

SMALL TEMNOSPONDYL AMPHIBIANS FROM THE MIDDLE PENNSYLVANIAN OF ILLINOIS

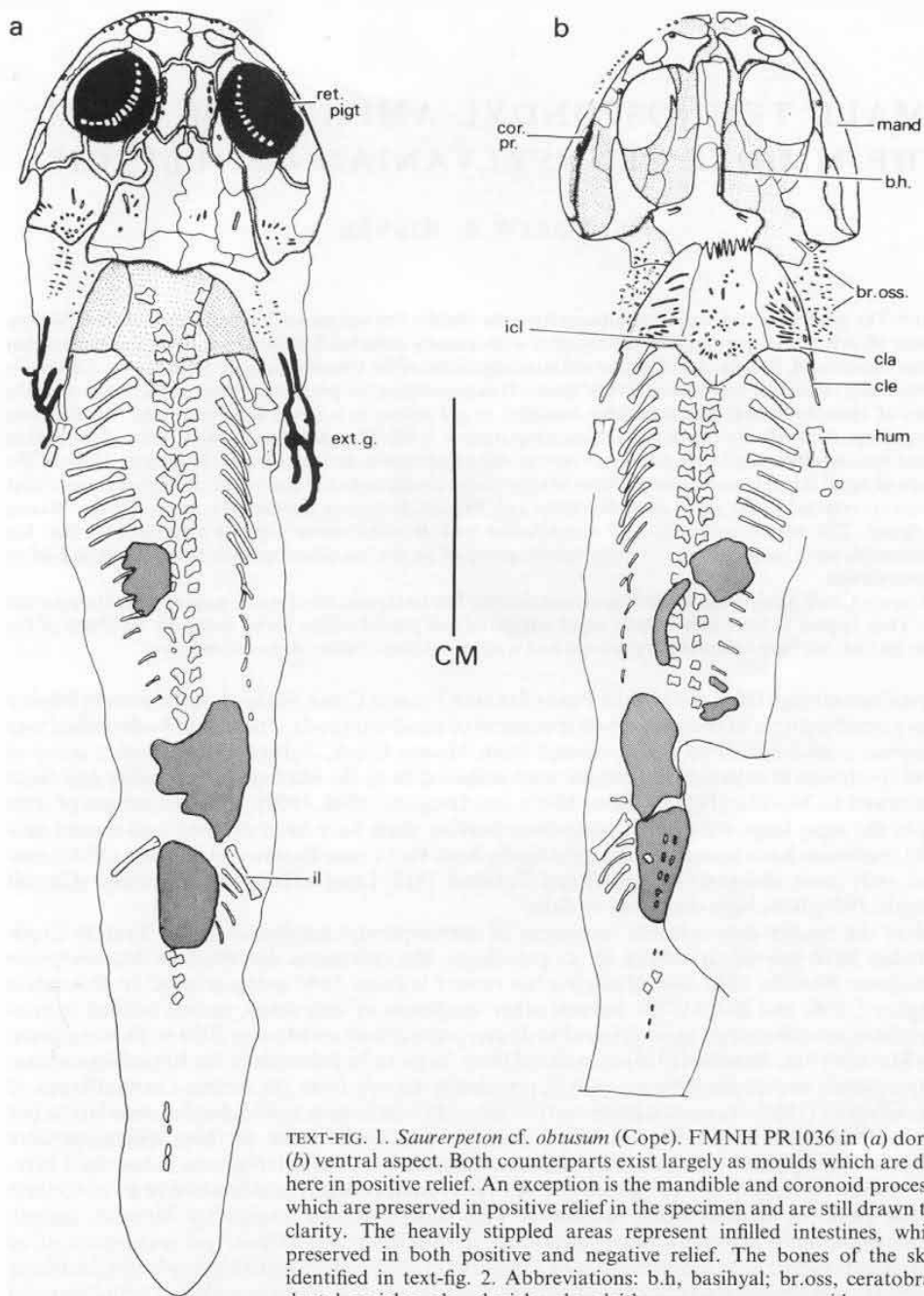
by ANDREW R. MILNER

ABSTRACT. The small temnospondyl amphibians from the Middle Pennsylvanian Francis Creek Shale of Mazon Creek near Morris, Illinois, are redescribed together with recently collected Francis Creek Shale specimens from Pit 11 near Braidwood, Illinois. A well-preserved larval specimen of the trimerorhachoid *Saurerpeton* cf. *obtusum* represents a new record for the 'Mazon Creek' fauna. It demonstrates the presence of three pairs of external gills and rows of ceratobranchial dental ossicles modified as gill rakers in a larval saurerpetontid. *Amphibamus grandiceps* Cope from Mazon Creek and the contemporary *A. lyelli* (Wyman) from Linton, Ohio, are shown to be distinct species which can be diagnosed on several size-independent and size-linked characters. Three of the specimens of small larval temnospondyls from Mazon Creek are identified as the larvae of *A. grandiceps* whilst two others are referred to the genus *Branchiosaurus* and, as such, constitute another new record for the 'Mazon Creek' fauna. The shared similarities of *Amphibamus* and *Branchiosaurus* support a hypothesis that the branchiosaurids are a monophyletic or polyphyletic group of neotenous dissorophoids most closely related to the Dissorophidae.

The Francis Creek Shale fossil assemblages contain very few tetrapods, all of which appear to be transported erratics. They appear to have been mostly small terrestrial and pool-dwelling forms living on the levees of the delta-fan and having been inundated by a flood and washed into an offshore depositional area.

THE fossil assemblage from the Middle Pennsylvanian Francis Creek Shale of north-eastern Illinois includes a small number of well-preserved specimens of small tetrapods. The first to be described was *Amphibamus grandiceps* Cope 1865 collected from Mazon Creek. Subsequently about a score of tetrapod specimens in sideritic concretions were collected from the Mazon Creek locality and these were reviewed by Moodie (1916), Olson (1946), and Gregory (1948, 1950). With the advent of strip mining in the area, large volumes of concretion-bearing shale have been exposed and several new tetrapod specimens have been collected, principally from Pit 11 near Braidwood, Illinois. Of this new material, only some aïstopods (Turnbull and Turnbull 1955; Lund 1978) and a microsauro (Carroll and Gaskill 1978) have been described to date.

Most of the readily determinable specimens of temnospondyl amphibian in the Francis Creek Shale fauna have proved to belong to *A. grandiceps*, the specimens described as *Mazonerpeton longicaudatum* Moodie 1912 and *Miobatrachus romeri* Watson 1940 being referred to this taxon by Gregory (1950) and Bolt (1979). Several other specimens of very small, poorly ossified temnospondyls have been described as, or referred to *Micrerpeton caudatum* Moodie 1909 or *Eumicrerpeton parvum* Moodie 1911. Moodie (1916) considered these forms to be referable to the Branchiosauridae, a family of small neotenous temnospondyls, principally known from the Permo-Carboniferous of Europe. Gregory (1950) reassessed them and considered them to be possible *Amphibamus* larvae but strictly indeterminate. Boy (1974, p. 261) concluded that, while some of these specimens were *Amphibamus*-like, others resembled *Branchiosaurus sens. strict.* These larvae are redescribed here, together with a recently collected specimen from Pit 11, and further consideration is given to their systematic position. Several other specimens were described and named by Moodie, namely *Erierpeton branchialis*, *Erpetobrachium mazonensis*, *A. thoracatus* and *Mazonerpeton costatum*, all of which were considered to be indeterminate by Gregory (1950). I concur with this conclusion and these specimens are not considered further in this study. Finally, another recently collected temnospondyl specimen is described here for the first time and constitutes the first record of a trimerorhachoid from the Francis Creek Shale fauna.



TEXT-FIG. 1. *Saurerpeton* cf. *obtusum* (Cope). FMNH PR1036 in (a) dorsal and (b) ventral aspect. Both counterparts exist largely as moulds which are depicted here in positive relief. An exception is the mandible and coronoid process in (b) which are preserved in positive relief in the specimen and are still drawn thus for clarity. The heavily stippled areas represent infilled intestines, which are preserved in both positive and negative relief. The bones of the skull are identified in text-fig. 2. Abbreviations: b.h, basihyal; br.oss, ceratobranchial dental ossicles; cla, clavicle; cle, cleithrum; cor.pr, coronoid process; ext.g, external gills; hum, humerus; icl, interclavicle; il, ilium; mand, mandible; ret.pigt, retinal pigment.

Material described or referred to in this study belongs to the collections of the American Museum of Natural History (AMNH); the British Museum (Natural History) (BMNH); the Field Museum of Natural History, Chicago (FMNH); the Department of Geology, University of Newcastle upon Tyne (KC); the Museum für Naturkunde, Humboldt University, Berlin (MB); the Museum of Comparative Zoology, Harvard University (MCZ); the National Museum of Natural History, Washington (USNM), and the Peabody Museum, Yale University (YPM).

SYSTEMATIC PALAEOONTOLOGY

Class AMPHIBIA
Order TEMNOSPONDYLI
Superfamily TRIMERORHACHOIDEA
Family SAURERPETONTIDAE Chase 1965
Genus SAURERPETON Moodie 1909

Type species. *Dendrerpeton obtusum* Cope 1868.

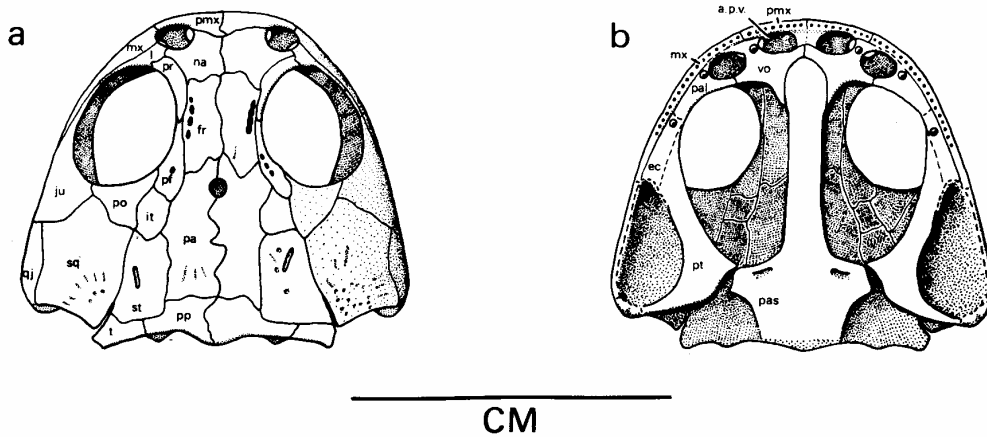
Saurerpeton cf. obtusum

Plate 64, figs. 1-4; text-figs. 1a, b, 2a, b

Material. FMNH PR1036 collected by Mr. J. Herdina of Berwyn, Illinois. At least two other specimens exist in private collections.

Locality. Peabody Coal Co. Pit 11 spoil heap, Will-Kankakee Counties, Illinois.

Horizon. Francis Creek Shale, Carbondale Formation, Desmoinesian, Middle Pennsylvanian (Westphalian D). The assemblage collected at Pit 11 is primarily of the marine Essex faunal type (Johnson and Richardson 1966) but contains some freshwater Braidwood faunal elements particularly at the northern end (Schram 1979, p. 176). The Braidwood faunal elements, including this specimen, are believed to have been washed into the sea by distributary flooding of the neighbouring swamps and delta levees (G. C. Baird 1979).



TEXT-FIG. 2. Reconstruction of skull of juvenile *Saurerpeton cf. obtusum* (Cope) based entirely on FMNH PR1036, (a) dorsal aspect, (b) palatal aspect. Abbreviations: a.p.v, anterior palatal vacuity; ec, ectopterygoid; fr, frontal; it, intertemporal; ju, jugal; l, lachrymal; mx, maxilla; na, nasal; pa, parietal; pal, palatine; pas, parasphenoid; pf, postfrontal; pmx, premaxilla; po, postorbital; pp, postparietal; pr, prefrontal; pt, pterygoid; qj, quadratojugal; sq, squamosal; st, supratemporal; t, tabular; vo, vomer.

DESCRIPTION

General features

The specimen is preserved in counterpart as a dorsoventral compression in the two halves of a sideritic concretion. Much of the kaolinite infilling has been removed, leaving moulds of both dorsal and ventral surfaces. Apart from the distal tail, the specimen is completely within the concretion although the fore limbs are very poorly preserved and the hind limbs are not visible. The specimen is small, the skull being 10 mm long and the snout to pelvis length being 33 mm. About 17 mm of tail is present.

Skull and mandibles

The general configuration of the skull is evident in text-figs. 1 and 2 and the following description is restricted to features of significance or interest. The construction of the skull closely resembles that of *Saurerpeton obtusum* from Linton, Ohio. Like the small, presumably juvenile specimens from that locality, it possesses proportionately large nares, orbits, pineal foramen and interpterygoid vacuities, simple sutures, very light pitting of the dermal bones, and traces of dermo-sensory pits on the frontals, postfrontals, and supratemporals. The reconstructions of the Linton *Saurerpeton* currently available in the literature are inadequate, being based on single incomplete specimens (Steen 1931, text-fig. 16; Watson 1956, text-fig. 24) or incompletely prepared material (Romer 1930, fig. 6; 1947, fig. 22). For this reason, a reconstruction of the skull of PR1036 has been prepared (text-fig. 2). Examination of casts of small *Saurerpeton* specimens from Linton has not revealed any significant features in which the Linton and Illinois specimens differ and the reconstruction may be taken to be representative of juvenile *Saurerpeton*.

