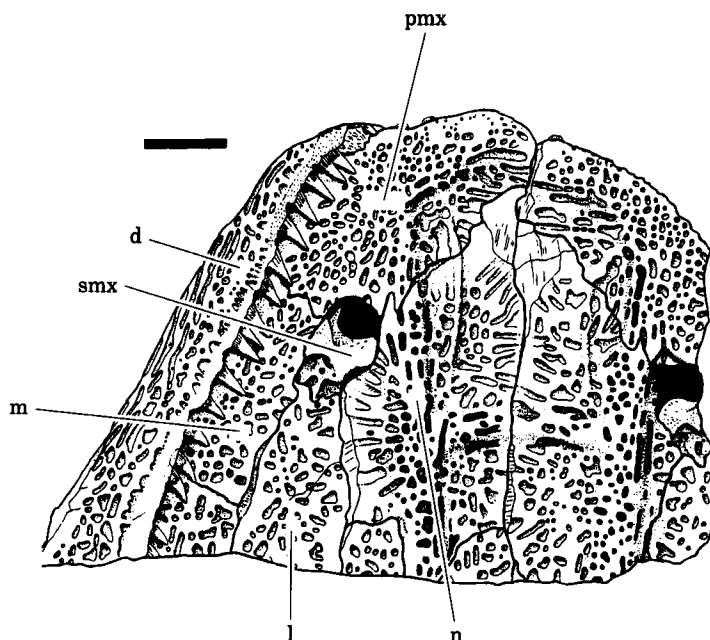


Figure 4. *Adamanterpeton ohioensis* gen. et sp. nov., Middle Pennsylvanian; Linton, Ohio. Holotype AMNH 2933. Snout tip.

and the posterior regions of the squamosal and quadratojugal are missing in the two specimens and cannot be described.

The premaxillae (Figs 3–6) are relatively massive elements. They have a long common suture, and they suture posteriorly with the nasals medial to the nares, and with the maxillae lateral to the nares. The suture between premaxilla and nasal is stepped with the lateral step level with the premaxilla–maxilla suture, and the medial step situated several millimetres anteriorly. The stepping results in a right-angled flange next to the external naris but there is no distinct pars dorsalis or alary process to the premaxilla. The stepping is less pronounced than in other cochleosaurids. The lateral premaxilla length: medial suture ratio is 1.4:1 whereas in other cochleosaurids it is 1.5–2.5:1. In *Edops*, the ratio is 1.3:1.

The maxillae are not well preserved in this material, the inner face of the left maxilla being visible in AMNH 2933 (Fig. 2) and part of the outer face of the right maxilla in AMNH 6954 (Fig. 6). The maxilla sutures broadly with the premaxilla at the level of the external naris. Medially, the pars dorsalis sutures with the septomaxilla, the lacrimal and the jugal, and the pars palatina sutures with the palatine and ectopterygoid. The maxilla is not a deep bone and narrows substantially posteriorly at the level of the anterior orbit margin. It appears to terminate posteriorly at the level of the posterior orbit margin (Figs 5, 6) and to be excluded from contact with the quadratojugal by the insula jugalis, a ventromedial process from the jugal which contacts the pterygoid, thus separating the maxilla from the quadratojugal.

Septomaxillae are well preserved in both specimens. In the smaller AMNH 6954

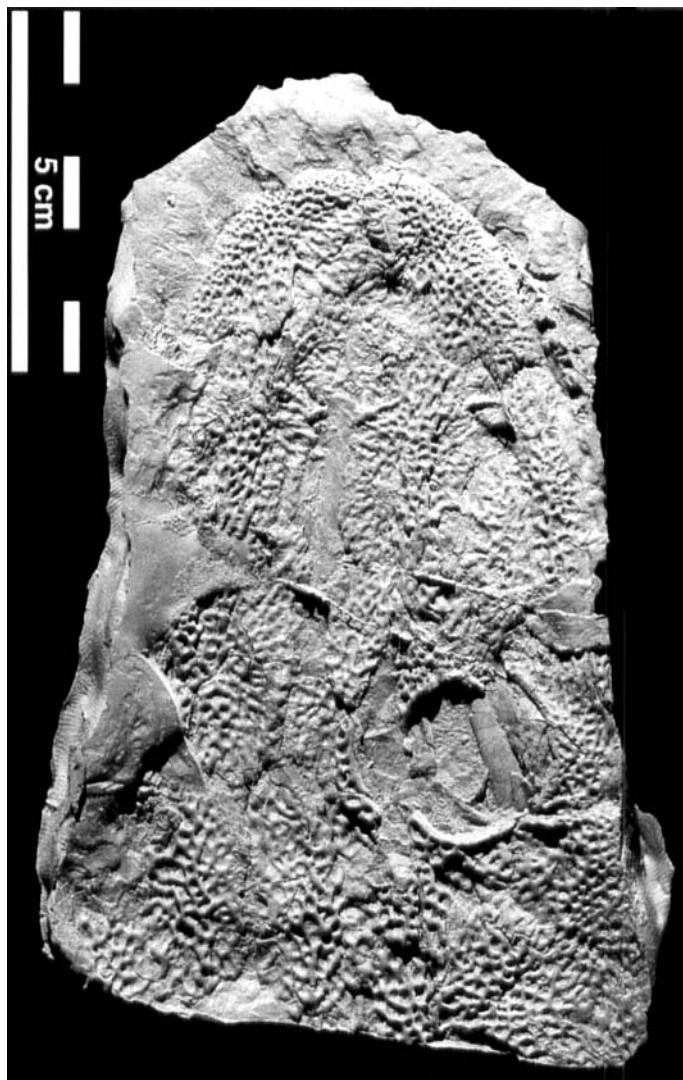


Figure 5. *Adamanterpeton ohioensis* gen. et sp. nov., Middle Pennsylvanian; Linton, Ohio. Silastomer cast of AMNH 6954. Skull roof.

(Fig. 6), the right septomaxilla is visible as a small triangular bone with a concave anterior edge bordering the external naris, a straight anteroposteriorly orientated lateral edge suturing with the maxilla, and a slightly convex medioposterior edge suturing with the nasal and lacrimal. The septomaxilla is less anteroposteriorly elongate than in other cochleosaurids. The dorsal surface of the septomaxilla of AMNH 6954 is covered in fine pitting much smaller than dermal ornament pits. In the left septomaxilla of the slightly larger AMNH 2933 (Figs 3, 4), the dorsal exposure is greater and more square in shape, and the posterior dorsal surface bears a few more typical large dermal ornament pits. Temnospondyl-type dermal ornament appears to occur where the bone is closely appressed to overlying skin and the

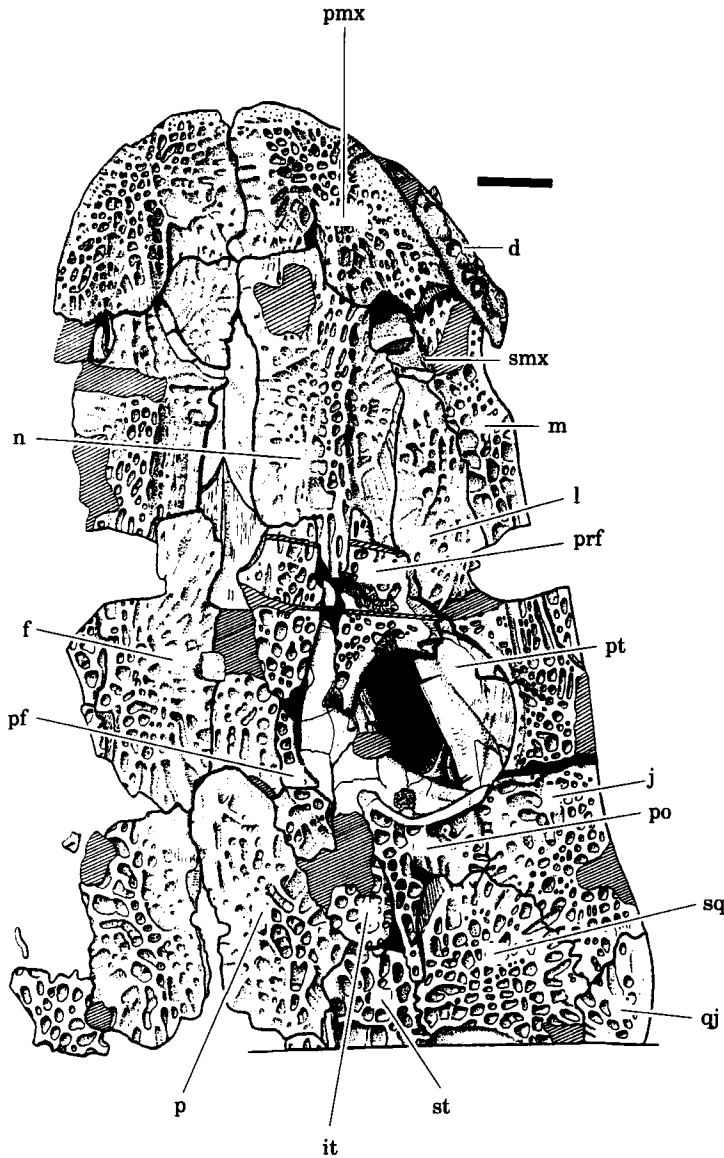


Figure 6. *Adamanterpeton ohioensis* gen. et sp. nov., Middle Pennsylvanian; Linton, Ohio. AMNH 6954 skull roof. Scale bar = 5 cm.

variation in the type of pitting over the posterior surface of the septomaxilla may reflect some variation in the relationship of this element to the skin around it.

