

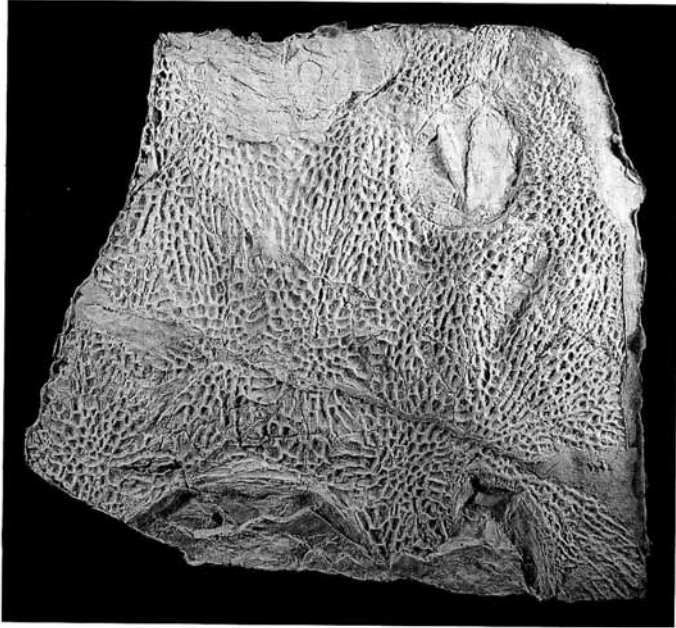
THE TEMNOSPONDYL AMPHIBIAN *CAPETUS* FROM THE UPPER CARBONIFEROUS OF THE CZECH REPUBLIC

by SANDRA E. K. SEQUEIRA and ANDREW R. MILNER

ABSTRACT. The Carboniferous temnospondyl amphibian *Capetus palustris* is reassessed on the basis of new and previously described specimens from the Gaskohle of Nýřany, Czech Republic. *Capetus* has frequently been synonymized with *Gaudrya*, also from Nýřany, but the holotype of *Gaudrya* is a fragment of a large specimen of *Cochleosaurus*. The phylogenetic position of *Capetus* within the primitive temnospondyls is uncertain and there is no support for a cladistic relationship to the typical long-snouted edopoids. Although a numerically rare element in the Nýřany assemblage, *Capetus* was one of the largest tetrapods present and was probably a major component of the tetrapod biomass in the Nýřany fauna.

ONE of the richest sources of Upper Carboniferous amphibians has been the Gaskohle from the Humboldt mine and other mines at Nýřany near Plzeň in the Czech Republic. Fossil vertebrates were collected from the Gaskohle from 1870 onwards and at least 700 amphibian specimens have been recorded from museums in Europe (Milner 1987). Taxonomic revisions of this fauna have reduced an initially large number of forms to about 25 monospecific genera, but some are still poorly known or poorly understood because of the fragmentary nature of most large specimens and the consequent difficulty of association. One such problematical series of specimens in the Nýřany assemblage is that of the large, superficially crocodile-like temnospondyl amphibians corresponding to the edopoid grade of organization. One form, *Cochleosaurus bohemicus* Fritsch, 1885, is usually readily recognizable from even fragmentary cranial material and its identity and characteristics present few difficulties. The remaining non-*Cochleosaurus* material consists of disparate large skull fragments of uncertain systematic position and this material is reviewed in the following account.

In his original series of papers on the Permo-Carboniferous vertebrates of Bohemia (now part of the Czech Republic), Fritsch (1885, 1901) described relatively few fragments of large temnospondyls, and most of these were clearly referable to *Cochleosaurus bohemicus*. A few specimens were placed in a second taxon *Nyrania trachystoma*, and one large anterior palatal fragment was made the holotype of a third form *Gaudrya latistoma*. In the first half of the twentieth century, several large temnospondyl skulls from Nýřany were described, all of which were clearly not *Cochleosaurus*. Broili (1908) described and figured three Nýřany skulls (housed at Munich) referring them to *Sclerocephalus credneri* which Fritsch (1901) had created for a specimen from the Permian of Ruprechtice, Bohemia. Jaekel (1911, 1913) figured a reconstruction of a temnospondyl skull roof based on a single specimen in the collection of Nýřany amphibians at the Museum für Naturkunde in Berlin, but did not describe or figure the original fossil. He referred this specimen to *Chelydosaurus vranýi*, a taxon established by Fritsch (1885) for material from the Permian of Olivětín and Ruprechtice in the Czech Republic. Steen (1938) described a further Nýřany skull fragment at the British Museum (Natural History) as the new taxon *Capetus palustris*. She noted that the largest of Broili's three specimens was probably the same form, whilst one of the others was a loxommatid. In their discussion of the relationships of *Edops craigi* from the Lower Permian of Texas, Romer and Witter (1942) suggested that *Capetus* was a close relative of *Edops* and comprised not only Steen's holotype but also Broili's largest specimen and Jaekel's specimen. In his