The snout is abbreviated, the nasals are broader than long, and there is no internasal foramen. It is difficult to assess whether the large external nares represent a specific resemblance to the condition in *Acroplopus* (Hotton 1959) or whether they are simply relatively large in a tiny individual. The asymmetry in the nasal region may be an artefact of compression although it does appear to be genuine and I have incorporated it in the reconstruction. The lacrymal extends from the external naris to the anterior orbit margin where it contacts the jugal. The jugal broadly borders the orbit margin. There is a prefrontal-postfrontal contact excluding the frontal from the orbit margin. Intertemporals are present. The posterior skull is elongate, particularly the parietals and supratemporals. The pineal foramen is situated at the anterior end of the interparietal suture. The postparietals have a stepped anterior edge, so that each one is the shape of a very thick L with the postero-distal end being as narrow as the tabular. The squamosals are squarish bones each with a shallowly concave posterior edge, presumably the vestige of an otic notch. This shape of squamosal is depicted in *Acroplopus* by Hotton (1959) although he identifies a tiny gap between the squamosal and supratemporal as a rudimentary otic notch. I suspect that this is just the outer end of a very open suture, probably a line of kinesis between the cheek and the skull table occurring in all saurerpetontids. Boy (1974) cites D. Baird's observation that the Linton *Saurerpeton* apparently possesses lines of kinesis between the cheeks and the skull table. FMNH PR1036 (text-fig. 1a) shows the squamosal sharing a non-undulating common border with the supratemporal which may represent a line of kinesis extending forwards between the postorbital and the supratemporal. It seems to me to be more likely that the shallowly concave posterior edge of the squamosal should represent the margin of an otic structure, functional or rudimentary, than that the widened end of a kinetic line should have an otic homology.

As in most Francis Creek Shale vertebrates, each orbit contains a black disc which appears to be the retina preserved as a degraded pigment (Richardson and Johnson 1971, p. 1228). Also visible in each orbit is part of a sclerotic ring. The incomplete ring in the morphological right orbit (left in text-fig. 1a; Pl. 64, fig. 3) contains fourteen plates and suggests the presence of a typical temnospondyl sclerotic ring of about thirty plates. Examination of several specimens of *S. obtusum* from Linton, all of which are well preserved and in articulation, revealed one (MCZ 2487) which possessed an incomplete ring of ten plates in one orbit. The rarity of preserved sclerotic plates in otherwise well-preserved specimens is neither surprising nor significant, as these structures are encountered only rarely in other genera where they are known to occur. Examination by the author of over

EXPLANATION OF PLATE 64

Figs. 1-2. *Saurerpeton* cf. *obtusum* (Cope), FMNH PR1036. Counterparts of concretion showing dorsal and ventral moulds of specimen, $\times 2.5$.

Figs. 3-4. *Saurerpeton* cf. *obtusum* (Cope), FMNH PR1036. Dorsal and ventral moulds of the skull, $\times 3$.



1



2



3



4

MILNER, temnospondyl amphibians

thirty skulls of *Cochleosaurus bohemicus* from Nýřany, Czechoslovakia, revealed only two specimens with sclerotic rings *in situ* although most of the material was preserved in articulation in a fine laminated coal. In both the Linton *Saurerpeton* and the Nýřany *Cochleosaurus* the widespread absence of sclerotic plates undoubtedly relates to prepreservational decomposition of the eyes of which the sclerotic plates are an integral part. The only trimerorhachoids in which sclerotic ossifications have been previously reported are the trimerorhachid *Lafonius* from the Upper Pennsylvanian of New Mexico (Berman 1973) and *Eugyrinus* from the Upper Carboniferous of England (Milner 1980a). No saurerpetontid has been previously reported with these structures.

The premaxilla and maxilla bear small marginal teeth, at least back to the level of the middle of the orbit. The small vomers bear a single pair of tusks anterior to the internal nares. The vomers form the mesial border of the internal nares and the posterior border of the paired anterior palatal vacuities. It is not possible to ascertain whether the vomers contact the palatines on the maxillary side of the internal nares as in *Acroplous*. The palatines are short V-shaped bones entering the margin of the interpterygoid vacuities and each bearing a single tusk. Ectopterygoid tusks are also visible although the bones themselves are not exposed. Each pterygoid has short palatine and quadrate rami and has a mobile contact with the braincase. The basal plate of the parasphenoid bears prominent carotid foramina and anterolateral 'wings' articulating with the pterygoids. The cultriform process is broad and appears to form a wedge between the vomers which have only a narrow sutural contact anterior to it. No denticles are visible on any palatal ossifications. The mandibles are poorly preserved and little can be made out except for the presence of a prominent coronoid process.

Hyobranchial skeleton

Superimposed on the cultriform process of the parasphenoid (text-fig. 1b) is a small rod-like ossification which is slightly expanded at both ends. Its shape and medial position indicate that it is a copula, a medial hyobranchial ossification of uncertain homology but probably the basihyal. Boy (1974) reported such an element in a large *Saurerpeton* from Linton (USNM 4471), an observation which I can confirm, although this ossification has not yet been described. Apart from the copula, the hyobranchial skeleton of FMNH PR 1036 was not ossified but can be inferred as having been present from the presence of several rows of dental ossicles modified as gill rakers (text-fig. 1). These have not previously been reported in *Saurerpeton*. At least four rows of these tooth-bearing ossicles are visible in the branchial region on each side of the specimen and six rows were probably present on each side as in *Branchiosaurus* (Boy 1972, fig. 39). In well-preserved *Branchiosaurus* cf. *petrolei* specimens from Odernheim, the six rows can be seen to occur in a 1-2-2-1 configuration on each side of the branchial region (Bulman and Whittard 1926; Boy 1972). As Bulman and Whittard noted, this configuration is consistent with the dental ossicles on each side having been attached to four cartilaginous ceratobranchials bordering three gill-slits. The dental ossicles of larval temnospondyls appear to have functioned as gill rakers with spike-like denticles extending across each gill-slit from the ceratobranchials on either side of it and acting as a filter preventing small food particles from being lost via the gill-slits. In several living neotenes urodeles, non-respiratory gill-slits are bordered by non-skeletal papillae which serve this purpose (Noble 1931) and may even be the homologues of the dental ossicles (Stadtmüller 1936, p. 659). Richardson and Johnson (1971, p. 1230) reported that one unidentified small amphibian from the Francis Creek Shale has ostracods in its gut, and gill rakers would have been essential for feeding on such organisms.

Ceratobranchial dental ossicles or comparable ossicles have been reported in eight genera of Palaeozoic amphibian, seven of which are temnospondyls, the other being a microsauro. They are the trimerorhachid *Lafonius* (Berman 1973, text-fig. 5), the saurerpetontid *Saurerpeton* (this paper, text-fig. 1), the actinodontid *Sclerocephalus* (Boy 1972, figs. 11, 69), the archegosaurid *Archegosaurus* (Meyer 1857, pl. 14), the micromelerpetontids '*Limmerpeton*' (Milner, unpubl.) and *Micromelerpeton* (Boy 1972, fig. 11), the branchiosaurid *Branchiosaurus* (Boy 1972, fig. 11), and the microbrachomorph microsauro *Microbrachis* (Carroll and Gaskill 1978, figs. 77 and 78 as 'gill-supports').

The structure of individual dental ossicles has been well illustrated by Boy (1972) for *Branchiosaurus*, *Micromelerpeton*, and *Sclerocephalus* and Berman (1973) for *Lafonius*. The dental ossicles in FMNH PR 1036 are not sufficiently well preserved for a consistent structure to be made out, but appear to have been rod-like ossicles with an expansion at one end, probably the insertion on the surface of the ceratobranchial. In this form, these structures must have functioned as gill rakers and would only have been of value to small aquatic plankton feeders. In forms such as *Sclerocephalus* and *Archegosaurus*, they occur only in the smallest individuals, presumably larvae, and are not retained in equally well-preserved adults. Their presence in a small *Saurerpeton* larva does not therefore imply that they were necessarily present in large individuals of the same species.

Ceratobranchial dental plates are a primitive character of the Osteichthyes (including Tetrapoda) and occur as platelets of bone bearing small teeth in such forms as the actinopterygian *Amia*, the osteolepiform *Eusthenopteron* (Jarvik 1980), and the coelacanth *Rhabdoderma* in which some of them also functioned as gill

rakers (Forey 1981). Dental plates modified as branchial gill rakers were taxonomically widely distributed in temnospondyl larvae and may be taken as characterizing the primitive temnospondyl condition, having presumably been present in the larva of the common ancestor of the above-listed temnospondyls. The further presence of these ossicles in *Microbrachis* implies that the common ancestor of temnospondyls and microsaur also possessed a larva with gill rakers. The relationships of the early tetrapods have yet to be established with any degree of certainty but the temnospondyls and microsaur have never been suggested as being closely related to each other, implying that the presence of larval gill rakers is either a primitive tetrapod character or a retention of a similar condition from larval choanate fishes. Ceratobranchial dental ossicles seem to have been lost as an adult characteristic in tetrapods except for neotenus temnospondyls such as *Gerrothorax*, a late Triassic plagiosaur which appears to bear denticles on ossified ceratobranchials (Nilsson 1946).

Also present in FMNH PR1036 are the carbonized remains of the external gills. There appear to have been three filamentous external gills on each side as in *Branchiosaurus* and many living urodeles. There is not good evidence that the gill filaments were pinnate. External gills have not previously been reported in any trimerorhachoid although, as with the gill rakers, they may occur only in the larvae. The only temnospondyls in which external gills have been widely reported are *Branchiosaurus* from Odernheim (Bulman and Whittard 1926) and Friedrichroda (Whittard 1930) and *Tungussogyrinus* from the Permian Tunguska basin in Siberia (Efremov 1939). Also from Odernheim, the temnospondyls *Micromelerpeton credneri* (Malz 1967, figs. 7 and 8) and *Sclerocephalus* are occasionally preserved with small external gills visible. Thus larval eryopoids, dissorophoids, and trimerorhachoids all possessed external gills and in none of these forms can more than three pairs of gills be seen, supporting Bystrow's (1939) contention that Palaeozoic amphibians possessed no more than three pairs of external gills. Sushkin (1936) and Schmalhausen (1968) have both argued that early tetrapods may have retained four pairs of external gills such as still occur in the larvae of lepidosirenid lungfish, recently argued to be the nearest living relatives of the tetrapods (Rosen, Forey, Gardiner and Patterson 1981). Sushkin's argument was based on the presence in the Upper Permian temnospondyl *Dvinosaurus* of a groove for a fourth branchial artery on the fourth ceratobranchial, implying the presence of a fourth external gill. Schmalhausen based his argument on the retention of a rudimentary fourth pair of external gills in the larva of the hynobiid salamander *Ranodon*, one of the most primitive living salamanders. The distribution of three or four pairs of external gills among Palaeozoic amphibians remains uncertain but in all small temnospondyls in which carbonized external gills can be counted, no more than three pairs are visible.

Postcranial skeleton

The vertebral column consists of an estimated twenty-four presacral vertebrae (two to three are obscured anterior to the pelvic region) and a few proximal caudal vertebrae are also preserved. Each vertebra consists of the paired halves of low neural arches but there are no ossifications corresponding to centra. The vertebrae thus correspond to the 'phylospondyl' condition which is simply a poorly ossified labyrinthodont condition as pointed out by Romer (1939). The ribs are straight, slender and slightly expanded at both ends. The anterior ribs of the pectoral region are larger and more fully ossified than those further back. The tail was laterally flattened.

The pectoral girdle includes a large rhomboidal interclavicle, slightly longer than broad and with a pectinate anterior edge as found in several genera of Palaeozoic temnospondyls (*Eugyrinus*, *Acroplopus*, and *Branchierpeton*). The clavicles are also proportionately large with broad triangular ventral blades overlapping the interclavicle. A tiny ossification representing the scapulo-coracoid is present as is a slender rod-like cleithrum. The fore limbs were tiny and only the shafts of the major limb bones are ossified. The humeri appear to have been short and stout. The ilium consists of a long slender blade expanded slightly at the acetabulum, resembling that of the Linton *Saurerpeton*. The ischia and pubes are not visible and may have been unossified. No hind limbs are visible. In the posterior abdominal region are several amorphous structures which, from their shape and position, appear to be endocasts of the intestines as reported by Moodie (1911) in some of the small temnospondyl larvae from Mazon Creek. No dermal scales are visible on the specimen.