The lacrimals are elongate rhomboidal elements. Each lacrimal sutures anteriorly to the septomaxilla, laterally to the maxilla, medially to the nasal and posteriorly to the jugal and prefrontal. The lacrimal is excluded from the dorsal edge of the naris margin by the septomaxilla, which it contacts broadly, and from the orbit margin by a prefrontal-jugal suture.

The nasals are large elongate rectangular bones forming the major area of the

preorbital snout. They suture anteriorly with the premaxillae, laterally with the septomaxillae and lacrimals, posteriorly with the prefrontals and frontals, and medially with each other. There is no sutural contact with the maxillae as in *Chenoprosopus* because of the lacrimal-septomaxilla contact. The length:width ratio of each nasal is about 2:1. The medial suture is straight and the medial regions of the nasals are apparently composed of very thin bone. The anterior edge of each nasal is stepped in correspondence to the posterior edge of the bordering premaxilla.

The frontals are a pair of narrow rectangular bones, about the same length as the nasals but with a length:width ratio of 2.6:1 (in AMNH 6954). They suture with the nasals, prefrontals, postfrontals, parietals and each other, and like the nasals, they have a straight common suture. They show some asymmetry both anteriorly and posteriorly with one frontal being more extensive than the other. Each frontal is excluded from the orbit margin by a narrow prefrontal-postfrontal sutural contact.

The circumorbital series comprises the prefrontals, postfrontals, postorbitals and jugals. The prefrontals, postorbitals and jugals all bear a characteristic thick smooth rim where they border the orbit margin. This is less pronounced on the postfrontals. The prefrontals are slightly elongate triangular elements, terminating in a point anteriorly at about the level of the anterior edge of the frontals. They are not greatly expanded anteriorly as are those of the large skull of *Edops*. The prefrontal makes narrow sutural contacts with the jugal and the postfrontal. The postfrontals are not well preserved in these specimens. They are the smallest elements of the circumorbital series and each appears to comprise a narrow anterior region bordering the orbit and a rectangular expanded posterior region suturing with the postorbital, intertemporal and parietal. The postorbital is a roughly triangular bone, similar in size to the prefrontal. The anterior edge is concave where it borders the orbit margin and the main body of the bone is a wide rectangle behind this. From the posteromedial corner of this rectangle, a narrow finger-like process extends posteriorly between the intertemporal and squamosal, separating them entirely, interdigitating between the supratemporal and squamosal very slightly (Fig. 6). About half of the anteroposterior length of the entire postorbital is composed of this process. The entire length of the postorbital represents about two-thirds of the distance from the orbit margin to the squamosal embayment. This is a characteristic primitive temnospondyl postorbital, in many more derived groups the postorbital is an anteroposteriorly narrow element. The ventral surface of the postorbital is visible in AMNH 2933 (Fig. 2) and can be seen to be smooth, unlike that in *Cochleosaurus bohemicus* which bears sculpture resembling dorsal dermal ornament despite its ventral position. The jugal forms the anterior cheek and the region lateral to the orbit. It is a large elongate bone, forming the lateral third of the orbit margin. Its dermal face sutures with the maxilla laterally, the lacrimal and prefrontal anteriorly and the squamosal and quadratojugal posteriorly. The anterior end is damaged in AMNH 6954 (Fig. 6) but can be seen to extend to meet the lacrimal broadly ahead of the level of the anterior orbit margin. The posterolateral edge is not preserved in AMNH 6954 but, in AMNH 2933, it appears to extend medially between the maxilla and quadratojugal to produce a flange, the insula jugalis which is situated between the ectopterygoid and the subtemporal fossa and may suture with the pterygoid (Fig. 2).

The skull table is composed of paired intertemporals, supratemporals, parietals, postparietals and tabulars. The intertemporals and supratemporals are known only from the right elements in AMNH 6954 (Fig. 6). The intertemporal is a small rectangular bone, similar in size to the postfrontal and smaller than the supratemporal.

The supratemporal is a roughly square element which can just be seen to contribute to the border of the squamosal embayment. In AMNH 2933, the underside of the left supratemporal is visible where it borders the embayment margin and it can be seen to bear dermal ornament wrapped around the embayment edge and extending on to the ventral surface of the bone (Fig. 2). The parietals are broadly rectangular bones, similar in length to the frontals but wider. A small pineal foramen is clearly present just posterior to the midpoint along the interparietal suture (Fig. 6). This is an unusual feature in cochleosaurids, the pineal foramen usually becoming closed in all but the smallest individuals. In *Cochleosaurus bohemicus*, the foramen is present as a prominent structure in skulls of 50–60 mm length, but is also retained in one 108 mm skull (MB Am.81) and is small and almost closed in another specimen with a 112 mm skull (MB Am.83.1). The postparietals can be inferred to be present from the fragment visible in AMNH 6954 but their configuration cannot be ascertained. The postparietal lappets present as large structures in *Cochleosaurus bohemicus* or smaller structures in *C. florensis* may or may not be present in *Adamanterpeton*. The morphological left tabular is visible in ventral aspect in AMNH 2933 (Fig. 2). It shows the present of a laterally directed posterolateral expansion as in *C. bohemicus*.

The cheek region is composed of the squamosal and quadratojugal. The anterior parts of both right elements are visible in AMNH 6954 but the suspensorial region is missing from the specimen (Fig. 6). The squamosal was a large rhomboidal bone in sutural contact with the supratemporal, postorbital, jugal and quadratojugal. It can just be seen to border a large squamosal embayment with a smoothly curved margin. The embayment was clearly laterally extensive but its full shape cannot be determined. The quadratojugal was a relatively stout bone occupying the post-eroventral corner of the cheek.

Palate and braincase
(Figs 1–2, 7–8, 10)

The palate of *A. ohioensis* is that of a primitive temnospondyl in that it possesses relatively small interpterygoid vacuities occupying only about half the palate width. There are paired vomers, palatines, ectopterygoids and pterygoids and a median parasphenoid.