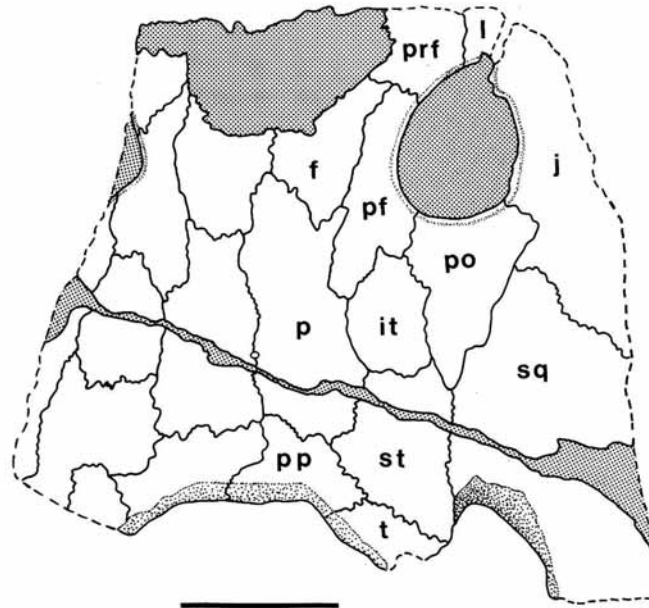


TEXT-FIG. 1. *Capetus palustris* Steen, 1938. BMNH R4706, latex cast of holotype specimen $\times 0.66$. For interpretation, see Text-figure 2.

comprehensive revision of the 'labyrinthodont' amphibians, Romer (1947) 'lumped' together all the large temnospondyl material from Nýřany which was not obviously assignable to *Cochleosaurus*. This was again based on the specimens described by Broili, Jaekel and Steen but also included the holotype palatal fragment of Fritsch's *Gaudrya latistoma* and some of the material that Fritsch referred to *Nyrانيا trachystoma*. The senior name for this combination of specimens thus became *Gaudrya latistoma* and his binomen was used for the large non-*Cochleosaurus* temnospondyl material from Nýřany by Romer (1947) and later authors, e.g. Langston (1953) and Milner (1980b). Romer (1966, 1968) briefly synonymized *Capetus* with a contemporary genus *Macrerpeton* from Linton, Ohio, USA, but this synonymy was never explained or justified in print, and the two genera are, in fact, distinct.

The discovery of an undescribed, largely complete skull of this type in Vienna in 1983, and its subsequent preparation, has permitted the authors to associate most of the non-*Cochleosaurus* specimens with greater confidence and also to reassign other specimens back to *Cochleosaurus*. As a result of this revision, briefly reported by Milner and Sequeira (in press), the senior name for this material reverts to *Capetus palustris*. In the following work this taxon is redescribed and its relationships are reconsidered.

Location of specimens. BMNH: Department of Palaeontology, Natural History Museum, London, UK. BSP: Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich, Germany. MB: Museum für Naturkunde, Humboldt Universität, Berlin, Germany. NMW: Naturhistorisches Museum, Vienna, Austria. UMZC: University Museum of Zoology, Cambridge, UK.



TEXT-FIG. 2. *Capetus palustris* Steen, 1938. BMNH R4706, holotype. Abbreviations: a, angular; bo, basioccipital; ch, choana; cor, coronoid; d, dentary; ect, ectopterygoid; eo, exoccipital; f, frontal; icl, interclavicle; it, intertemporal; j, jugal; l, lacrimal; m, maxillary; n, nasal; p, parietal; pal, palatine; pas, parasphenoid; pf, postfrontal; pmx, premaxillary; po, postorbital; pp, postparietal; pra, prearticular; prf, prefrontal; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; sc, sphenethmoid; smx, septomaxillary; spl, splenial; spp, postsplenial; sq, squamosal; st, supratemporal; t, tabular; v, vomer. Scale bar = 50 mm.