SYSTEMATIC POSITION

PR1036 is clearly a small temnospondyl of the trimerorhachoid-brachyopoid complex, having an elongate skull-table, a poorly developed otic notch, paired anterior palatal fenestrae, a broad cultriform process, and reduced limbs. The retention of primitive tetrapod features such as the presence of intertemporals, a movable basiptyergoid-basisphenoid articulation, and unossified ceratobranchials preclude it from being *dvinosaurus*, *kourerpetontid*, or *brachyopid*, and identify it as

one of the trimerorhachoids which characterize the late Palaeozoic tetrapod assemblages of North America. These Upper Carboniferous and Lower Permian forms are currently divided into two families, the Trimerorhachidae (including *Trimerorhachis*, *Neldasaurus*, and *Lafonius*) and the Saurerpetontidae (including *Saurerpeton*, *Acroploous*, and *Isodectes*). In recent years they have been the subject of studies by Hotton (1959), Chase (1965), Baird (1966—and in Welles and Estes 1969), Berman (1973), and, from a cladistic viewpoint, by Coldiron (1978). Chase's family group Saurerpetontidae is considered by Coldiron to be a paraphyletic grade and hence an artificial group in his hypothesis of relationships. The family name is retained in this work as a useful label for the *Saurerpeton*-*Acroploous*-*Isodectes* group. The Francis Creek Shale specimen may be identified as a saurerpetontid by the presence of the following characters as well as those listed above:

- L-shaped postparietals and slender tabulars.
- Jugal broadly entering the orbit margin.
- Palatine broadly bordering the interpterygoid vacuity.
- Absence of palatal denticles or tooth-rows.
- Presence of a pronounced coronoid process on the mandible.
- Presence of a kinetic line between the cheek and the skull-table.
- A 'winged' basal plate to the parasphenoid.
- Ilium with a long slender blade.

Referring the specimen to a given genus of saurerpetontid is rendered difficult by the unsatisfactory comparative diagnoses of the material available in the literature. *Saurerpeton* has not been studied recently and the older published first-hand descriptions are not entirely accurate. For example, acid-etching of the Linton material by Dr. D. Baird has revealed that it does not possess the distinct otic notches depicted by Romer (1947) and Watson (1956), the squamosals showing only shallow posterior concavities as in *Acroploous* and *Isodectes* (*Eobrachyops*). Furthermore, new specimens of *Acroploous* from the Lower Permian Speiser Shale of Kansas (Schultze 1980) and of *Isodectes* from the Upper Pennsylvanian Burlingame Limestone, also in Kansas (Baird 1966 and 1969 in Welles and Estes), have recently been collected and are currently being studied respectively by Mr. Brian Foreman and Mr. John Chorn of Kansas University, Lawrence, Kansas. Mr. Foreman and Mr. Chorn have kindly permitted me to examine their material and it is clear that a substantial re-evaluation of the characteristics of *Acroploous* and *Isodectes* will be necessary and that *Acroploous* at least possesses undescribed derived conditions not found in the Linton *Saurerpeton* or in the Francis Creek Shale specimen. The characters of the type of *Isodectes* from the Texas red-beds are ill-defined in the literature and this, combined with the close resemblance of the contemporary Linton and Francis Creek Shale specimens, leads me to refer the Francis Creek Shale specimen to the genus *Saurerpeton*.

The type species *Saurerpeton obtusum* is based on material described from the Westphalian D coal-swamp assemblage from Linton, Ohio. At least twelve specimens were collected at Linton and several were described under different names. The valid binomen is derived from *Dendrerpeton obtusum* Cope 1868 (AMNH 6928) and *S. latithorax* (Cope) Moodie 1909 (USNM 4471). Similar material has been described from the contemporary Kittanning Coal of Cannelton and is currently reported in the literature under the undiagnosed binomen of *S. minimum* (Moodie 1909), see D. Baird 1964, 1978. It is probably not distinguishable from *S. obtusum*. The Francis Creek Shale is contemporaneous with the Linton and Cannelton horizons and the *Saurerpeton* specimens from all three localities are extremely similar. As the two named species have not been comparatively diagnosed and are doubtfully distinct, the Francis Creek Shale specimen is referred to *S. obtusum* as the senior species. Ultimately, comparative study of the material from the three localities may reveal from one to three species.

Superfamily DISSOROPHOIDEA
Family DISSOROPHIDAE Williston 1910
Genus AMPHIBAMUS Cope 1865

Type species. *Amphibamus grandiceps* Cope 1865.

Diagnosis. Primitive dissorophids growing to about 300 mm total length. The skull is unusually broad in large specimens, being almost circular in dorsal aspect, and the skull table is more abbreviated than in any other dissorophoid with the occiput being clearly anterior to the level of the quadrates. Other characteristics of the genus are primitive retentions as *Amphibamus* lacks several of the derived conditions characterizing most or all other dissorophids. Retained primitive features include the presence of a prefrontal-postfrontal suture, the presence of a stapedial foramen, the absence of dermal armour plates on the tops of the neural spines, and the absence of rugose ridges on the dermal skull roof. All described material is from the Westphalian D of North America and Europe.

Amphibamus grandiceps Cope 1865

Text-figure 3a, b

Diagnosis. (For 'post-metamorphic' material only.)

As for genus, plus:

Parasphenoid bears a slender cultriform process with a single medial row of denticles.

Space for forty-eight marginal teeth in each jaw ramus.

Twenty to twenty-one presacral vertebrae.

Ossified ventral dermal scales present.

At 14 mm mid-line skull length, the skull of *A. grandiceps* has the following characteristics: undulating medial sutures between frontals and parietals; postfrontals expanded posteriorly behind level of posterior orbit margin; and pineal foramen posterior to level of posterior orbit margin.

(See remarks below for discussion of this diagnosis.)

Selected synonymy. (For 'post-metamorphic' material only.)

1865 *Amphibamus grandiceps* Cope, p. 134.

1866 *Amphibamus grandiceps* Cope; Cope, p. 135, pl. 32, fig. 8.

1912 *Mazonerpeton longicaudatum* Moodie, p. 337, pl. 3, figs. 1, 2; pl. 7, fig. 3.

1916 *Mazonerpeton longicaudatum* Moodie; Moodie, p. 61, pl. 3, figs. 5, 6; text-fig. 14a.

1916 *Amphibamus grandiceps* Cope; Moodie, p. 126, pl. 3, fig. 7; pl. 4, figs. 5, 6; pl. 14, figs. 1, 2; text-figs. 26-28.

1940 *Amphibamus grandiceps* Cope; Watson, p. 195, fig. 1.

1940 *Miobatrachus romeri* Watson, p. 198, figs. 2-10.

1950 *Amphibamus grandiceps* Cope; Gregory, p. 841, figs. 1-6.

1964 *Amphibamus grandiceps* Cope; Carroll, p. 242.

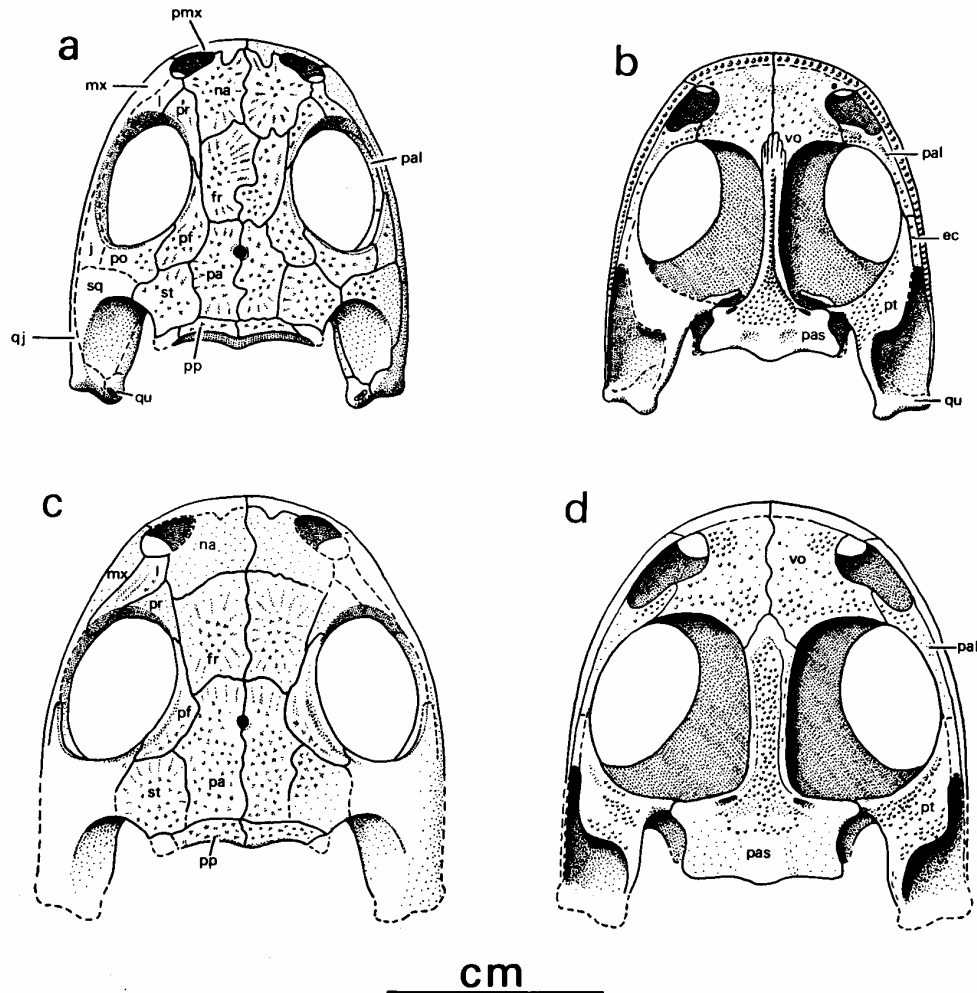
1979 *Amphibamus grandiceps* Cope; Bolt, p. 529, figs. 1-3, 5-9.

Surviving material. YPM 794, the neotype of *A. grandiceps*. YPM 795, the type of '*Mazonerpeton longicaudatum*'. FMNH UC2000, the type of '*Miobatrachus romeri*'. FMNH PR558, an undescribed but poorly preserved specimen in counterpart.

The holotype of *A. grandiceps* was destroyed in a fire (Moodie 1916, p. 126) and a further specimen (Moodie 1916, pl. 14, figs. 1, 2) is now unlocatable (Gregory 1950, p. 842).

Localities and horizons. The five described specimens all appear to have been collected in Mazon Creek, near Morris, Grundy County, Illinois. The undescribed FMNH PR558 is from the Pit 11 spoil heap, Will-Kankakee Counties, Illinois. All are from the Francis Creek Shale, Carbondale Formation, Desmoinesian, Middle Pennsylvanian (= Westphalian D).

Remarks. The above synonymy and list of material is incorporated for the sake of completeness. The material has been studied in recent years by Gregory (1950), Carroll (1964), and Bolt (1979) and Dr. J. R. Bolt is undertaking further study of it. The reconstruction of the skull (text-fig. 3a, b) is primarily based on YPM 794 although the jaw suspensorium incorporates information from FMNH UC2000. It is an original reconstruction based on first-hand examination of latex casts, but does not include any new information which cannot be gleaned from the recent published work listed above.



TEXT-FIG. 3. Reconstructed skulls of small post-metamorphic individuals of *Amphibamus*. (a, b) *Amphibamus grandiceps* Cope from Mazon Creek. Reconstruction of skull roof and palate based on YPM 794 with details of the jaw suspensorium and otic region based on FMNH UR2000. (c, d) *A. lyelli* (Wyman) from Linton, Ohio. Provisional reconstructions of the skull roof and palate based on MB 1888-1456. Abbreviations: ec, ectopterygoid; fr, frontal; j, jugal; l, lachrymal; mx, maxilla; na, nasal; pa, parietal; pal, palatine; pas, parasphenoid; pf, postfrontal; pmx, premaxilla; po, postorbital; pp, postparietal; pr, prefrontal; pt, pterygoid; qj, quadratojugal; qu, quadrate; sq, squamosal; st, supratemporal; vo, vomer.

The reconstruction is provided in order to facilitate comparison with a reconstruction of a similar size skull of *Amphibamus lyelli* in order to establish some diagnostic characters of the two species.

The species of Amphibamus

Carroll (1964) demonstrated that 'Pelion' *lyelli* from the Westphalian D of Linton, Ohio, was, when stripped of some *Saurerpeton* specimens, sufficiently similar to *A. grandiceps* as to merit inclusion in the same genus, as the new combination *A. lyelli*. Bolt (1979, p. 552) concurs with this. Carroll also referred contemporary material from Nýřany, Czechoslovakia, to the genus as the new combination *A. calliprepes* (Steen). This material requires redescription before it can be comparatively diagnosed against the North American species of *Amphibamus* and it is not discussed further here except to note that, from my examination of the material, it is indeed a distinct species, either of *Amphibamus* or a closely related but distinct genus.

Carroll (1964) differentiated the two North American species of *Amphibamus* on the following criteria which appeared to him to be size-independent.

- (i) Marginal tooth-rows. The number of tooth-spaces per jaw ramus is forty-eight in *A. grandiceps* and seventy-six in *A. lyelli*.
- (ii) Number of presacral vertebrae. *Circa* twenty-one in *A. grandiceps* and twenty-five in *A. lyelli*.
- (iii) Prefrontal-postfrontal suture. Relatively wide in *A. grandiceps* and relatively narrow in *A. lyelli*.
- (iv) Postparietals. Relatively anteroposteriorly deep in *A. grandiceps* and relatively slender in *A. lyelli*.