The vomers are large and elongate, of a configuration characteristic of the Cochleosauridae. They suture with the premaxillae anteriorly, the palatines posterolaterally, the pterygoids posteriorly and with each other medially (Figs 2, 8). There may be some sutural connection to the anterior of the cultriform process but this is not clear. The anterior region of each vomer extends well ahead of the choana and bears a series of four thickened struts radiating out from the position of the vomerine fangs at the anteromedial margin of the choana. One strut extends anterolaterally along the leading edge of the choana, one extends slightly anterolaterally and a third extends slightly anteromedially. The fourth extends directly medially towards the opposite vomerine fangs. These struts presumably help to brace the narrow interchoanal region and its fangs against the thickened margin of the premaxillae. The anteromedial struts are seen in *Edops* and *Cochleosaurus bohemicus* but not in *Cochleosaurus florensis* or *Chenoprosopus*. The choana resembles that of *Cochleosaurus* combining the primitive edopoid features of a straight anterior edge extending anterolaterally, and a sharply rounded anteromedial corner next to the

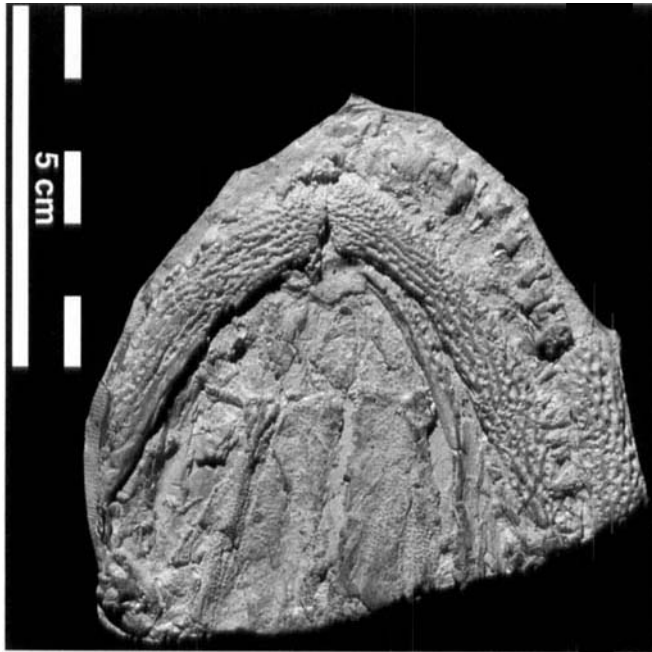


Figure 7. *Adamanterpeton ohioensis* gen. et sp. nov., Middle Pennsylvanian; Linton, Ohio. Silastomer cast of AMNH 6954. Palate.

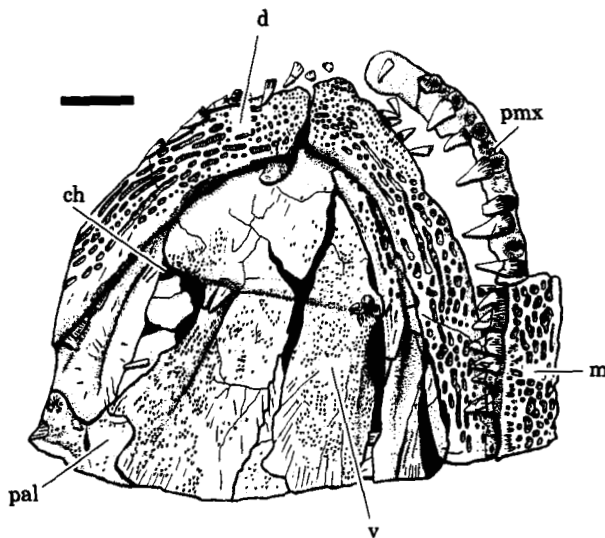


Figure 8. *Adamanterpeton ohioensis* gen. et sp. nov., Middle Pennsylvanian; Linton, Ohio. AMNH 6954 palate. Scale bar = 5 cm.

vomerine fangs, with the derived coelosaurid feature of a straight posteromedial edge formed by vomer and palatine extending back to a rounded posterior margin formed by the palatine. The posterior region of each vomer is also unusually elongate

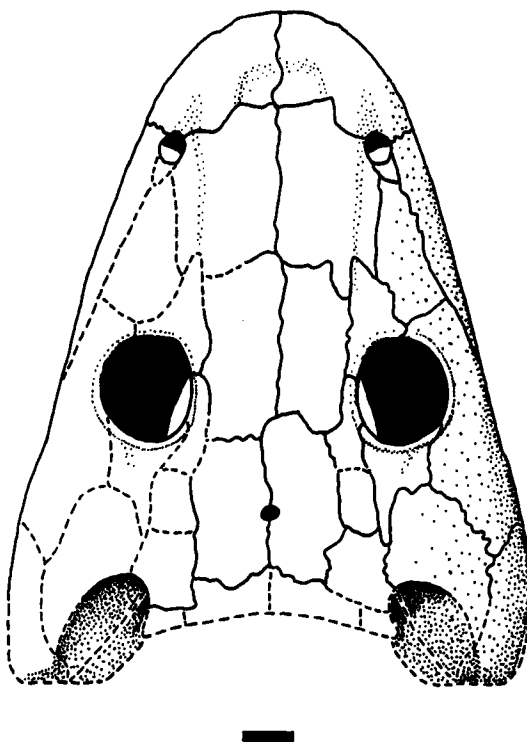


Figure 9. *Adamanterpeton ohioensis* gen. et sp. nov., Reconstruction of the skull roof, based mainly on AMNH 6954. Scale bar = 5 cm.

and forms a large rectangular extension behind the interchoanal region. The squared-off posterior end of the vomer is excluded from the margin of the interpterygoid vacuity by the palatine ramus of the pterygoid which extends behind it to contact the anterior end of the cultriform process. Although the vomers appear to be excluded from the margin of the interpterygoid vacuity, there is some suggestion that they might support the anterior end of the cultriform process by extending a short distance posteriorly along the sides of the cultriform process. This region is present but crushed in AMNH 2933, but appears to have this structure (Fig. 2). The palatine is an elongate bone, slightly broadened anteriorly with a concave anterior edge bordering the choana. The anterolateral lappet bordering the choana also bears the fangs, but does not extend far up the lateral edge of the choana. The ectopterygoid is shorter than the palatine and is a relatively small rectangular bone bearing the ectopterygoid fang and pit at its anterior end. The posterior region of the ectopterygoid and associated region of the pterygoid are both crushed but the ectopterygoid appears to be excluded from the subtemporal fossa margin by the insula jugalis, which is represented by a block of bone crushed through the posterior end of the ectopterygoid. The pterygoid is a large element showing the typical temnospondyl triradiate condition. The basisphenoid and quadrate rami are both relatively small whereas the palatine ramus is large. The palatine ramus extends broadly anteriorly to suture with the anterior cultriform process, to suture anteriorly with the full posterior edge of the vomer, and the medial edges of the palatine and ectopterygoid. It is wider than these elements throughout its length. The region of

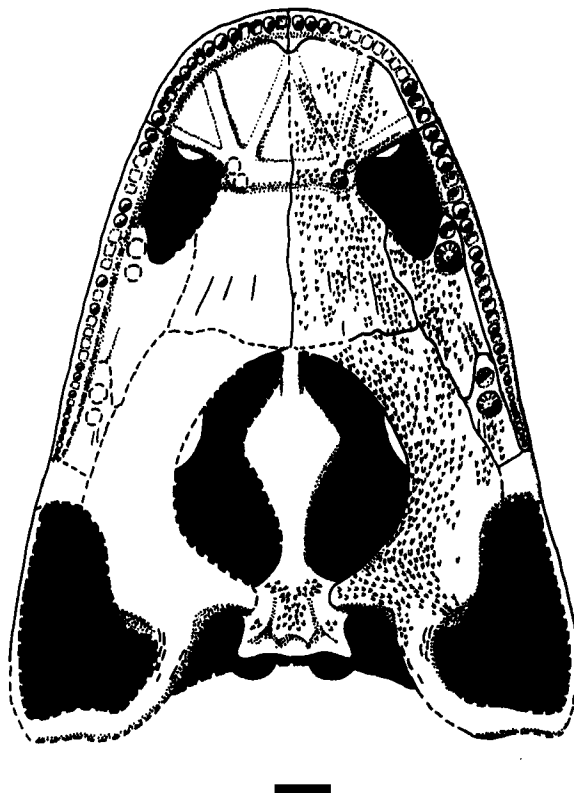


Figure 10. *Adamanterpeton ohioensis* gen. et sp. nov., Reconstruction of the palate, based mainly on AMNH 2933. Scale bar = 5 cm.

the pterygoid bordering the subtemporal fossa is not well preserved, a layer of coal having been stripped away from its surface. As a result, not only are denticles not preserved but it is unclear whether there are any sutures in this region and hence whether the ectopterygoid or the insula jugalis extend over this region as in *Cochleosaurus*. There is a small rounded flange on the posterolateral edge bordering the subtemporal fossa. The basisphenoid–basispterygoid articulation comprises two round ventrally directed robust condyles on the anterolateral corners of the parasphenoid basal plate and there were presumably corresponding dorsal condyles on the basispterygoid processes.

The parasphenoid basal plate was wider than long with a width:length ratio of 1.43, similar to that of *Cochleosaurus bohemicus*. It appears to have had a straight posterior edge with three shallow depressions across the ventral surface, and to have been 'waisted' laterally, just posterior to the condyles. There are no traces of grooves or foramina for the carotid arteries as in most temnospondyls. Much of the cultriform process is not preserved but the anterior tip is present in AMNH 2933 (Fig. 2) and appears to have been spatulate at the tip in the region just above or between the posterior end of the intervomerine suture. AMNH 2933 also bears the remnants of a large fully ossified sphenethmoid comparable to that in *Edops* in its relative size, rhomboidal shape and degree of ossification.