SYSTEMATIC PALAEOLOGY

Class AMPHIBIA
 Order TEMNOSPONDYLI Zittel, 1888
 Family *incertae sedis*
 Genus CAPETUS Steen, 1938

Type species. *Capetus palustris* Steen, 1938.

Diagnosis. As for the type (and only) species.

Capetus palustris Steen, 1938

Plates 1–3; Text-figs 1–10

- 1908 *Sclerocephalus credneri* Fritsch; Broili [*partim*] p. 55, pl. 1 figs 1, 3 [*non* Fritsch 1901].
- non* 1908 *Sclerocephalus credneri* Fritsch; Broili, pl. 1 fig. 2.
- 1911 *Chelydosaurus vranyi* Fritsch; Jaekel, fig. 124 [*non* Fritsch 1885].
- 1913 *Chelydosaurus vranyi* Fritsch; Jaekel, fig. 5 [*non* Fritsch 1885].
- 1938 *Capetus palustris* Steen, p. 241, text-fig. 27.

- 1947 *Gaudrya latistoma* Fritsch; Romer, p. 104, fig. 20 [non Fritsch 1885].
 1953 *Gaudrya* Fritsch; Langston, p. 374 [non Fritsch 1885].
 1980b *Gaudrya latistoma* Fritsch; Milner, p. 453 [non Fritsch 1885].
 1987 *Gaudrya* Fritsch; Milner, p. 506 [non Fritsch 1885].
 1987 'Unnamed stem-eryopoid'; Milner, p. 506.

Holotype. BMNH R4706, acid-etched mould of a skull table and cheek, in coal, figured by Steen (1938, text-fig. 27; Text-figs 1–3).

Diagnosis. A primitive temnospondyl with a mixture of unique, derived and primitive characters which does not readily permit it to be placed in a pre-existing family. The only possibly unique character is: pterygoid–vomere sutures extending anterolaterally from the midline to the choanae at about 45°. Derived characters shared with higher temnospondyls are: premaxillary antero-posteriorly abbreviated with prominent alary process running mesial to large external naris (shared with most Palaeozoic temnospondyls other than *Edops*, *Cochleosaurus*, *Chenoprosopus* and *Dendrerpeton*); jugal extending broadly anteriorly to level of anterior orbit margin (shared with edopoid and 'eryopoid'-grade temnospondyls). Retained primitive characters include: lacrimal entering orbit margin in large specimens; intertemporals present; elongate postorbital; pineal foramen retained in large specimens; postparietal lappets absent; maxillary contacting quadrato-jugal; vomers not elongate at level of choanae; interpterygoid vacuities narrow and terminating anteriorly as points; pterygoids broadly suturing with vomers and probably excluding vomers from margin of interpterygoid vacuity; large rhomboidal interclavicle.

Locality and horizon. Nýřany, 13 km southwest of Plzeň, Czech Republic. Gaskohle, Nýřany Series of the Plzeň Basin, Westphalian D, Upper Carboniferous.

Referred Material

BSP. A partial skull and a fragment of snout tip, figured by Broili (1908 pl. 1, figs 1, 3). These two specimens were probably destroyed in 1944. It is now uncertain whether they represented part of a single skull.

MB Am.84. Acid-etched mould of a skull roof, mandible and interclavicle – the reconstructed skull roof figured by Jaekel (1911, 1913) and Romer (1947) (Pl. 1, fig. 1; Text-fig. 4).

MB Am.92. Bitumen cast of a skull table and cheek. Location of original specimen unknown. Previously undescribed (Text-fig. 5).

NMW 1893.32.53. Incomplete skull table and left cheek in counterpart and NMW 1895.2366, fragments of a large snout and left mandible, all previously undescribed. These are unprepared fragments attributable to *Capetus* and, despite the two catalogue numbers, represent a single specimen. Part of mandible figured here (Text-fig. 8B).