However, the largest surviving specimen of *A. grandiceps* has a mid-line skull length of 14 mm whilst the smallest *A. lyelli* available to Carroll had a mid-line skull length of 26 mm, the other *A. lyelli* skulls being up to 50 mm long. Thus the possibility exists that some or all of these characters might actually be the product of ontogenetic changes rather than species-diagnostic characters and Bolt (1979, p. 552) has suggested that further study might result in the conclusion that the two populations were, to all intents and purposes, conspecific. Bolt also notes other differences in the marginal dentition (pedicellate teeth in *A. grandiceps*, conical teeth in *A. lyelli*) and presacral vertebral construction (gastrocentrous in *A. grandiceps*, rhachitomous in *A. lyelli*) which he suggests may also represent ontogenetically changing features in a single growth series.

I have been able to resolve some of these character differences as being ontogenetic or specifically diagnostic by reference to a hitherto undescribed small specimen of *A. lyelli* from Linton. A latex cast of this specimen MB 1888-1456 has been made available to me through the generosity of Dr. R. L. Carroll and Dr. R. Reisz. It is preserved in counterpart and is the anterior half of a small *A. lyelli* with a 17 mm long skull. It is thus only slightly larger than the neotype of *A. grandiceps* (14 mm skull) and permits the identification of character differences which are non-ontogenetic or the product of different rates of ontogeny. I hope to describe MB 1888-1456 more fully at a later date but include here a provisional reconstruction of the skull to facilitate comparison (text-fig. 3c, d).

It can be seen from text-fig. 3a-d that the 14-17 mm skulls of the two species are broadly comparable in the possession of proportionately large orbits, nares and pineal foramen that characterize juvenile temnospondyls. Both also lack any trace of lateral-line pits or sulci. Characters (iii) and (iv) used by Carroll (1964) to differentiate the two species appear to be simply the products of ontogeny. Comparison of text-figs. 3a and 3c shows the prefrontal-postfrontal sutures to be very similar in width and the postparietals to be equally slender in both skulls. The character-states for (iii) and (iv) which Carroll ascribes to *A. lyelli* are those of a larger *Amphibamus* skull and not necessarily species-diagnostic. Likewise MB 1888-1456 does not possess vomerine or palatine tusk-pairs (the ectopterygoids are obscured by the mandibles) although larger *A. lyelli* skulls do possess such tusks (Carroll 1964). This then is also an ontogenetic feature. Another feature of all small *Amphibamus* skulls of both species is the absence of tabulars. MB 1888-1456 has both tabulars missing as do all *A. grandiceps* specimens. Tabulars are certainly present in larger *A. lyelli* specimens (AMNH 6841, BMNH R2670) indicating that their absence in smaller skulls is due to post-mortem detachment

rather than natural absence or non-ossification. It is unlikely that the tabulars are only apparently absent due to delayed ossification as Boy's studies on ossification sequences in temnospondyls show the tabulars to ossify in the middle larval phase prior to the circum-orbital series (Boy 1974, table 1).

However, in some ontogenetically variable features, the two *Amphibamus* skulls do differ as follows:

- (a) The 14 mm long *A. grandiceps* skull shows some interdigitation of the medial sutures between the frontals and parietals (a feature associated with older individuals) while the 17 mm long *A. lyelli* skull has simpler sutures.
- (b) The *A. grandiceps* skull has a parietal foramen which is situated more posteriorly relative to the orbits than in the *A. lyelli* skull, suggesting again a greater ontogenetic age for the *A. grandiceps* skull.
- (c) The postfrontals are posteriorly expanded in the *A. grandiceps* skull but are slender crescent-shaped bones in the *A. lyelli* skull. In larger *A. lyelli* (BMNH R2670) the postfrontals are also expanded posteriorly, indicating that this expansion takes place ontogenetically in *A. lyelli* but has not yet occurred in MB 1888-1456 although it has already occurred in the smaller *A. grandiceps* YPM 794.

Thus three separate cranial features suggest that *A. grandiceps* at 14 mm skull length is ontogenetically older than *A. lyelli* at 17 mm skull length. *A. lyelli* is known to grow to 60 mm mid-line skull length whereas *A. grandiceps* is not known to have grown to more than 20 mm skull length. This may be more than negative evidence. If *A. grandiceps* matured at a smaller size than *A. lyelli*, it is probably because it had a smaller adult size. Whether this was so or not, the difference in relationship of size and ontogenetic development in the two species is a diagnostic character.

Four apparently size-independent characters further serve to distinguish *A. grandiceps* from *A. lyelli*, two of which were reported by Carroll and two of which are recorded here for the first time.

- (d) As noted by Carroll (1964), the number of marginal teeth in *A. grandiceps* is forty-eight per ramus whereas in *A. lyelli* it is about seventy-six per ramus. MB 1888-1456 does not possess a visible complete tooth-row but one sequence of twenty-two teeth and spaces is visible at the back of the right maxilla and these suggest a total per ramus of sixty to seventy although this sequence may include smaller posterior teeth. However, the discrepancy of tooth-counts between species seems too great to be a by-product of ontogeny because, although the number of teeth is known to increase with growth in some temnospondyls, this is much less dramatic. In Bystrow and Efremov's (1940) description of *Benthosuchus sushkini*, they report a 28 mm long skull with fifty-three premaxillary + maxillary teeth (op. cit., fig. 58) and a longer snouted 124 mm skull with seventy-four marginal teeth (op. cit., fig. 30). The proportional length of the snout increases with growth in *Benthosuchus* and the increase in numbers of marginal teeth is a consequence of this and the greater discrepancy in size between the two *Benthosuchus* specimens. In the two *Amphibamus* species, the difference in marginal tooth-count is greater considering that no snout elongation occurs, and is probably a valid specific difference.
- (e) The other distinction recorded by Carroll (1964) which seems indisputable is the number of presacral vertebrae. In the type of *A. lyelli* (AMNH 6841) there are certainly twenty-five presacrals while in *A. grandiceps* there are either twenty or twenty-one (Bolt 1979, p. 547).
- (f) As can be seen in text-fig. 3, the two species differ in the width of the medial region of the skull, *A. lyelli* having broader medial-region ossifications than *A. grandiceps*. On the dorsal surface of the skull, this is most conspicuous for the nasals and frontals, whilst in the palate, the parasphenoid shows the difference in width most obviously. In both *A. grandiceps* specimens with good parasphenoids (YPM 794 and UC2000), the cultriform process bears a single medial row of denticles along most of its length and the basal plate is antero-posteriorly narrow. In *A. lyelli* (MB 1888-1456) the cultriform process bears a broad medial strip of denticles, about four denticles in width and the basal plate is much less narrow antero-posteriorly.
- (g) Dr. Donald Baird (*in litt.*) has pointed out to me, and I have subsequently confirmed for myself, that whereas the *A. grandiceps* specimens all possess chevrons of ossified gastralia

(ventral dermal scales), no *A. lyelli* specimens show any trace of ossified scales. The preservation of vertebrates from Linton is extremely fine and all the *Amphibamus* specimens are articulated and show no evidence of disintegration, dermal structures such as the palpebral cup being present. As most other Linton tetrapods have prominent dermal scales present, one must conclude that *A. lyelli* lacked ossified scales throughout its known size range whereas *A. grandiceps* retained them. The absence of scales in *A. lyelli* inevitably suggests that it may have been one of the earliest amphibians to adopt cutaneous gas-exchange through a vascular skin.

Thus the two North American species of *Amphibamus*, though similar, can be distinguished by seven characters (*a-g* above), some of which reflect different rates of ontogenetic change (*a-c*) while others are more or less size-independent (*d-g*). Other differences between the two species, which Bolt (1979) has attributed to ontogenetic processes may yet prove to be divergent adaptations. The pedicellate teeth and pleurocentrum-dominated presacral vertebrae of *A. grandiceps* may or may not metamorphose into the conical teeth and rhachitomous vertebrae of the larger *A. lyelli*. Unfortunately MB 1888-1456 sheds no light on these characters. The possibility remains, however, that *A. grandiceps*, *Doleserpeton annectens*, and some of the small *Tersomius* material may represent a radiation of small unarmoured dissorophids uniquely characterized by pedicellate teeth and gastrocentrous vertebrae while the other larger, mostly armoured, dissorophids retained rhachitomous vertebrae and simple teeth throughout their life-history.

THE MAZON CREEK 'BRANCHIOSAURS'

Between 1909 and 1916 Moodie described a series of very small temnospondyl specimens from Mazon Creek under a variety of names as outlined in the introduction. He noted their resemblance to the European *Branchiosaurus* material and referred them to the Branchiosauridae. Romer (1939) demonstrated that the characteristics of the amphibian order Phyllospondyli (the 'branchiosaurs') were those of small or larval labyrinthodonts and concluded that most 'branchiosaurs' were the larvae of contemporary larger temnospondyls. Gregory (1950) comprehensively reviewed the Mazon Creek 'branchiosaurs', concluding that several of Moodie's specimens were completely indeterminate and that the remaining material represented a single type of temnospondyl larva. The senior name for this material was *Micrerpeton caudatum* and Gregory concluded that it was strictly indeterminate although possibly the larvae of *A. grandiceps*. Gregory's reluctance to place this material in the synonymy of *A. grandiceps* was based, in part, on five observable different characters (1950, p. 862) quoted here:

1. Skull length $\frac{1}{3}$ to $\frac{1}{2}$ total length, compared to about $\frac{1}{4}$ total length in *Amphibamus*.
2. Skull width appreciably greater than skull length instead of about the same.
3. Tail longer.
4. Pineal foramen between orbits instead of behind them.
5. Possibly less-developed horn on tabular (or supratemporal).

However, Gregory noted that all these characters were susceptible to alternative explanations (ontogenetic change, artefacts of preservation), but also argued that *M. caudatum* showed no positive resemblances to *A. grandiceps* and could have been the larval form of almost any contemporary temnospondyl. Boy (1971, 1972) has subsequently demonstrated the distinct nature of the Branchiosauridae as a family of small neotenus dissorophoids and has commented (1974) that some of the Mazon Creek larvae resemble *Amphibamus*, taking ontogenetic changes into account, while others bear a closer resemblance to *Branchiosaurus sensu stricto*. My re-examination of all the material, including the previously undescribed specimen FMNH PR664 from Pit 11 (text-fig. 4), has led me to agree with Boy's conclusion. The following systematic re-assessment of the Francis Creek Shale larvae (i.e. from both Mazon Creek and Pit 11) is restricted to five potentially determinable specimens—namely FMNH UR38 (the type of *M. caudatum*), FMNH PR664, USNM 4400, YPM 802, and YPM 803 (the type of *Eumicrerpeton parvum*). I agree with Gregory's conclusion that the type and

only specimens of *Eriperpeton branchialis* (YPM 801), *Mazonerpeton costatum* (YPM 800), *Erpetobranchium mazonensis* (YPM 799), and *A. thoracatus* (USNM 4306) are all indeterminate.

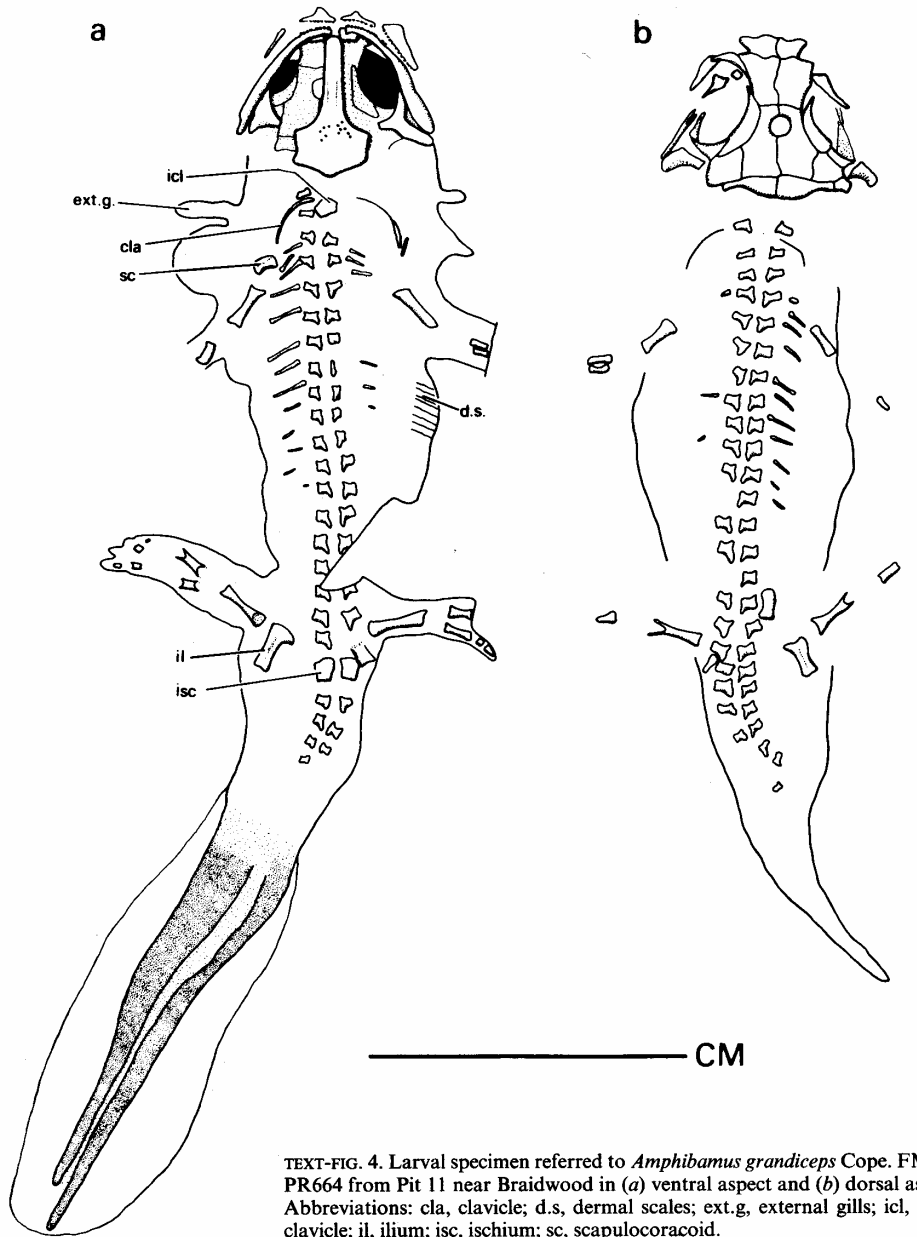
The five specimens studied are all certainly small temnospondyls and have the potential to be:

- (i) Larvae of *A. grandiceps* which occurs in the same assemblage.
- (ii) Small specimens of *B. sensu stricto* to which they bear a general resemblance and which occurs in the contemporary assemblage from Nýřany, Czechoslovakia. The earliest record of *Branchiosaurus* in North America is the only specimen of *B. darrahi* from the slightly younger Stephanian horizon at Montrose, near Pittsburgh, Pennsylvania.
- (iii) Larvae of some other temnospondyl, known or unknown.