Little of the occiput can be seen, but one element underlying the region of the

left postparietal in AMNH 2933 may have been a left exoccipital. It comprises a diamond-shaped plate with a curved rod of bone emerging from the middle of it (Fig. 2).

Mandible
(Figs 2, 8, 11)

The mandible is best seen in the palatal aspect of AMNH 2933 (Fig. 2) but some anterior elements can also be seen on the palate fragment of AMNH 6954 (Fig. 8). The mandible appears to have been comprised of the normal complement of temnospondyl elements. It was relatively shallow, reaching its greatest depth just posterior to the orbits where it was probably equivalent in depth to the cheek. The symphyseal region was about half the maximum depth. The coronoid-surangular process was low. The posterior region is not well preserved but there appears to have been no retroarticular process. The anterior splenial (presplenial) was about two-thirds of the length of the posterior splenial (postsplenial) and was excluded from the symphyseal region by a ventral expansion of the dentary. The prearticular bore a small foramen, just anterior to the prearticular-articular suture.

Dentition

The marginal teeth and palatal fangs of *A. ohioensis* were simple sharply pointed conical teeth with smooth enamel surfaces and of oval to slightly rectangular section at the base. Broken teeth and tooth-bases show them to have been of labyrinthodont construction.

The premaxilla has space for 14 teeth (AMNH 6954) and the maxilla has space for about 30, giving a potential upper marginal dentition of about 44 teeth and spaces. There is some pseudocanine peaking around the premaxilla-maxilla suture.

Each dentary has space for about 45 teeth and there is no size discrepancy between the upper and lower marginal teeth. The symphyseal region is not visible on either specimen and the presence or absence of symphyseal fangs is unknown. The coronoids bear plates of bone covered in tiny denticles, combining to produce a denticle field over the entire coronoid region.

The major elements of the palatal dentition are three pairs of fang + pit on the major paired palatal bones. This is the typical primitive temnospondyl condition. The vomerine fangs are the smallest of the palatal fangs and are situated at the anteromedial corners of the choanae. Each is situated at the intersection of the thickened struts within each vomer. The palatine fangs are larger than other fangs or any marginal teeth, and are situated on the outer anterior lappet of the palatine immediately posterolateral to each choana. On the morphological left side of AMNH 2933, two fangs are present simultaneously instead of the usual fang + replacement pit condition, and the larger fang is 13 mm long with a 6 mm diameter base. The ectopterygoid fangs are situated at the anterior end of each ectopterygoid and are intermediate in size between the vomerine and palatine fangs.

All the paired palatal bones are covered in small denticles over their remaining palatal surface. The denticles are generally slightly curved and backwardly directed diminutive cones. On the vomers, denticles seem to be arranged in rows radiating

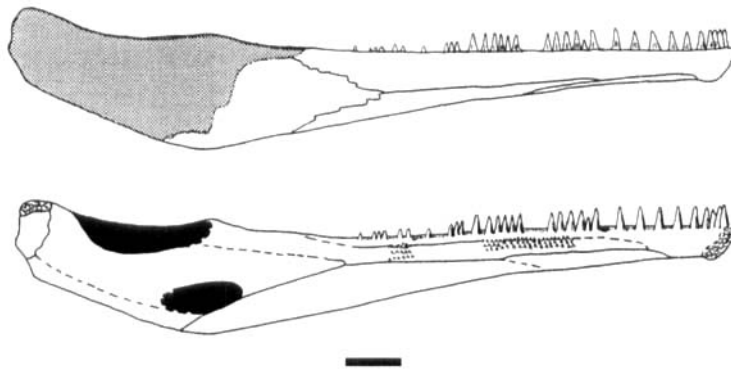


Figure 11. *Adamanterpeton ohioensis* gen. et sp. nov., Reconstruction of the mandible based mainly on AMNH 2933. Scale bar = 5 cm.

from the fangs, and are present in the anteromedial region of each vomer as in *Cochleosaurus bohemicus* but unlike *Cochleosaurus florensis* or *Chenoprosopus*. On the palatines and pterygoids, no pattern of distribution can be ascertained. On the pterygoids, the denticles in the region of the posterolateral flange bordering the subtemporal fossa are slightly larger, and there are also anteroposterior rows of particularly small denticles extending back along the medial surface of the quadrate ramus of the pterygoid. Denticles are also scattered over much of the ventral surface of the basal plate of the parasphenoid, and do not form a discrete triangular patch as in species of *Cochleosaurus*. There are numerous isolated denticle-bearing platelets of bone in the palatal region indicating that the skin over the interpterygoid vacuities was also covered with sheets of denticle-bearing platelets in the living animal.

SYSTEMATIC POSITION

Edopoidea

Adamanterpeton ohioensis is clearly a temnospondyl amphibian belonging within the taxon Edopoidea (Fig. 12)—a clade as defined by Sequeira & Milner (1993) and Milner & Sequeira (1994a, b)—because it possesses the following derived character-states:

- (1) premaxilla is anteroposteriorly elongate marginally but not medially (the primitive condition as seen in *Greererpeton*) but has a substantial flat and expanded dorso-medial surface—a unique feature associated with a small dorsally placed external naris (Milner & Sequeira 1994a: Character state 1A).
- (2) Anterior region of the jugal sutures with the prefrontal excluding the lacrimal from the orbit margin (also in eryopoid-grade temnospondyls) (Milner & Sequeira [1994a]: Character state 2A).
- (3) Anterior region of the jugal broadens and sutures broadly with the lacrimal to contribute substantially to the width of the preorbital region (Milner & Sequeira [1994a]: Character state 11A).

As well as these derived character-states, *A. ohioensis* shares with the Edopoidea

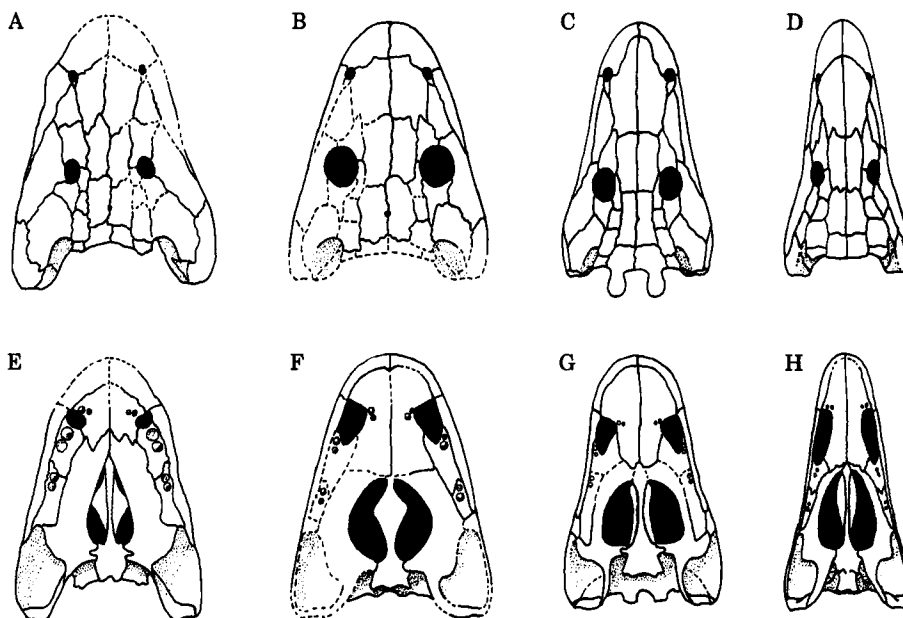


Figure 12. Comparative skulls (A–D) and palates (E–H) of edopoid temnospondyls. A, *Edops craigi*; B, *Adamanterpeton ohioensis*; C, *Cochleosaurus bohemicus*; D, *Chenoprosopus milleri*; E, *Edops craigi*; F, *Adamanterpeton ohioensis*; G, *Cochleosaurus florensis*; H, *Chenoprosopus milleri*. Sources: A,E, after Romer & Witter, 1942; B, F, this work; C, original; D,H, after Langston, 1953; G, after Godfrey & Holmes, 1995.

some primitive character-states otherwise unusual within the temnospondyls, namely the retention of intertemporal ossifications, and the palatine rami of the pterygoids meeting anteriorly to exclude the palatines and vomers from the interpterygoid vacuity margins.