NMW 1898.X.51. Mould of a large skull and mandibles in counterpart with some original palate material remaining. Acid etched by S.E.K. Sequeira in 1989. Previously undescribed (Pls 2–3; Text-figs 6–7, 8C).

UMZC T.144. Previously part of the D.M.S. Watson collection as DMSW B.77. Acid-etched mould of outer face of posterior right mandible and associated cheek. Previously undescribed (Pl. 1, fig. 2; Text-fig. 8A).

Description and comparisons

General cranial features. The skull of *Capetus* is superficially alligator-like in shape. The most complete specimens (MB Am.84 and NMW 1898.X.51) possess a moderately elongate snout accounting for about 59 per cent of the total skull length. The skull broadens posteriorly to reach its maximum width at the level of the anterior edge of the prominent otic notches. These demarcate the posterolateral edges of the skull table, which is slightly wider than long, and which possesses a markedly concave posterior margin. Dermal bone surfaces have typical temnospondyl pit and ridge ornament radiating outward from the centres of ossification. No specimen shows any trace of lateral-line sulci or pits. The material comprises fragments or casts of incomplete skulls, most of which were in the 230–300 mm range and had firmly interlocking sutures. The smallest skull (MB Am.84) is 180 mm long and may have belonged to a subadult individual as the sutures are relatively open and some bones have slipped relative to one another (Pl. 1, fig. 1; Text-fig. 4). Comparative cranial dimensions

TABLE 1. *Capetus palustris*. Cranial dimensions in mm. (e) = estimated dimension.

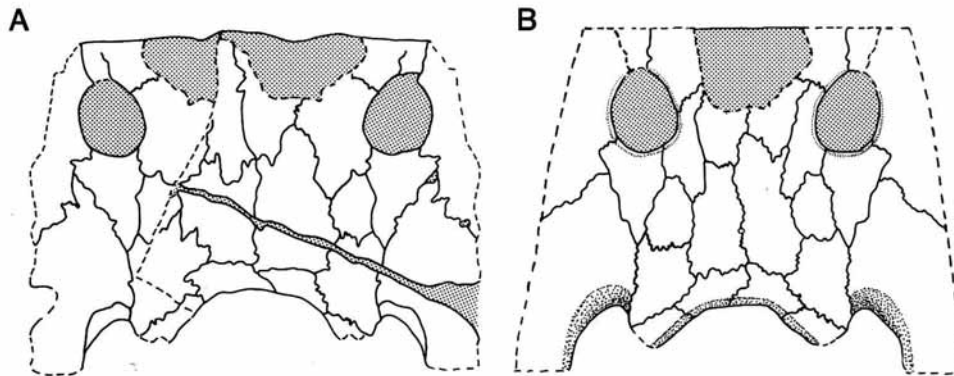
Dimension	MB Am.84	NMW 1898.X.51	MB Am.92	BMNH R4706
Midline skull length	180	235	—	—
Snout length—midline snout tip to mid-orbit	110	138	—	—
Skull table length, midline mid-orbit to posterior margin	70	97	102(e)	114
Minimum interorbital width	53	69	74(e)	79
Orbit width	28	33	36(e)	37
Midline to tabular tip	40	54	64	65

are given in Table 1. Some fragmentary material (NMW 1893.32.53 and NMW 1895.2366) represents a distinctly larger skull, perhaps 400 mm in length.