The characters that Gregory used to differentiate the Mazon Creek larvae from *Amphibamus* are mostly, as he himself observed, known to change during ontogeny or be susceptible to other explanations. The apparently relatively greater skull length of *Amphibamus* (Gregory, characters 1 and 2) is partly attributable to a slight increase in relative skull length produced by the posterior movement of the dissorophid jaw suspensorium during ontogeny to give a deeper gape for terrestrial feeding while retaining a large otic notch. The skull: total length ratio is also in part an artefact (as is Gregory character 3) of the lack of a complete tail in any specimen of *A. grandiceps* which, as Gregory notes, effectively negates the characters of tail length and ratio of skull length to total length. If, as seems possible from the work of Watson (1940) and Bolt (1979), *Amphibamus* is the closest Carboniferous relative of the Anura, then the reduction of the size of the tail at metamorphosis is more to be expected in *Amphibamus* than in any other Carboniferous temnospondyl. The width to length ratio of the skull (character 2) is partly attributable to the different degree of post-mortem crushing in the large and small skulls. In the small skulls, the cheeks and mandibles are spread out to the side to a much greater extent than in the larger *Amphibamus* skulls. The pineal foramen position relative to the orbits (Gregory, character 4) most certainly does shift backwards during ontogeny within a temnospondyl species as demonstrated by Bystrow and Efremov (1940) in *Benthosuchus sushkini*. The 'tabular' shape (character 5) is, in fact, the supratemporal shape, the tabulars being detached in USNM 4400 but visible as tiny ossifications in FMNH UR38 and PR664. The tabulars, and possibly the underlying distal edge of the supratemporal, elongate anteroposteriorly with growth, providing support for the dorsal edge of the tympanum in those forms which have a large otic notch such as *Dendrerpeton* (Milner 1980a) and *A. lyelli* (Steen 1931, text-fig. 11). Thus Gregory's characters do not preclude the Mazon Creek larvae from being synonymous with *A. grandiceps* and can all be attributed to ontogenetic changes or to artefacts of preservation. Gregory noted that this was not enough to justify assigning them to *A. grandiceps* as many of the features of the larvae were equally consistent with their being juveniles of other temnospondyls and they showed no special resemblance to *A. grandiceps*. This observation was substantially influenced by Romer's (1939) view that 'branchiosaurs' all metamorphosed into larger temnospondyls and hence that all their characteristics were merely those of larvae. As Boy (1972) has demonstrated, *Branchiosaurus sensu stricto* is not a larval taxon and many of the characters of this genus have systematic validity.

In order to attempt the determination of the 'Mazon Creek larvae', ten of their observable characters were identified and the distribution of these characters, both primitive and derived, among other Palaeozoic temnospondyls, was examined. The ten characters together with their status and general distribution are as follows, the sequence of characters commencing with the widespread primitive features and leading to the more precisely defining derived characters.

1. Preorbital region is very abbreviated. Probably both a primitive and larval tetrapod character retained in branchiosaurids, dissorophids, most trimerorhachoids, *Dendrerpeton*, and small larvae of long-snouted temnospondyls.
2. Prefrontal-postfrontal contact. A primitive tetrapod character, widespread in early temnospondyls but most dissorophids and branchiosaurids share a derived condition in which the reduced prefrontal and postfrontal do not meet and the frontal enters the orbit margin. However, *Amphibamus* and some primitive species of *Branchiosaurus* retain the primitive condition.



TEXT-FIG. 4. Larval specimen referred to *Amphibamus grandiceps* Cope. FMNH PR664 from Pit 11 near Braidwood in (a) ventral aspect and (b) dorsal aspect. Abbreviations: cla, clavicle; d.s, dermal scales; ext.g, external gills; icl, interclavicle; il, ilium; isc, ischium; sc, scapulocoracoid.

3. Large interpterygoid vacuities, palatine rami of the pterygoids with concave mesial margins. A derived character within the temnospondyls, occurring in most temnospondyls, the Anura, the microsauro *Hyloplezion*, and the diplocauline nectrideans. Primitive temnospondyls such as the colosteids, loxommatoids, *Edops*, and *Caerorhachis* all possess small or no interpterygoid vacuities as do the ichthyostegids and choanate fish.
4. Intertemporals absent. A derived condition within the temnospondyls although widespread in post-Carboniferous forms. Intertemporals are retained in most Carboniferous temnospondyls, only the loxommatid *Megaloscephalus*, the colosteids *Colosteus* and *Erpetosaurus*, and the dissorophoids and eryopids lacking them.
5. Large otic notch extending as a shallow or deep concavity from tabular to quadrate and hence a relatively large structure occupying the entire posterior edge of the squamosal. This appears to be a derived condition characterizing *Dendrerpeton* and the Dissorophoidea (comprising the Dissorophidae, Trematopidae, Micromelerpetontidae, and Branchiosauridae). The primitive tetrapod and temnospondyl condition is either no notch or a small spiracular-type otic notch bordered by the tabular, supratemporal and part of the squamosal but not extending to the quadrate. The former condition occurs in colosteids, nectrideans, microsaurids, and captorhinomorphs, the latter condition occurs in ichthyostegids, loxommatids long-snouted edopoids, and eryopids. In *Dendrerpeton* and the dissorophoids, the enlargement of the notch and, by implication, the tympanum, to occupy most of the posterolateral region of the head, is a derived condition not occurring in other early tetrapods, except by obvious convergence in some seymouriamorphs.
6. Jugal terminating in a point anteriorly and failing to contact the lachrymal. The primitive tetrapod and temnospondyl condition is a broad sutural contact between lachrymal and jugal at the level of the anterior orbit margin. In the Dissorophoidea and many of the Trimerorhachoidea, the larger orbits are distally bordered by the maxillae and the lachrymal and jugal do not meet. In larger individuals with proportionately small orbits, the cheeks tend to be broader or deeper but instead of reversion to the primitive condition, the intervening 'gap' is filled by the palatine (Dissorophoidea and Saurerpetontidae, see Bolt 1974b) or the postorbital (Trimerorhachidae).
7. Relatively long slender humerus, lacking a supinator process. The primitive tetrapod humerus as found in ichthyostegids, anthracosaurs, and colosteids is a stout 'tetrahedral' structure and in most temnospondyls it is a short 'waisted' bone with expanded ends and a prominent supinator process. However, in dissorophids (DeMar 1968) and branchiosaurids (Boy 1972), the humerus is more than twice as long as its greatest width and lacks a supinator process. Other dissorophoids such as the trematopids retain a short humerus with supinator process (DeMar 1968).
8. Slender clavicles and a relatively small interclavicle which is wider than long and has no posteromedial stem. Within the temnospondyls, this is a derived condition restricted to *Branchiosaurus*, some dissorophids (including *Amphibamus*), and also *Eryops*. The majority of temnospondyls, including primitive forms such as *Greererpeton*, *Dendrerpeton*, *Cochleosaurus*, and the trimerorhachoids, possess large, rhomboidal, heavily ornamented interclavicles bordered by clavicles with large broadly triangular blades. In the derived state, the clavicle blades are narrow and the interclavicle is a small bone, poorly ossified or unossified in *Branchiosaurus* but always slightly wider than long.
9. Twenty to twenty-two vertebrae. Most temnospondyls have twenty-five or more presacral vertebrae and there is no evidence to suggest that the primitive tetrapod or primitive temnospondyl condition were characterized by less than twenty-five presacrals. A smaller number occurs in *Eryops* (twenty-three) and in several, but not all, dissorophoids including *Cacops aspidephorus*, *Amphibamus grandiceps*, and *Branchiosaurus* spp. (twenty to twenty-one) and appears to represent a derived condition in these forms.
10. Extremely abbreviated skull-table, the tabular-tabular width being almost twice the length from the posterior orbit margin to the tabular. Among the temnospondyls, this type of

abbreviated skull-table appears to occur in a few eryopoid (*Eryops*, *Zatrachys*) and dissorophoid (*Branchiosaurus*, *Amphibamus*, *Broiliellus*) genera, and thus appears to be a derived character of at least double origin. The skull-table is relatively conservative in shape during ontogenetic change and the larvae of most temnospondyls do not have such abbreviated skull-tables as *Amphibamus* or *Branchiosaurus* (e.g. *Saurerpeton* larva—this paper, *Micromelerpeton* and *Sclerocephalus* larvae—Boy 1972, fig. 69).

Of the above listed ten characters, FMNH PR664 shares 1–10; USNM 4400 shares 1–5 and 7–10; FMNH UR38 shares 1–4, 7, 9, and 10; YPM 803 shares 1–3, 5, 8, and 10; and YPM 802 shares 1, 3, 8, and 10. The only described temnospondyl genera which include species sharing all ten characters, particularly derived characters 7–10 combined with primitive character 2, are the primitive dissorophoids *Amphibamus* and *Branchiosaurus*. None of the Francis Creek Shale larvae have characters inconsistent with their being either *A. grandiceps* larvae or small *Branchiosaurus* and there is no reason to conclude that they are anything other than one of these two. My initial attempts to identify all of these larvae as belonging to one of these two genera failed with the realization that some shared further characters with *Amphibamus* while others of similar size shared characters with *Branchiosaurus*. I have finally concluded that three of the specimens are larvae of *Amphibamus* while the other two are probably specimens of *Branchiosaurus*. They are discussed separately in the following systematic section together with the reason for the generic assignments.

Family DISSOROPHIDAE Williston 1910
Genus AMPHIBAMUS Cope 1865
Amphibamus grandiceps Cope (attributed larvae)

Text-figs. 4, 5a–d, f, g, 6b

Selected synonymy. (Larvae only.)

- 1909 *Micrerpeton caudatum* Moodie, p. 39, figs. 1–6.
- 1916 *Micrerpeton caudatum* Moodie; Moodie, p. 52, pl. 2; pl. 52, fig. 4.
- 1916 *Eumicrerpeton parvum* Moodie; Moodie, p. 57 *partim!* non Moodie 1910, 1911.
- 1950 *Micrerpeton caudatum* Moodie; Gregory, p. 857, figs. 7, 9 *partim!*

Included material. FMNH UR38 (previously Walker Museum 12313) (text-fig. 5c, d). The type (in counterpart) of *M. caudatum* figured extensively by Moodie. Gregory's figure (1950, fig. 7) is difficult to relate to the original specimen. USNM 4400 (text-figs. 5f, g, 6b). Specimen in counterpart referred by Moodie (1916) to *E. parvum* and by Gregory (1950) to *M. caudatum*. FMNH PR664 (text-figs. 4, 5a, b). An undescribed specimen in counterpart.

Localities and horizon. FMNH UR38 and USNM 4400 are from Mazon Creek near Morris, Grundy Co., Illinois. FMNH PR664 is from Peabody Coal Company Pit 11 spoil heap, Will-Kankakee Counties, Illinois. Horizon as for previously described material.