Cochleosauridae

Sequeira & Milner (1993) and Milner & Sequeira (1994a) defined the Cochleosauridae on five characters, taken from seven listed in a typescript by Godfrey and Holmes. Sequeira & Milner (1993) cited Godfrey and Holmes' numbers for these characters, but these were not used in the published version (Godfrey & Holmes, 1995), which is referred to here.

Adamanterpeton ohioensis shows four of the five derived character-states listed by Sequeira & Milner (1993) (as CO.2–CO.5) and Milner & Sequeira (1994a) (as 3A and 5A–7A). They are, slightly reworded, as follows:

CO.2. (5A) Depressed areas with subdued sculpture between parallel anteroposterior sculpture ridges on either side of the skull table. Hook (1993) rejected this character but, like Godfrey & Holmes (1995), we continue to be impressed by the differential depth of sculpture across the skull table in cochleosaurids.

CO.3. (3A) Elongate vomers, with elongate prechoanal region and elongate interchoanal region associated with long choanae. Interpterygoid vacuities set back in

posterior half of skull. This character-state is also accepted by Hook (1993) as a valid defining character for the Cochleosauridae.

CO.4. (6A) Extensive contact between insula jugalis (medial extension of jugal) and lateral extension of pterygoid, separating the maxilla from the quadratojugal, and the ectopterygoid from the subtemporal fossa. This character-state is also accepted by Hook (1993) as a valid defining character for the Cochleosauridae, although as he notes, a less extensive state of this character occurs in the Saurerpetontidae.

CO.5. (7A) Choanae wider anteriorly than posteriorly. This character-state is also accepted by Hook (1993) as a valid defining character for the Cochleosauridae.

These four character-states serve to distinguish the Cochleosauridae from the Edopidae (effectively *Edops*).

One other character used previously does not hold for *A. ohioensis*, namely CO.1. (4A), the closure of the pineal foramen in medium-large skulls. In the 120 mm long skull of AMNH 6954, the pineal foramen is clearly visible, although somewhat small. The pineal foramen is obliterated by bone in large (120 mm+) skulls of *Cochleosaurus bohemicus*, in 190–300 mm skulls of *Chenoprosopus milleri* and in known specimens of *Cochleosaurus florensis*. In the 84 mm skull of *Procochleosaurus jarrowsensis*, the 80 mm skull of *Chenoprosopus lewisi* and skulls of *Cochleosaurus bohemicus* up to 60 mm long, the pineal foramen remains prominent. However, in 60–120 mm skulls of *Cochleosaurus bohemicus*, it can be seen to be progressively obliterated by ossification. The pineal foramen is still fully formed in one 108 mm skull (MB Am.81) of *C. bohemicus* and also visible in the process of obliteration in a 112 mm skull of the same species. Therefore its presence in the 120 mm skull of *C. ohioensis* is not a radical negation of the diagnostic character, but it does tend to weaken it. It can still be argued that the Cochleosauridae may be characterized by obliteration of the pineal foramen in skulls of 120 mm length or more. We simply do not know whether larger *A. ohioensis* existed and, if so, whether they possessed a pineal foramen or not.

Because it is a primitive cochleosaurid, *Adamanterpeton* shares more primitive features with *Edops* than other cochleosaurids and so has a general resemblance to what a small *Edops* might be expected to look like. However all the shared features with *Edops* appear to be primitive and the patterns of anterior palate elongation are distinct in the two genera, *Edops* elongating the anterior pterygoids and retaining short vomers, while *Adamanterpeton* and other cochleosaurids elongated the posterior vomers and not the anterior pterygoids.

Generic and specific identity

As reviewed in the introduction, the Family Cochleosauridae is currently recognized to comprise three genera: *Cochleosaurus* Fritsch, 1885, *Chenoprosopus* Mehl, 1913 and *Procochleosaurus* Sequeira, 1996. *Adamanterpeton* cannot be placed readily in any of these genera and appears to be a plesiomorphic stem-cochleosaurid. Only limited comparison with *Procochleosaurus* is possible because of the restricted material of the latter, and most of the following discussion concerns the relationship of the Linton form to the genera *Cochleosaurus* and *Chenoprosopus*.

The Linton material does not appear to share any derived character-state uniquely with the species of *Cochleosaurus*. *Cochleosaurus* is usually characterized by the presence

of prominent posteriorly directed lappets of bone on the postparietals, but this region of the skull is not visible in the Linton specimens and no useful comparison can be made.

(1) One character-state shared by both species of *Cochleosaurus* which *Adamanterpeton* does not possess is the presence of a distinct patch of denticles in the shape of an inverted triangle on the basal plate of the parasphenoid. *Adamanterpeton* shares with the outgroup *Edops*, the presence of a diffuse patch of denticles over the basal plate surface. The state of this character in *Chenoprosopus* is not known.

Adamanterpeton also lacks the derived character-states found in either *Cochleosaurus* species.

(2) *Adamanterpeton* lacks the striate-radiate dermal ornament seen in 120 mm skulls of *C. bohemicus* having a uniformly rugosely pitted skull as in *Edops* and *C. florensis*.

(3) *Adamanterpeton* lacks the sculptured underside to the postorbital in *C. bohemicus*, having a primitively smooth underside to the postorbital.

(4) *Adamanterpeton* lacks the narrow sphenethmoid of *C. florensis*, having an anteriorly broadened sphenethmoid like *Edops* and *Cochleosaurus bohemicus*.

(5) *Adamanterpeton* lacks the concave prefang region of the vomers which occurs in *C. florensis* and *Chenoprosopus*, having vomers with a flat denticle-bearing prefang region with an anteromedial ridge, like *Edops* and *C. bohemicus*.

(6) *Adamanterpeton* has a vomer with a prefang length equal to or shorter than the postfang length as in most cochleosaurids. In *C. florensis* the prefang length is significantly greater at a smaller size.

The Linton material does not appear to share any derived character-state uniquely with the species of *Chenoprosopus* as defined by Hook (1993). Primitive character-states *contra* *Chenoprosopus* are as follows:

(7) *Adamanterpeton* has a broadly rounded snout like *Edops* and *Cochleosaurus*, unlike the more narrowly pointed snout of *Chenoprosopus*.

(8) *Adamanterpeton* retains a broad lacrimal-septomaxilla contact as in *Edops* and *Cochleosaurus*, clearly separating the nasal from the maxilla, whereas in *Chenoprosopus* the septomaxilla and lacrimal have only a point contact or are completely separate permitting a maxilla-nasal contact.

(9) *Adamanterpeton* retains a choana with straight anterior edge and sharply angled anteromedial corner as in *Edops* and *Cochleosaurus*, whereas in *Chenoprosopus* the anteromedial margin of the choana is rounded.

(10) *Adamanterpeton* retains an anteriorly broad jugal making a broad suture with lacrimal. In *Chenoprosopus* the anterior region of the jugal is narrow and makes a reduced contact with the lacrimal.

(11) In *Adamanterpeton* the dorsal face of the postorbital is not triangular but bears a long finger-like process extending back between the supratemporal and squamosal. This is the configuration of the ventral side of the postorbital in most primitive temnospondyls, but within the Edopoidea it occurs only on the dorsal surface in *Edops*, *Adamanterpeton*, and large *Cochleosaurus*. In juvenile *Cochleosaurus* and *Chenoprosopus*, the bone is a simple triangular shape in dorsal aspect.

(12) In *Adamanterpeton*, *Edops* and *Cochleosaurus* the posterior region of vomer is covered with small denticles; there is no localization to a posterolateral ridge bordering the choana as in *Chenoprosopus*.

(13) In *Adamanterpeton*, the splenial is primitively separated from symphyseal region by a downgrowth of dentary; in *Chenoprosopus*, the splenials meet.

Not only does the Linton material not share any derived characters with either *Cochleosaurus* or *Chenoprosopus*, it also lacks some character-states that they share.

(14) The snout of *Adamanterpeton* is less elongate than those of *Cochleosaurus* or *Chenoprosopus* at about 120 mm skull length, particularly the premaxillae. In particular, the premaxillae of *Adamanterpeton* have a lateral length: medial suture length ratio of 1.4. It is 1.3 in *Edops* and 1.5–2.5 in other cochleosaurids.