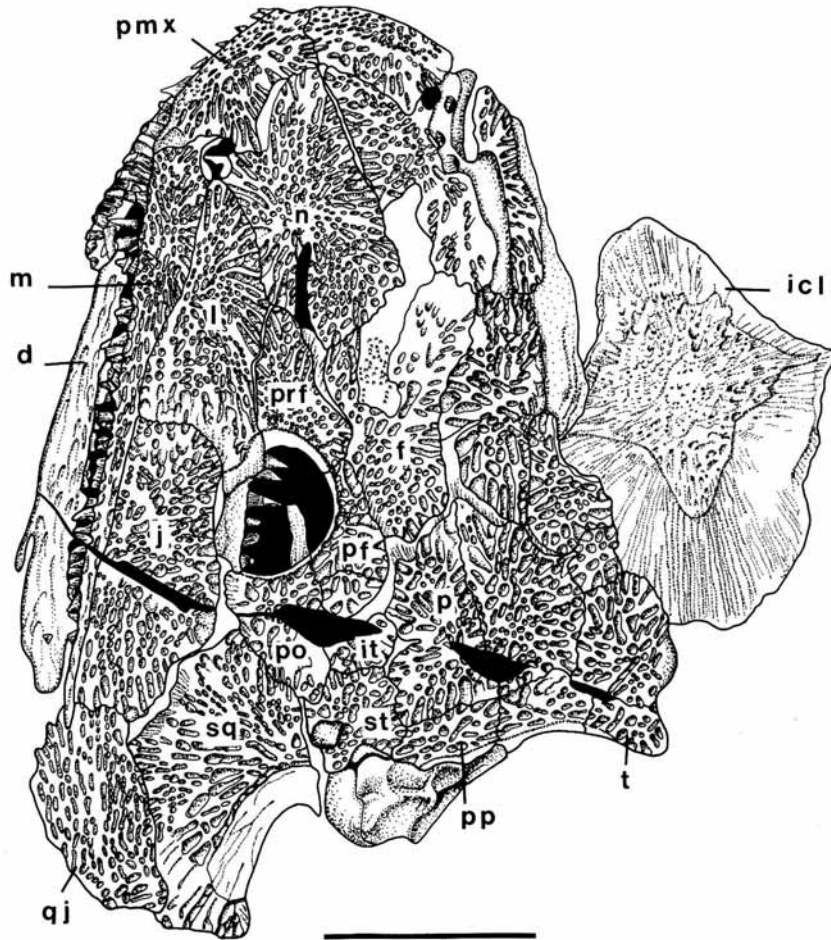
Skull roof. The dermal skull roof of *Capetus* comprises the full complement of dermal bones typical of primitive temnospondyls and only elements of particular systematic significance are described.

The configuration of the premaxillaries is unusual among early temnospondyls. Each premaxillary forms a narrow border along the anterior edge of the snout, and extends a pronounced wedge-like alary process posteriorly over the anterior edge of the nasal. The alary process is situated slightly mesial to the medial edge of a large external naris in MB Am.84 (Text-fig. 4) and NMW 1898.X.51 (Text-fig. 6). Edopoids such as *Edops*, *Cochleosaurus* and *Chenoprosopus* possess much larger premaxillaries, which lack alary processes and which border small inset external nares. *Dendrerpeton* appears to possess narrow premaxillaries with no alary processes. In the more derived temnospondyls of the eryopoid grade (*sensu* Milner 1990a), the premaxillaries are similar in shape to those of *Capetus* but the alary processes may either border the nares or lie medially to them (e.g. *Scleurocephalus* Boy, 1988; *Onchiodon* Boy, 1990).

The large nasals are about twice as long as wide. They occupy most of the surface area of the anterior snout and extend anteriorly between the posterior ends of the premaxillaries. The external naris is bordered posteriorly by a small septomaxillary which probably sutured with the anterior edge of the lacrimal. The septomaxillary is visible as a disarticulated element in the left naris of MB Am.84 (Text-fig. 4). The lacrimal extends posteriorly to enter the anterior orbit margin and, in doing so, separates the prefrontal from the jugal.



TEXT-FIG. 3. *Capetus palustris* Steen, 1938. A, Steen's reconstruction in which right postfrontal and frontal were combined as a massive right postfrontal, giving an unusually large interorbital width and an apparent resemblance to *Edops*. B, new reconstruction with frontals and postfrontals identified correctly, giving a skull of more *Scleurocephalus*-like proportions.