Diagnostic characters. As described above, these three specimens share a suite of characters with *A. grandiceps*, several of these characters being relatively rare in Palaeozoic temnospondyls but which also occur in *Branchiosaurus*. Despite a general similarity to *Branchiosaurus* based on primitive and larval features, these three specimens each share characters with the larger *Amphibamus* specimens which distinguish them from *Branchiosaurus*. These are as follows:

- (i) Absence of hyobranchial ossifications. A negative and perhaps a weak character but the palates of all three specimens are clearly preserved (text-fig. 5b, d, g) and none of the specimens show signs of disintegration. The only dissorophid known to possess hyobranchial ossifications is *Micropholis stowi* from the Lower Triassic of the Karroo, none of the smaller Permian-Carboniferous dissorophids showing any trace of such structures. *Branchiosaurus* species possess hyobranchial ossifications which are usually visible in well-preserved specimens in palatal aspect.
- (ii) None of the three specimens possess visible internal carotid foramina on the basal plate of the parasphenoid. In *A. grandiceps* there are no clear foramina but distinct grooves on either side

of the base of the cultriform process (Watson 1940, fig. 4; this paper, text-fig. 3*b*). In *Branchiosaurus* the condition is variable but the foramina are usually prominent in small individuals comparable in size to the Mazon Creek larvae (Boy 1972, fig. 31*a*). In larger *Branchiosaurus* the foramina may be prominent holes or be replaced by deep grooves in the sides of the cultriform process (Boy 1972, figs. 31*b*, 32).

- (iii) In FMNH UR38 and PR664 the ventral surface of the basal plate of the parasphenoid bears a patch of denticles on its anterior half. Post-metamorphic *A. grandiceps* also possess a patch of denticles in this area whereas *Branchiosaurus* species either possess no parasphenoid denticles at all (Boy 1972) or possess a small patch at the posterior end of the cultriform process (*B. humbergensis*, Boy 1978).
- (iv) In FMNH PR664 and USNM 4400 the skull-tables can be seen to be extremely abbreviated antero-posteriorly and the supratemporals are about half the surface area of the parietals (text-fig. 5*a*, *f*). This corresponds to the condition in *Amphibamus*, particularly the ontogenetically younger specimen of *A. lyelli* (text-fig. 3*c*), more nearly than to the condition in *Branchiosaurus* (Boy 1972, fig. 24). FMNH UR38 appears similar in palatal aspect (text-fig. 5*d*) but in dorsal aspect, the supratemporals and parietals seem to be similar in surface area, giving the skull-table a more *Branchiosaurus*-like appearance (text-fig. 5*c*). This conflicts with the *Amphibamus*-like parasphenoid denticles and the longer quadrate ramus of the pterygoid (text-fig. 5*d*) and on balance I conclude that the specimen bears most resemblance to *Amphibamus* although it is less certainly assigned here than are the other two specimens.

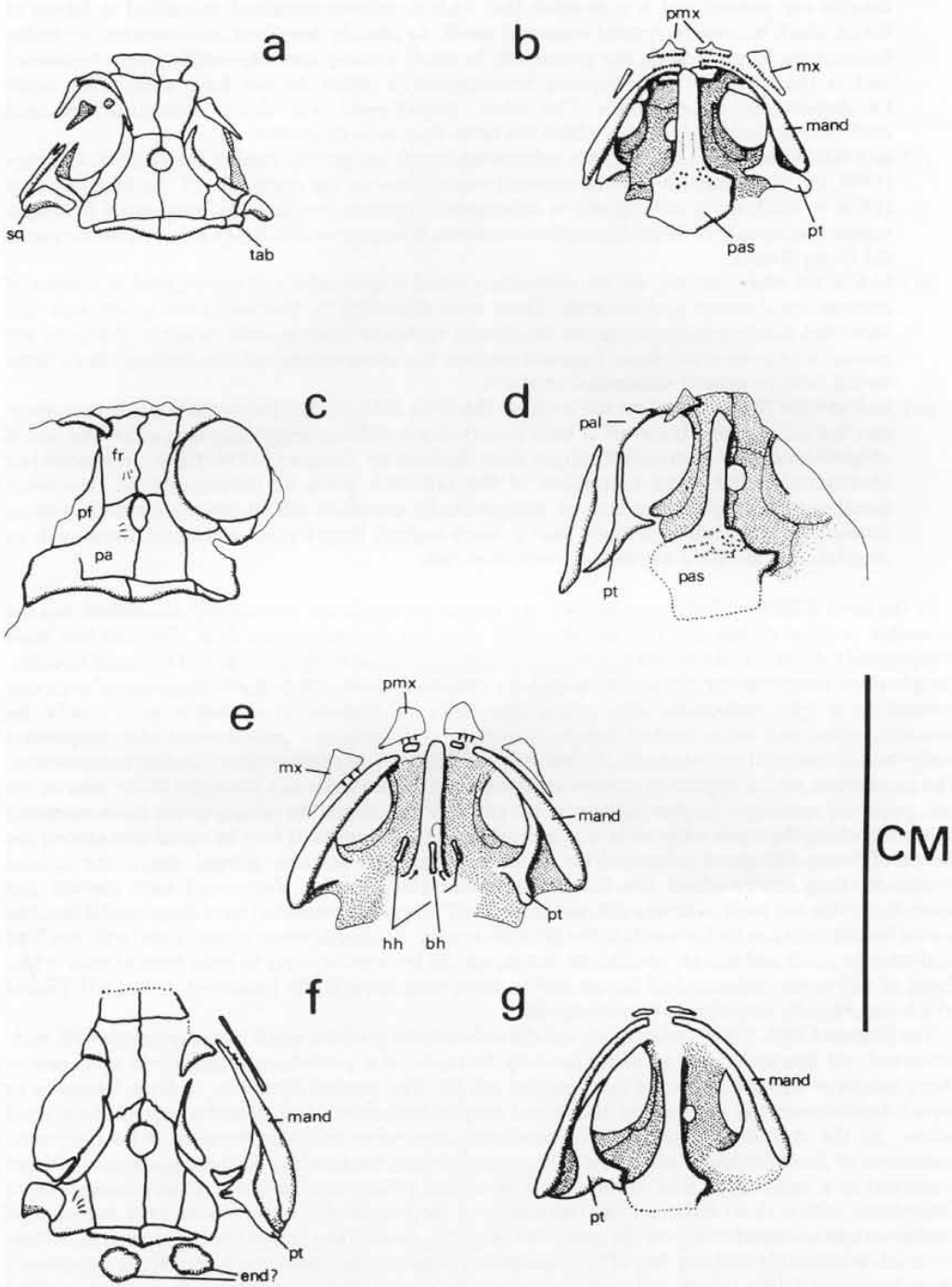
The above characters, which are all that the material permits, are all specific resemblances to *Amphibamus* rather than to *Branchiosaurus* and form the basis of this material being referred to *A. grandiceps*. I have not attempted to assess these character-states as being primitive or derived. As the attribution is to a slightly larger amphibian in the same assemblage, I believe the identification of typological similarities to be adequate.

Remarks. If these three specimens are accepted as aquatic larvae of *A. grandiceps*, they support Bolt's (1979, p. 549) conclusion that the previously recognized *A. grandiceps* specimens are post-metamorphic and that individuals underwent a relatively rapid metamorphosis between 7 and 14 mm mid-line skull length. During this metamorphosis the jaws elongated backwards, the suspensorium swinging back behind the level of the occiput with the result that the shallow larval otic notch grew into the deep semicircular otic notch characterizing post-metamorphic dissorophoids. The maxilla elongated posteriorly, as did the outer region of the squamosal. The vertebral centra presumably ossified at a slightly later stage, they are unossified in FMNH PR558 which has large notches in a skull about 12 mm long. The carpals and tarsals remain unossified in the larger *A. grandiceps*.

Among the characteristics of the *Amphibamus* larvae which have not been commented on so far, as they are not of immediate systematic significance, are the following:

- (i) In FMNH PR664, external gills are visible (text-fig. 4*a*) indicating that the premetamorphic stage of *Amphibamus* was indeed aquatic. At least two pairs of external gills were present but the condition of preservation only permits the main filament of each gill to be identified and it is not possible to determine whether the gills were pinnate or not. No ceratobranchial dental

TEXT-FIG. 5. Skulls of larval dissorophoids from the Francis Creek Shale. (*a*, *b*) *Amphibamus grandiceps* Cope. FMNH PR664, dorsal and ventral counterparts. (*c*, *d*) *A. grandiceps* Cope. FMNH UR38, dorsal and ventral counterparts. (*e*) ?*Branchiosaurus* sp. YPM 803, in ventral aspect showing basihyal and hypohyals. (*f*, *g*) *A. grandiceps* Cope. USNM 4400, dorsal and ventral counterparts. Abbreviations: bh, basihyal; end?, endolymphatic sacs?; fr, frontal; hh, hypohyal; mand, mandible; mx, maxilla; pa, parietal; pal, palatine; pas, parasphenoid; pf, postfrontal; pmx, premaxilla; pt, pterygoid; tab, tabular.

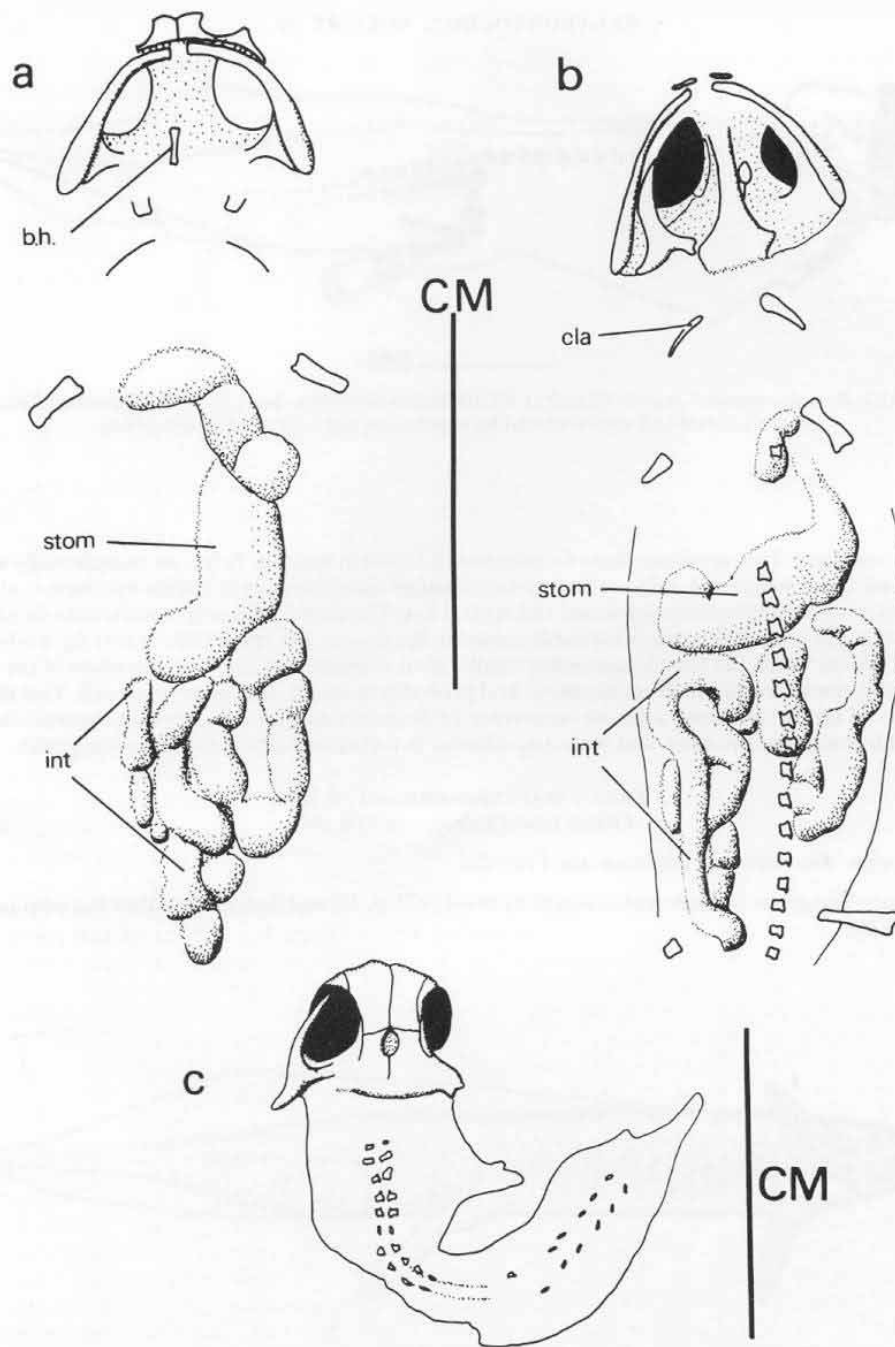


ossicles are present and it is possible that such structures remained unossified in larvae of forms which became terrestrial while still small. As already described, such ossicles, probably functioning as gill rakers, are prominent in small aquatic temnospondyls (*Branchiosaurus*) and in the larvae of large aquatic temnospondyls which do not have them when adult (*Archegosaurus*, *Saurerpeton*). The adult *Amphibamus* was clearly terrestrial and had undoubtedly lost any gill-slits which the larva may have possessed.