(15) The palatine fangs of *Adamanterpeton* are relatively massive, like those of *Edops*, significantly larger than vomerine fangs or marginal teeth. The palatine fangs are only slightly enlarged in other cochleosaurids.

(16) The dentition of *Adamanterpeton* comprises fewer teeth than other cochleosaurids. The mandible has space for about 44 teeth, as in the outgroup *Edops* and in contrast to 48 in *C. bohemicus*, 55 in *C. florensis*, and 56–60 in *Chenoprosopus*. The premaxilla has space for 14 teeth (12 in *Edops*) in contrast to 14–18(–20?) through *C. bohemicus* ontogeny, 18 in *C. florensis* and 20 in *Chenoprosopus*.

(17) The pineal foramen is fully open in an *Adamanterpeton* skull of 120 mm length. It is obliterated by bone growth in *Cochleosaurus florensis* of similar size and in larger *Chenoprosopus*, and is in the process of obliteration in some *C. bohemicus* skulls of similar size, though still present in others.

In conclusion, this material cannot be placed within either *Cochleosaurus* (Character 1) or *Chenoprosopus* (Characters 7–13) and such evidence as is available suggests that it forms the sister-taxon to those two genera together (Characters 14–17). It must thus be placed in a new genus, although we have been unable to detect any autapomorphic character-states. The cladogram in Figure 13 summarizes the information presented here and incorporates data from Sequeira & Milner (1993), Hook (1993), Milner & Sequeira (1994a), and Godfrey & Holmes (1995).

ADAMANTERPETON AND THE LINTON FAUNA

Hook & Baird (1986) recorded, from collections, the existence of over a thousand tetrapod specimens from the canneloid shale at Linton. Of these, between 200 and 300 were classified by Hook and Baird as temnospondyls (including colosteids and baphetids). *Adamanterpeton ohioensis* is represented only by the two specimens described in this paper, making it the rarest temnospondyl and one of the rarest tetrapods in the Linton fauna. The recently collected contemporaneous assemblage from Five Points, Ohio, has most of the Linton tetrapod taxa present, but *Adamanterpeton* has not yet been identified (Hook & Baird, 1994) and is presumably equally rare. This contrasts with *Cochleosaurus bohemicus* from the contemporaneous fauna from Nýřany which is represented by about ten large and 60–70 smaller specimens out of 600 tetrapods. Clearly *C. bohemicus* reproduced in the Nýřany water-body and at least one age-class of juveniles is preserved as well as several adults. *A. ohioensis* appears to have been a more exotic element in the Linton fauna, probably a rare terrestrial accidental occurrence. The presence of the similar *C. florensis* in the lycopsid-stump assemblage from Florence, Nova Scotia in association with a suite of presumed terrestrial amniotes, suggests the possibility that some cochleosaurs were relatively

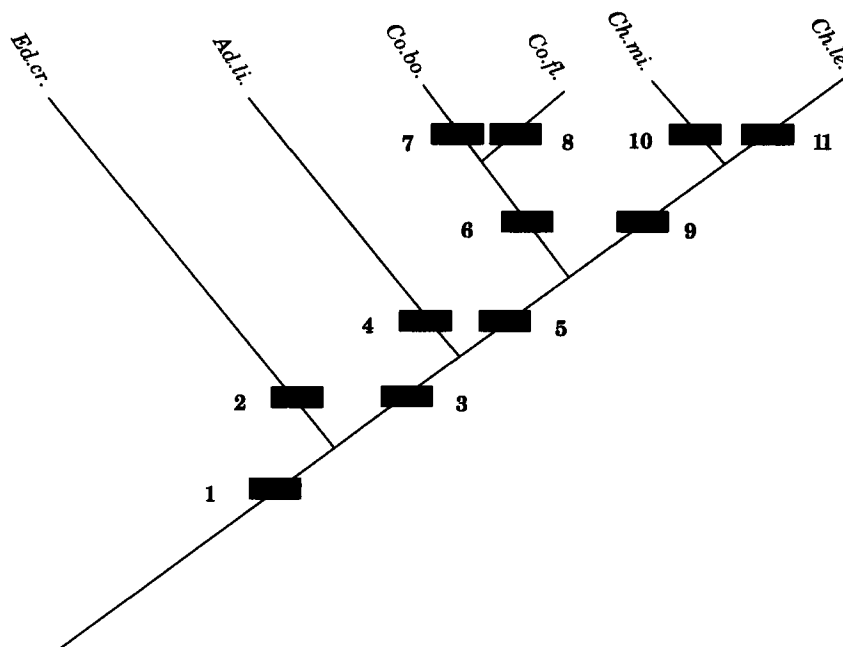


Figure 13. Cladogram depicting the hypothesis of relationships for the Edopoidea as discussed in the text. Characters defining nodes are as follows: 1 – Edopoidea; premaxilla elongate marginally but not medially, giving a substantial flat and expanded dorsomedial surface; jugal–prefrontal suture excluding lacrimal from orbit margin; broad anterior region of jugal suturing broadly with lacrimal. 2 – Edopidae = *Edops* (= *Ed. cr.*); marginal dentition shows pseudocanine peaking with characteristic maxillary swellings above the peaks; ilium with expanded dorsal blade. 3 – Cochleosauridae; depressed areas with subdued sculpture between parallel sculpture ridges on skull table; elongate vomers with both elongate prechoanal region, and elongate interchoanal region associated with long choanae, interpterygoid vacuities in posterior half of skull; choanae wider anteriorly than posteriorly; extensive contact between insula jugalis and lateral extension of pterygoid, separating maxilla from jugal, and ectopterygoid from subtemporal fossa. 4 – *Adamanterpeton* (= *Ad. li.*); no derived character. 5 – Unnamed node; premaxillaries with lateral:medial length ratio of at least 1.5: 1; palatine fangs reduced little larger than marginal teeth; pineal foramen generally obliterated at 120 mm skull length; mandible with space for at least 48 teeth. 6 – *Cochleosaurus*; postparietal lappets; distinct triangular patch of denticles on basal plate of parasphenoid. 7 – *C. bohemicus* (= *Co. bo.*); striate–radiate dermal ornament on large skulls; postorbital sculptured on ventral surface. 8 – *C. florensis* (*Co. fl.*); narrow spenethmoid. 9 – *Chenoprosopus*; narrow acuminate snout; little–no septomaxilla–lacrimal contact; short jugal–lacrimal contact; premaxilla with space for at least 20 teeth; choana with rounded anteromedial margin; vomerine denticles localized to posterolateral ridge bordering choana; splenials contributing to mandibular symphysis (Hook, 1993). 10 – *C. milleri* (*Ch. mi.*); squamosal–intertemporal contact (Hook, 1993). 11 – *C. lewisi* (*Ch. le.*); nasal–maxilla contact (Hook, 1993).

terrestrial. Both these species have relatively rugose sculpture in skulls of 100–150 mm length, a feature sometimes associated with terrestriality in temnospondyls such as the armoured dissorophids. Perhaps the Cochleosauridae encompassed both amphibious and terrestrial small carnivores, with *C. florensis* and *A. ohioensis* representing the terrestrial part of the adaptive radiation.

THE EDOPOID AND ERYOPOID RADIATIONS

With the recent description of some new primitive temnospondyls (*Balanerpeton woodi* Milner & Sequeira, 1994; *Procochleosaurus jarroensis* Sequeira, 1996; and *Chenoprosopus lewisi* Hook, 1993) and the redescription of several previously known taxa (*Capetus palustris* Steen by Sequeira & Milner [1993], *Cochleosaurus florensis* Rieppel by Godfrey & Holmes [1995], and *Dendrerpeton* spp. by Milner [1996]), we can construct a slightly clearer perspective of the evolutionary history of these forms. The edopoid clade and eryopoid grade of temnospondyl can be seen to be distinct sequential adaptive radiations filling the 'crocodilomorph' niches through the Carboniferous and early Permian.

*Edopoids**The edopoid clade*

The edopoid clade, formally the superfamily Edopoidea, comprises the families Edopidae (*Edops*) and the Cochleosauridae (*Procochleosaurus*, *Adamanterpeton*, *Cochleosaurus* and *Chenoprosopus*). The defining characters of the clade Edopoidea may be briefly summarized as:

- (1) Premaxilla is anteroposteriorly elongate marginally but not medially but has a substantial flat and expanded dorso-medial surface—a unique feature associated with a small dorsally placed external naris (Milner & Sequeira, 1994a).
- (2) Anterior region of the jugal sutures with the prefrontal excluding the lacrimal from the orbit margin (also in many but not all eryopoid grade temnospondyls) (Milner & Sequeira, 1994a).
- (3) Anterior region of the jugal broadens and sutures broadly with the lacrimal to contribute substantially to the width of the preorbital region (Milner & Sequeira, 1994a).

As well as these derived character-states, the Edopoidea possess several primitive character-states otherwise unusual within the temnospondyls, namely the retention of intertemporal ossifications, and the palatine rami of the pterygoids meeting anteriorly to exclude the palatines and vomers from the interpterygoid vacuity margins. The defining characters of the Cochleosauridae, and the relationships of the included genera have already been presented in this work.

The edopoid radiation

The edopoid clade, superimposed on a stratigraphical chart (Fig. 14), can be theorized to have appeared by the Viséan, not on the basis of diagnostic fossil material, but by phylogenetic inference from other taxa present. The presence of the more derived temnospondyl *Balanerpeton woodi* in the Brigantian (Upper Viséan) East Kirkton assemblage (Milner & Sequeira, 1994a) implies that the dichotomies giving rise to the Edopoidea and to *Dendrerpeton* had already occurred. There is no critically diagnostic edopoid material from the Viséan or Namurian, but there are non-diagnostic elements such as large temnospondyl ribs from East Kirkton (Milner & Sequeira, 1994a) and large rhachitomous vertebrae from Greer, West Virginia (Godfrey, 1988) which are consistent with the presence of large *Edops*-like forms, as

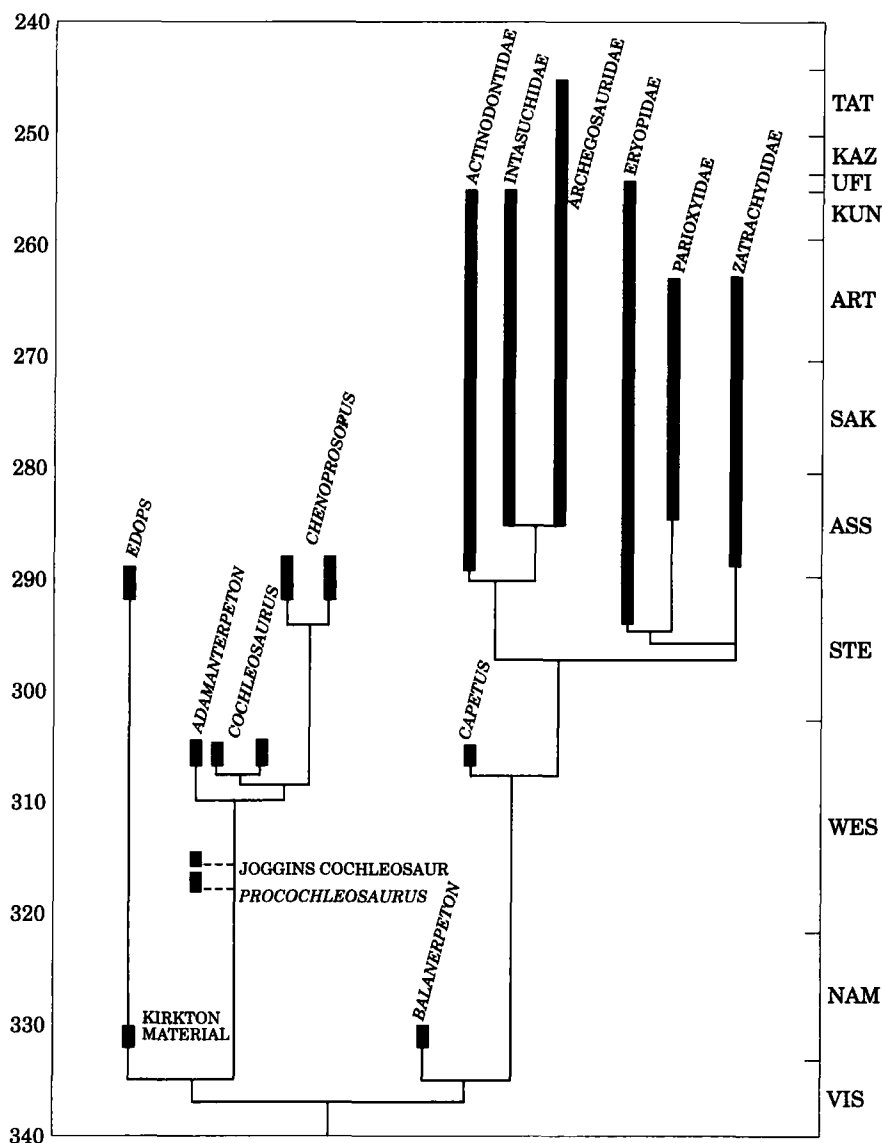


Figure 14. Phylogeny of the edopoid clade and eryopoid grade of temnospondyls produced by superimposing the cladograms of these groups on the Carboniferous-Permian timescale. Nodes as depicted represent the latest possible dates of dichotomies. Abbreviations: ART = Artinskian; ASS = Asselian; KAZ = Kazanian; KUN = Kungurian; NAM = Namurian; SAK = Sakmarian; STE = Stephanian; TAT = Tatarian; UFI = Ufimian; VIS = Viséan; WES = Westphalian.

noted by Milner & Sequeira (1994a). The earliest diagnostic edopoid specimen is *Procochleosaurus jarowensis*, a cochleosaurid from the Upper Langsettian (= Upper Westphalian A) of Jarrow, Kilkenny, Ireland (Sequeira, 1996). Although difficult to place within the Cochleosauridae, this specimen demonstrates that the edopid-cochleosaurid dichotomy had already occurred by the Langsettian and this conclusion is supported by a set of cochleosaurid vomers from the late Langsettian of Jogjins,

Nova Scotia (Milner, 1996). In the Westphalian D, the Cochleosauridae is represented by *Adamanterpeton* and *Cochleosaurus*, and at the Stephanian–Asselian boundary by *Chenoprosopus*, the latest genus of the family. The Edopidae, though the sister-family to the Cochleosauridae, is known only on the basis of *Edops* from the Stephanian–Asselian boundary in Texas. In general then, the edopoid radiation can be summarized as having appeared in the Viséan, diversified through to the Westphalian and ceased to appear in the record during the Asselian. The radiation comprised broad-skulled forms (*Edops*)—perhaps the primitive morphology; narrow-skulled forms (the alligator-like *Cochleosaurus*, *Adamanterpeton* and *Procochleosaurus*) and the slender-skulled gharial-like forms (*Chenoprosopus*).

Eryopoids

The eryopoid grade

The eryopoid grade has been argued to be paraphyletic with respect to the Stereospondyli and probably the Dissorophoidea and Lissamphibia (Milner, 1990a, 1990b). We endorse the paraphyly with respect to the stereospondyls but are now less certain about the position relative to the dissorophoid–lissamphibian clade. The possibility that the latter clade is related to *Balanerpeton* is one that we are currently exploring.

The eryopoid grade has the genus *Capetus* as a primitive immediate relative or outgroup (Milner & Sequeira, 1994a). Following Boy (1990, 1993) and Milner (1990a, b) the eryopoid grade itself comprises the families Eryopidae (*Eryops*, *Onchiodon*, *Clamorasaurus*), Zatrachydidae (*Acanthostomatops*, *Dasyceps*, *Zatrachys*), Parioxyidae (*Parioxy*), Actinodontidae (*Sclerocephalus*, *Syndiodosuchus*), Intasuchidae (*Cheliderpeton*, *Intasuchus*), and Archegosauridae (*Archegosaurus*, *Bashkirosaurus*, *Collidosuchus*, *Kashmirosaurus*, *Konzhukovia*, *Melosaurus*, *Platyposaurus*, *Prionosuchus* and *Tryphosuchus*). The internal relationships of the eryopoids have been discussed by Milner (1990a) and Boy (1990, 1993). There is general agreement in these three studies that the principal taxa can be divided into two major subgroups, one comprising *Sclerocephalus*, *Cheliderpeton* and the Archegosauridae (the Archegosauroida of Boy [1993]), and the other comprising the Eryopidae, Parioxyidae and Zatrachydidae (the Eryopoidea of Boy [1993]). The position of *Intasuchus* and *Syndiodosuchus* is not yet resolved. This set of relationships is followed here.