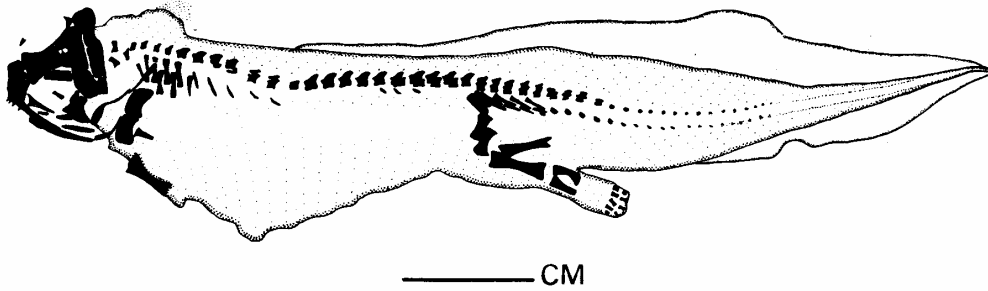
- (ii) In USNM 4400 (text-fig. 5f), two calcareous lumps are present behind the occiput. Gregory (1950, fig. 9) appears to have interpreted one of these as the occiput itself. As noted by Boy (1974, p. 261), these correspond to structures occurring frequently in very small *Branchiosaurus* and appear to be endolymphatic calcium storage glands such as occur in the larvae of the living Anura.
- (iii) In USNM 4400 (text-fig. 6b) the alimentary canal is unusually well represented as a series of casts of the stomach and intestine. These were described by Moodie (1916, p. 60) who also identified two impressions next to the cloacal region of the specimen as either glands or the posterior regions of oviducts. I cannot confirm this observation and it is unlikely that a larva would have possessed substantial oviducts.
- (iv) In FMNH UR38 most of the tail is visible (Moodie 1916, pl. 2). I have examined this specimen and the tail contains traces of at least twenty-five vertebrae, suggesting that either the tail of *Amphibamus* was substantially larger than depicted by Gregory (1950, fig. 6, 16 caudals) or alternatively, that some resorption of the tail took place at metamorphosis. No post-metamorphic *Amphibamus* has an unequivocally complete tail so the matter must remain unresolved although it is likely that a short-bodied, long-limbed terrestrial form such as *Amphibamus* did have a comparatively short tail.

In the larva FMNH PR664 (text-fig. 4a), the caudal vertebrae are presumably unossified, but the muscular portion of the tail can be identified as a heavily carbonized film. The tail has been compressed sideways and the two carbonized strips correspond to the epaxial and hypaxial muscles. Peripheral to the muscular portion of the tail is a smooth surface with a clearly demarcated edge and covered by a light carbonized film which represents the remains of a membranous caudal fin extending above and below the tail. Because the trunk of the specimen is dorso-ventrally compressed while the tail is laterally compressed, the tail must have been twisted through 90° during compression. The caudal fins, which appear to narrow anteriorly and to terminate just posterior to the base of the tail, probably extended further forwards, particularly the dorsal fin which could have extended anteriorly along the trunk without being detectable in this specimen. It may be noted that among the larvae of living European salamandrids which resemble this larva in general shape, the upland stream-dwelling larvae which live in running water (*Salamandra*, *Euproctus*) have slender fins restricted to the tail itself, whereas still-water larvae (*Triturus*, *Pleurodeles*) have deep caudal fins, the dorsal fin extending as far forwards as the pectoral region. As *Amphibamus* is associated with lowland coal-swamp pools and deltaic conditions, the larval tail fin is more likely to have been extensive like those of still-water salamandrid larvae and to have been imperfectly preserved in FMNH PR664 which superficially resembles a stream-dweller.

The Francis Creek Shale localities are not the only ones to produce small temnospondyls with well-preserved tail fins and mention might usefully be made of a previously undescribed specimen of *Branchiosaurus* which also shows an extensive tail fin. The general similarity of *Branchiosaurus* to larval *Amphibamus* has been noted above and may be indicative of relationship, as will be argued below. At the Autunian 'branchiosaur'-producing exposures at Oederheim in West Germany, specimens of *Branchiosaurus* are frequently preserved with the musculo-skeletal portion of the tail preserved as a carbonized film. Bulman and Whittard (1926) reconstructed *Branchiosaurus* from Oederheim with a short flattened tail two-thirds of the length of the trunk with only five ossified caudal vertebrae, based solely on the preserved musculo-skeletal portion of the tail as present in their material. Whittard (1930) and Boy (1972) had access to better specimens and were able to reconstruct *Branchiosaurus* with a longer tail terminating in a point and containing eleven to eighteen ossified



TEXT-FIG. 6. Entire specimens of larval dissorophoids from the Francis Creek Shale. (a) *?Branchiosaurus* sp. YPM 802. (b) *Amphibamus grandiceps* Cope. USNM 4400. (c) Indeterminate larval dissorophoid, USNM 4319. Abbreviations: b.h, basihyal; cla, clavicle; int, intestine; stom, stomach.



TEXT-FIG. 7. *Branchiosaurus* cf. *petrolei* (Gaudry). KC106 from Odernheim, Saarpfalz, West Germany. Specimen showing dorsal and ventral caudal fin membranes and terminal filament of tail.

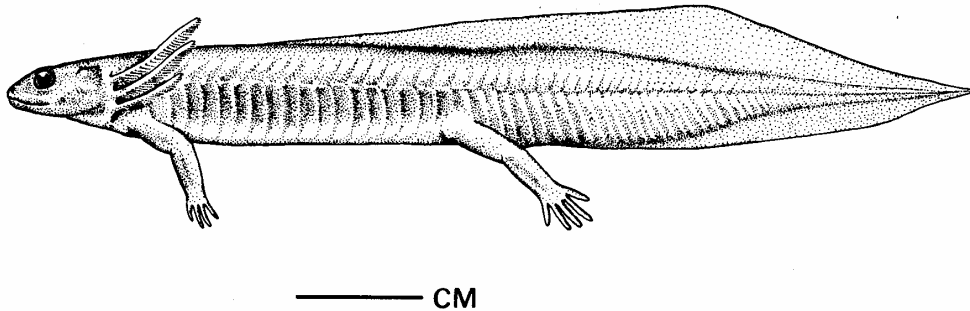
caudal vertebrae. One specimen from Odernheim (KC 106 in text-fig. 7) has an exceptionally well-preserved tail in which not only are twenty-four ossified caudal vertebrae visible but there is also a terminal filament and substantial dorsal and ventral fins. The dorsal fin is deep and extends along the back whilst the ventral fin extends forwards almost to the cloaca. The restoration in text-fig. 8 is based on KC 106 (in which the head is somewhat smaller than average) and gives an indication of the true shape and size of the tail in *Branchiosaurus* and probably in larval *Amphibamus* as well. This shape and size of tail is consistent with the occurrence of *Branchiosaurus* in shallow lake deposits in the Saarpfalz intermontane basin and with *Amphibamus* in deltaic and coal-swamp pool deposits.

Family BRANCHIOSAURIDAE Frič 1883

Genus BRANCHIOSAURUS Frič 1876

Type species. *Branchiosaurus salamandroides* Frič 1876.

Diagnosis. The genus is diagnosed at length by Boy (1972, p. 39) and further described in a later paper (Boy 1978).



TEXT-FIG. 8. Restoration of *Branchiosaurus* based on specimen KC106.

?Branchiosaurus sp. indet.

Text-figs. 5e and 6a

Selected synonymy

- 1910 *Eumicrerpeton parvum* Moodie; p. 367, figs. 1–4.
 1911 *Eumicrerpeton parvum* Moodie; p. 427, fig. 1.
 1916 *Eumicrerpeton parvum* Moodie; p. 57, fig. 15b, c, pl. 3, figs. 1, 2.
 1950 *Micrerpeton caudatum* Moodie; Gregory p. 857, fig. 8 *partim! non Moodie.*

Material. YPM 803 (text-fig. 5e). The type of Moodie's *E. parvum*, included by Gregory in *M. caudatum*. YPM 802 (text-fig. 6a). Referred to *E. parvum* by Moodie and to *M. caudatum* by Gregory.

Locality and horizon. Mazon Creek. Details as for *A. grandiceps*.

Remarks. These two specimens were first described by Moodie as a new species of branchiosaurid *E. parvum* and later reduced in synonymy with *M. caudatum* Moodie by Gregory (1950). Both specimens are small and poorly preserved but, as noted by Boy (1974, p. 261), both possess characters which suggest that their affinities lie with *Branchiosaurus* rather than with the *Amphibamus* material described above. These characters are:

- (i) Possession of an ossified basihyal (YPM 803, 802) and ossified hypohyals (YPM 803).
- (ii) Presence of prominent internal carotid foramina on the basal plate of the parasphenoid (YPM 803).
- (iii) Absence of denticles on the ventral surface of the parasphenoid (YPM 803). I cannot confirm Gregory's observation of a patch of denticles on this specimen.

As described previously, the small specimens attributed to *A. grandiceps* do not possess hyobranchial ossifications or visible internal carotid foramina but do possess a denticle field across the anterior region of the base of the parasphenoid. Some of these specimens (FMNH PR664) are just as small as YPM 803 and 802, suggesting that these are size independent characters rather than ontogenetic differences. The attribution of YPM 803 and 802 to *Branchiosaurus* is necessarily tentative because of their poor preservation, but in such features as can be observed they correspond to *Branchiosaurus*. A possibility that cannot be excluded is that all the 'Mazon Creek larvae' belong to *Amphibamus* and that some are large premetamorphic aquatic larvae while others are small metamorphosing individuals which have acquired some *Amphibamus* palatal characters while still retaining gills (FMNH PR664). In this instance I think that this is less economical than referring the larvae to two taxa as they are typologically different at the same body size. Ultimately, collection of a larger sample of larvae would permit us to establish if more than one growth series is present, as Boy (1972) was able to do with the Oderenheim assemblage of 'branchiosaurs'.

Although more precise determination is not possible, two further observations can be made. YPM 803 shows a prefrontal-postfrontal suture excluding the frontal from the orbit margin (text-fig. 5e) and also ossified ventral dermal scales, both of which are primitive characters within the genus *Branchiosaurus*. The prefrontal-postfrontal contact characterizes *B. salamandroides* Frič from the Westphalian D of Nýřany and Třemošná, *B. fayoli* Thevenin from the Stephanian of Commentry, and *B. dracyi* Boy (attributed to Milner) from the basal Autunian of Dracy St. Loup. Ossified dermal scales occur in small specimens, only in *B. salamandroides* and *B. fayoli*. The Mazon Creek material is thus comparable to *B. salamandroides* and *B. fayoli* in these features, but can neither be diagnosed as referable to any of the European species nor can it be separately diagnosed to justify the specific name *parvus*. Hence the material is simply identified as *?Branchiosaurus* sp. indet.

Indeterminate dissorophoid larvae.

With so few characters distinguishing *Branchiosaurus* from *Amphibamus* larvae, it is inevitable that some of the smaller Francis Creek Shale larvae will be indeterminate. Two such are USNM 4319 (text-fig. 6c), described by Gregory (1950, p. 860) but not previously illustrated, and USNM 4432. USNM 4319 is undoubtedly referable to one of the above-described taxa but is not critically diagnostic.

ON THE RELATIONSHIP OF THE BRANCHIOSAURIDAE TO THE
DISSOROPHIDAE

In recent years the families Branchiosauridae and Dissorophidae have been much studied, the former by Boy (1971, 1972, 1974, 1978) and the latter by Carroll (1964), DeMar (1966, 1968), and Bolt (1974a, b, 1977, 1979) and both families are now recognized as representing major radiations of small temnospondyls during the Permo-Carboniferous. The difficulties encountered during this study in differentiating larval *Amphibamus* from *Branchiosaurus*, even using derived characters, leads to the conclusion that branchiosaurids are more closely related to dissorophids than to any other family of temnospondyls and may even be more closely related to some dissorophids than to others. Boy (1978) has argued, I believe correctly, that branchiosaurids were either facultatively or permanently neotenuous relatives of small terrestrial temnospondyls, exploiting plankton-feeding niches in the Autunian intermontane lakes. That their closest terrestrial relatives were the dissorophids is suggested by the following shared derived characters, some of which have already been itemized in the discussion of the identity of the 'Mazon Creek' larvae.