Monophyletic origin of the eryopoid grade

The monophyly or polyphyly of the relationship of the eryopoids to the edopoids has been discussed by Milner (1990b), Boy (1990), Sequeira & Milner (1993), Hook (1993), and Milner & Sequeira (1994a). Boy (1990), followed by Hook (1993) suggested that the eryopoids might have a diphyletic origin from among the edopoids, with *Edops* related to the eryopid–zatrachyd–parioxyid clade and *Chenoprosopus* related to the actinodontid–archegosaurid clade (Boy, 1990) or *Chenoprosopus* specifically related to the Archegosauridae (Hook, 1993). *Cochleosaurus* was not included in these analyses. Sequeira & Milner (1993: 675–676) discussed Boy's conclusions and argued that most of the characters used were invalid because of inappropriate outgroups, non-incorporation of *Cochleosaurus*, and use of both alternative states of a character as derived. Sequeira & Milner argued that there was no support for a

Chenoprosopus–actinodontid–archegosaurid relationship and that the two characters supporting an *Edops*–eryopid–zatrachyd–parioxyid relationship were probably convergence associated with semi-terrestriality and were outnumbered by five characters uniting the higher (post-edopoid) temnospondyls. Hook (1993) has pointed out similarities specifically between *Chenoprosopus* and *Archegosaurus* and has suggested that the nasal configuration of *Archegosaurus* “could be derived directly from a cochleosaurid with small external nares simply by enlarging the narial opening” and that other archegosaurid characters “could be obtained independently by slight modification of a *Chenoprosopus*-like cochleosaurid”. These are transformationist arguments, impossible to falsify or verify, and we see no purpose in arguing on this basis. We restate our arguments, for the monophyly of the eryopoid temnospondyls in relation to the edopoid temnospondyls and against a *Chenoprosopus*–archegosaurid relationship, as follows:

(1) *Chenoprosopus* and *Cochleosaurus* share five derived characters, namely: (i) depressed areas with subdued sculpture between parallel anteroposterior sculpture ridges on either side of the skull table; (ii) elongate vomers, with elongate prechoanal region and elongate interchoanal region associated with long choanae. Interpterygoid vacuities set back in posterior half of skull; (iii) extensive contact between insula jugalis (medial extension of jugal) and lateral extension of pterygoid, separating the maxilla from the quadratojugal, and the ectopterygoid from the subtemporal fossa; (iv) choanae wider anteriorly than posteriorly; (v) pineal foramen obliterated by bone in skulls of over 120 mm length. The eryopoids are primitive for these five derived character-states. All would have to be reversed to modify a cochleosaurid to obtain the archegosaurid condition.

(2) *Balanerpeton*, trimerorhachoids, *Capetus* and eryopoids share: (i) a premaxilla which is a small, generally anteroposteriorly narrow structure with a prominent alary process extending over the adjoining nasal, associated with an enlarged naris; (ii) anteriorly rounded interpterygoid vacuities. *Balanerpeton*, trimerorhachoids and eryopoids share (iii) reduced palatine ramus of the pterygoid permitting the vomers to border the interpterygoid vacuity margin. The condition is unknown in *Capetus* but may be a reversal of this. Eryopoids share (iv) loss of the intertemporal; (v) enlargement of the exoccipitals to give a bilobed occipital condyle; (vi) bilobed or divided anterior palatal fossa on the premaxilla and vomer (Boy, 1993). Boy (1993: Abb.7) has recently demonstrated that the Archegosauridae nest within a clade in which *Cheliderpeton* and *Sclerocephalus* are sequentially more primitive members. Some of the character-states used by Boy do also occur in *Chenoprosopus*, e.g. lacrimal excluded from naris by nasal–maxilla contact and prefrontal anteriorly constricted, but others, such as (vii) the development of tooth rows on the palatine and ectopterygoid, are not found in cochleosaurs.

Some of these character-states have certainly been acquired convergently elsewhere and are not unique, but this neither invalidates them, nor does it negate the validity of a scheme which seeks to minimize the number of character-state changes. Hook (1993) has argued that the above seven character-states could all have been acquired convergently in a *Chenoprosopus*–*Archegosaurus* relationship, but it must also be accepted that the five cochleosaurid characters would have to be reversed as well. This group of 12 convergences and reversals must be set against a set of resemblances between *Chenoprosopus* and *Archegosaurus*, most of which can be argued to be manifestations of

having a long slender skull, namely prechoanal elongation of the vomer, nasal-maxilla contact ahead of the lacrimal, slender triangular prefrontals, elongate premaxilla and antorbital length greater than midorbital width. We suggest that these are the convergences and that *Chenoprosopus* and *Archegosaurus* are fundamentally unrelated temnospondyls filling a gharial-like niche, and are consequently convergently long-skulled with slender muzzles and with elongate elements comprising these skulls.

In conclusion, it is argued that the eryopoids are a grade of monophyletic origin in relation to the Edopoidea. In the following discussion this is assumed.

The eryopoid radiation

The first known member of this adaptive radiation is the stem-eryopoid *Capetus palustris* from the Westphalian D (Sequeira & Milner, 1993). The family Eryopidae first appears in the mid-Stephanian (*Eryops avinoffi* from the Tri-State area) which implies that the *Sclerocephalus*–*Cheliderpeton*–archegosaurid clade must also have been present. All the other families make their first appearance in beds believed to be of Asselian age or equivalent, thus Parioxyidae (*Parioxys bolli* from the Bowie Group of Texas), Zatrachydidae (*Acanthostomatops vorax* from the Niederhässlich-Schweinsdorf Beds of Niederhässlich, Germany), Actinodontidae (*Sclerocephalus bavaricus* from the Altenglan Beds of Homberg, Germany), Intasuchidae (*Cheliderpeton latirostre* from the Lauterecken-Odernheim Beds of Lebach, Germany) and Archegosauridae (*Archegosaurus decheni* from the Lauterecken-Odernheim Beds of Lebach, Germany). These families make last appearances in the record between the Sakmarian (Parioxyidae) and the Tatarian (Archegosauridae). In general then, the eryopoid radiation can be summarized as having appeared in the Westphalian, diversified in the Stephanian/Upper Pennsylvanian to give full diversity in the Asselian and gradually ceased to appear in the record through the Permian. The radiation included broad-skulled forms (Eryopidae); slightly broad-skulled alligator-like forms, perhaps the primitive morphology for this radiation (*Capetus* and the Actinodontidae), narrow-skulled forms (the crocodile-like *Cheliderpeton*, *Intasuchus* and some archegosaurids) and the slender-skulled gharial-like forms (typical Archegosauridae). The Zatrachydidae and Parioxyidae exhibit more peculiar morphologies apparently not represented in the edopoid radiation.

Evolutionary scenario

The edopoid clade and eryopoid grade appear to be sequential adaptive radiations filling the spectrum of 'crocodilomorph' niches through the Carboniferous and Permian (Fig. 14). The edopoid radiation can be inferred to have appeared by the late Viséan, to have diversified by or in the Westphalian across Euramerica and to have made its last appearances at the Stephanian–Asselian boundary in North America. In the late Westphalian, when *Cochleosaurus* was present and *Edops* and *Chenoprosopus* or their predecessors can be inferred to have been present, the group was at its peak of known diversity, and at this time, the first immediate relative of the eryopoids *Capetus palustris* appears in the fossil record in Europe. By the late Stephanian, the Eryopidae were present and by phylogenetic inference, other eryopoid families may well have diversified. Certainly by the Asselian, the full range

of eryopoid families are represented in the fossil record (mainly in Europe but with some families in North America) and the edopoids have ceased to appear. The diversification of eryopoids in the Stephanian–Asselian appears to have been contemporaneous with the last appearances of the edopoids and it is a reasonable scenario that the eryopoid radiation replaced the edopoid radiation. There is no compelling evidence for a major taxonomic tetrapod extinction in the Stephanian–Asselian when the edopoids cease to appear, and this, combined with the overlap of the two radiations suggests that replacement may have been a competitive niche-by-niche phenomenon rather than the occupation of vacant niche space resulting from a mass-extinction.

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(From ARM). This paper is dedicated to Alec Panchen, whose teaching persuaded me to become a vertebrate palaeontologist, resulting in 29 fascinating and extremely fulfilling years so far. I have never been able to achieve Alec's high standard of description and illustration but have made a career out of trying to do so.

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