1. Centre of ossification of the jugal behind the level of the posterior edge of the orbit, with the jugal narrowing to a point anteriorly and never reaching the lachrymal. A dissorophoid character shared by the families Trematopidae, Micromelerpetontidae, Dissorophidae, and Branchiosauridae.
2. Extreme abbreviation of the skull-table, the distance from the posterior edge of the orbit to the tabular being about half the tabular-tabular width. Within the Dissorophidae this character is restricted to the Branchiosauridae and the dissorophid genera *Amphibamus*, *Tersomius*, and *Doleserpeton*.
3. Reduction of the ectopterygoid. In most dissorophids the ectopterygoid is a tiny bone bearing a 'tusk-pair', in branchiosaurids and *A. grandiceps* it is a slip of bone bearing a few small teeth and in *Doleserpeton* it appears to be absent.
4. Vomers bearing clumps or rows of teeth as well as or instead of 'tusks'. This also characterizes branchiosaurids, *Amphibamus*, *Tersomius*, and *Doleserpeton*.
5. Large otic notch, either deep or shallow, extending from the tabular to the quadrate, giving the squamosal an entirely concave posterior margin. A dissorophoid character occurring in all the dissorophoid families, although a more derived slit-like notch occurs in large, presumably adult, trematopids.
6. Pedicellate teeth? Pedicellate teeth are certainly present in several genera of dissorophid (Bolt 1977, 1979) and Boy has recently (1978) described structures resembling fused pedicels on the dentary of a large *Branchiosaurus*.
7. Presacral vertebral column reduced to twenty to twenty-one vertebrae. This is the normal condition in *Branchiosaurus* and occurs in some dissorophid genera (*Amphibamus*, *Cacops*).
8. Clavicles with narrow ventral blades and interclavicle reduced to a small rhomboidal plate usually smaller than one clavicle blade. Ossification of the interclavicle may be delayed in *Branchiosaurus*. This type of pectoral girdle occurs in dissorophids, branchiosaurids, and probably in trematopids but not in micromelerpetontids.
9. Long slender humerus with no supinator process. Occurs only in dissorophids and branchiosaurids.
10. Ribs reduced to very short straight structures. In small dissorophids such as *Amphibamus* and in branchiosaurids the ribs are much shorter than in any other small temnospondyl.
11. Although not strictly a shared derived character, it may be noted that in the Carboniferous *Branchiosaurus* species and in the Carboniferous dissorophid *Amphibamus* there is a prefrontal-postfrontal contact excluding the frontal from the orbit margin, whereas in the Permian *Branchiosaurus* and the Permian dissorophids the pre- and postfrontals are reduced and the frontal enters the orbit margin.

Characters 7-9 represent a functional complex of shorter trunk, longer limbs, and a pectoral girdle

with reduction of the ventral dermal components. This is a complex that one might expect to find in small terrestrial amphibians such as the dissorophids but it also occurs in the manifestly aquatic *Branchiosaurus* and is one of the principal lines of evidence that has led Boy (1978) to deduce that *Branchiosaurus* is a neotenuous relative of a terrestrial form. Because *Branchiosaurus* is clearly an aquatic form and smaller than most dissorophoids, those characteristics of the dissorophoids which are associated with large size and terrestriality need not be expected in a form in which metamorphosis does not appear to have occurred. Thus *Branchiosaurus* lacks the dorsal process on the quadrate, the posteromedial process on the quadratojugal and the lateral exposure of the palatine, all of which characterize the superfamily Dissorophoidea as originally conceived by Bolt (1969). The former two structures are probably intimately involved in the formation and support of a frog-like tympanum and need not be expected in an aquatic paedomorphic form in which the ontogenetic changes associated with terrestriality had been suppressed. The lateral exposure of the palatine likewise need not be expected in a tiny individual with very large orbits, this structure developing only as an 'infilling' of the cheek in larger skulls with relatively smaller orbits. The absence of such characters does not necessarily negate an immediate relationship between the branchiosaurids and the dissorophids. This is not to suggest that the Branchiosauridae and Dissorophidae are sister groups but rather that the Branchiosauridae represents a subgroup within the Dissorophidae as presently conceived, or in cladistic terms that the Dissorophidae is paraphyletic with respect to the Branchiosauridae. However, it is premature to suggest any change in classification at our present state of knowledge, for two reasons.

1. The Dissorophidae is widely agreed to be the group of Palaeozoic temnospondyls from which the Anura (and more controversially, the Urodela) evolved, and as such is almost certainly paraphyletic with respect to the Anura. In a strict cladistic classification, the Dissorophidae would be considered as a grade and fragmented into subgroups ranked according to their similarity to the Anura as manifested by derived skeletal characters. The Dissorophidae, as currently conceived, is made up of two major subfamilies of armoured forms, the Aspidosaurinae and the Dissorophinae which are not necessarily immediately related (DeMar 1966), plus several non-armoured forms of uncertain relationship. Bolt (1974a, 1977) has noted several of the potential ontogenetic complexities in systematizing these forms. Until we understand more fully the relationships of the dissorophids to one another and to the Anura, there is little purpose in attempting to determine the precise relationships of the Branchiosauridae.

2. The Branchiosauridae may be polyphyletic with respect to the Dissorophidae and may represent more than one lineage of paedomorphic forms. In both families the Carboniferous representatives retain a prefrontal-postfrontal contact while the Permian forms have the frontal entering the orbit margin. This may be convergence or coincidence or it may indicate that the Carboniferous *Branchiosaurus* is a neotenuous relative of *Amphibamus* while the Permian *Branchiosaurus* is more closely related to the Permian dissorophids. Likewise, *Branchiosaurus humbergensis* Boy 1978, which is unusual in combining retention of parasphenoid denticles (otherwise unknown in *Branchiosaurus*) with an advanced skull construction, may represent a third *Branchiosaurus* lineage. In other words, it remains possible that the shared derived characters of *Branchiosaurus* are unrecognized larval dissorophid characters rendered more conspicuous in two or three independent lineages of large neotenuous individuals. Alternatively the Branchiosauridae may prove to be a valid clade of neotenuous dissorophids.

In conclusion, the Branchiosauridae is here suggested to consist of one or more lineages of paedomorphic dissorophids and hence to be more closely related to the Dissorophidae than to any other family of Palaeozoic temnospondyls.

THE FRANCIS CREEK SHALE TETRAPOD ASSEMBLAGE

Several recent discoveries and systematic reassessments of the tetrapods from the Francis Creek Shale permit a revised tetrapod faunal list to be compiled, updating that of Gregory (1950) and complementing the recent review of the Mazon Creek fish fauna provided by Bardack (1979). Further

Francis Creek Shale tetrapods are still known only from single specimens in private collections and are currently unpublished. The following listing refers only to published material in the collections of recognized institutions. It is also restricted to specimens which are determinate at some level.

Order TEMNOSPONDYLI

Dissorophidae: *Amphibamus grandiceps*—six 'adults', three larvae.

Branchiosauridae: ?*Branchiosaurus* sp. indet.—two specimens.

Saurerpetontidae: *Saurerpeton* cf. *obtusum*—one specimen.

This material has been listed and described in the systematic section of this paper.

Order BATRACHOSAURIA

Embolomeri *incertae sedis*: *Spondylrpeton spinatum*—one specimen.

A single specimen (YPM 793) consisting of two caudal vertebrae of a large embolomerous anthracosaur. This is the only large tetrapod fragment represented in the Francis Creek Shale assemblage. Panchen (1970) noted that the material is indeterminate at a generic level and that the binomen is a *nomen vanum* (more precisely a *nomen dubium*). Panchen initially assigned the specimen to the Archeriidae solely on the criterion of size but as the larger eogyrinid anthracosaurs had to pass through the archeriid size range during growth, this was hardly a valid taxonomic character used in isolation and Panchen later (1977) noted that it could equally belong to a leptophractine eogyrinid. The specimen appears to be indeterminate at family level and is here assigned to the Infraorder Embolomeri only.

Order AIȘTOPODA

Phlegethontiidae: *Aornerpeton mazonensis*—five specimens.

First described as *Phlegethontia mazonensis* by Gregory (1948). Subsequently, further specimens were described by Turnbull and Turnbull (1955), McGinnis (1967), and Lund (1978), the latter author raising the Francis Creek Shale material to separate generic status. The reported specimens are USNM 17079, MCZ 2204, FMNH PR291, FMNH PR400, and FMNH MCP501. A further specimen reported by Gregory (1950 p. 867) was reidentified as a lysorophid by Baird (1964)—see below.

Order NECTRIDEA

Urocordylidae: *Ptyonius marshii*—one specimen.

A single specimen (USNM 18125) first described by Gregory (1950, p. 866, fig. 10) as *Sauropleura* sp. but reidentified by Bossy (1976).

Order LYSOROPHIA

Lysorophidae: *Cocytinus* sp.—one specimen.

A single specimen (USNM 4313) first described by Gregory (1950, p. 867) as a specimen of *Phlegethontia* but reidentified by Baird (1964, p. 14, note 7) as *Cocytinus*.

Order MICROSAURIA

Family *incertae sedis*: unnamed specimen.

The only specimen (FMNH PR981) first described by Carroll and Gaskill (1978, p. 134). In their monograph, Carroll and Gaskill cautiously refer this specimen to the Hyloplesiontidae but note that because of poor preservation of the skull and manus, there is nothing to preclude assignment of this specimen to the tuditanomorph microsauro families Tuditanidae or Hapsidopareiontidae. The specimen, though of inherent interest, is thus strictly indeterminate at family level and I am treating it as such.

Order CAPTORHINOMORPHA

Family Protorothyrididae: *Cephalerpeton ventriarmatum*—one specimen.

The only specimen (YPM 796) was recently redescribed by Carroll and Baird (1972). It is probably a juvenile animal.

The above-listed material makes up a small sample of twenty-two specimens, an insignificant number in relation to the thousands of non-tetrapod specimens collected from the Francis Creek Shale concretions. The tetrapods are clearly transported erratics which do not relate directly to the environment of preservation but which may provide some information about the neighbouring terrestrial and freshwater environments. With the identification of further specimens, the Francis Creek tetrapod assemblage bears an increasing resemblance to the contemporary tetrapod assemblage from Linton, Ohio, but is not simply a smaller sample of an identical assemblage as at least two filters appear to have operated. One such filter apparently controlled the size of the preserved, or at least the collected material, as only one Francis Creek Shale tetrapod fossil is a fragment of a large animal. The others are all remains of animals less than 20 cm long. Richardson and Johnson (1971, p. 1230) note that the larger fish are also known only from fragments, some of which are from associated skeletons and they suggest that the larger vertebrates were buried intact and that complex nodules formed around them which broke up on re-exposure. However, the scarcity of described fragments of large tetrapods suggests that they may have been rarely preserved in the Francis Creek Shale, either because of the effects of current sorting of corpses or because the deltaic system was predominantly inhabited by small tetrapods. The second filter has operated in such a way that, although the range of tetrapod taxa resembles a small sample of the contemporary assemblage from Linton, Ohio, at least at the family level, the relative numbers of the different forms are quite distinct. This is not an observation on which great weight can be put because of the small size of the sample and the certainty that it is made up of erratics. Nevertheless, the relative numbers of tetrapod types present suggest that the Francis Creek Shale tetrapod assemblage is not just a small sample of a typical coal-swamp pool assemblage such as those from Linton or Nýřany. In a recent reassessment of the contemporary Nýřany assemblage (Milner 1980b), I interpreted that large assemblage of tetrapods from a small lake in a swamp-forest as comprising three different tetrapod associations. These were: an open water-lacustrine association characterized by eogyrinids and loxommatids; a terrestrial-marginal association characterized by many families including dissorophids, phlegethon-tiids, gymnarthrid, tuditanid and hapsidopareiontid microsaur, and protorothyridid (romeriid) reptiles; and, thirdly, a swamp pool association characterized by ophiderpetontids, urocordylids, and the larvae of temnospondyls and microsaur. Using the same family-to-association assignments as for the Nýřany and, by analogy, the Linton faunas, the Francis Creek Shale assemblage appears to contain:

One open water-lacustrine specimen—the embolomere *Spondylorpeton*.

Twelve terrestrial-marginal specimens—the adult *Amphibamus*, *Aornerpeton*, *Cephalerpeton*, and the microsauro.

Eight swamp pool specimens—the larval *Amphibamus*, *Branchiosaurus*, *Saurerpeton*, and specimens of *Ptyonius* and *Cocytinus*.

These relative numbers suggest that the Francis Creek Shale tetrapods derive as significantly from a terrestrial association as from a swamp pool association, unlike the Nýřany tetrapods, over 75% of which appear to derive from the swamp pool in which they were preserved. The conclusion that slightly over half of the Francis Creek Shale tetrapods, although erratics, were probably terrestrial, corroborates the observation of Johnson and Richardson (1966, p. 627) that the Braidwood fauna contained 85% terrestrial species, 11% fresh- or brackish-water species, and 4% marine species. These high representations of terrestrial forms are consistent with the interpretation that the Francis Creek Shale assemblages are the product of an active deltaic system subject to occasional channel diversions and river floods (Shabica 1979). Of the known tetrapods, the embolomere, as a probable open-water form, may have lived in the delta river itself. The small terrestrial- and pool-dwelling forms were

probably inhabitants of the deltaic lobes and were flushed into the sea along with considerable quantities of mud, either by a storm-surge (Richardson and Johnson 1971) or more probably by a river flood (G. C. Baird 1979). The limited diversity of inferred terrestrial forms (*Amphibamus*, *Aornerpeton*, and *Cephalerpeton*) may represent a small association of specialized forms adapted to life on the levees of the delta fan lobes, while the pool-dwellers and larvae inhabited freshwater pools in the delta.

No observations of geographical significance appear to be possible, except that the closest resemblance of the assemblage is to that from Linton, Ohio. Except for the Branchiosauridae, all the tetrapod families recorded from the Francis Creek Shale occur at Linton, whereas the Saurerpetontidae, Lysorophidae, and *Ptyonius* do not occur in the Nýřany assemblage. Only *Branchiosaurus* is a specific similarity to the Nýřany assemblage, but although this genus is unrecorded from Linton, it is described from the Stephanian of the Tristate area (Romer 1939). Thus the Francis Creek Shale tetrapod assemblage is geographically entirely consistent with other contemporaneous coal-swamp tetrapod assemblages from North America.

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