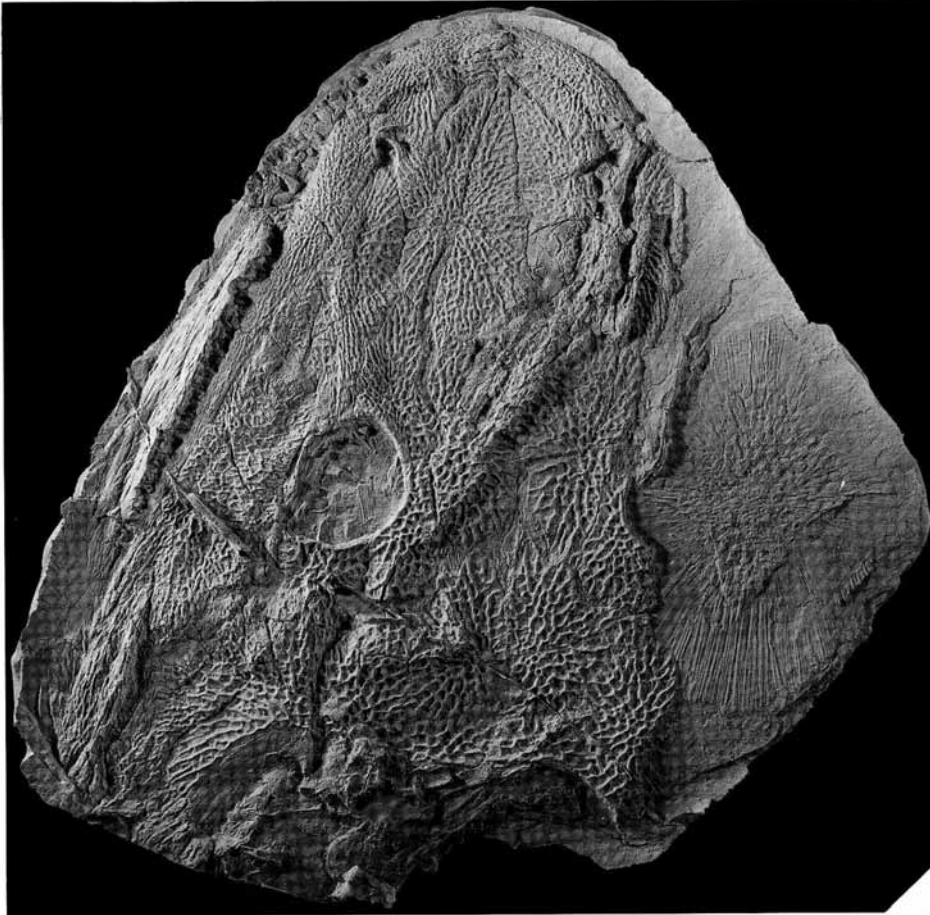


TEXT-FIG. 4. *Capetus palustris* Steen, 1938. MB Am.84, the specimen figured by Jaekel (1911, 1913) as *Chelydosaurus vranji*. For list of abbreviations, see Text-fig. 2. Scale bar = 50 mm.

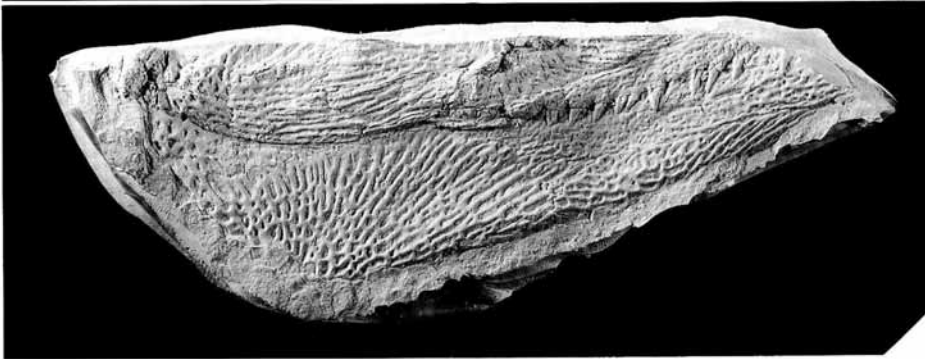
This is visible in BMNH R4706 (Text-fig. 2), MB Am.84 (Text-fig. 4), NMW 1898.X.51. (Text-fig. 6) and one of the lost BSP specimens figured by Broili (1908, pl. 1 fig. 1). This is the primitive tetrapod condition and is an unusual symplesiomorphy to be found in a long-snouted temnospondyl. A thickened ridge extends from the posterior end of the lacrimal anteriorly to a point partway along the lacrimal-maxillary suture. The two ridges

EXPLANATION OF PLATE I

Capetus palustris Steen, 1938. 1. MB Am.84, silicone-rubber cast of specimen $\times 0.66$. For interpretation, see Text-figure 4. 2. UMZC T.144, silicone-rubber cast of posterior region of right mandible $\times 1$. For interpretation, see Text-figure 8A.

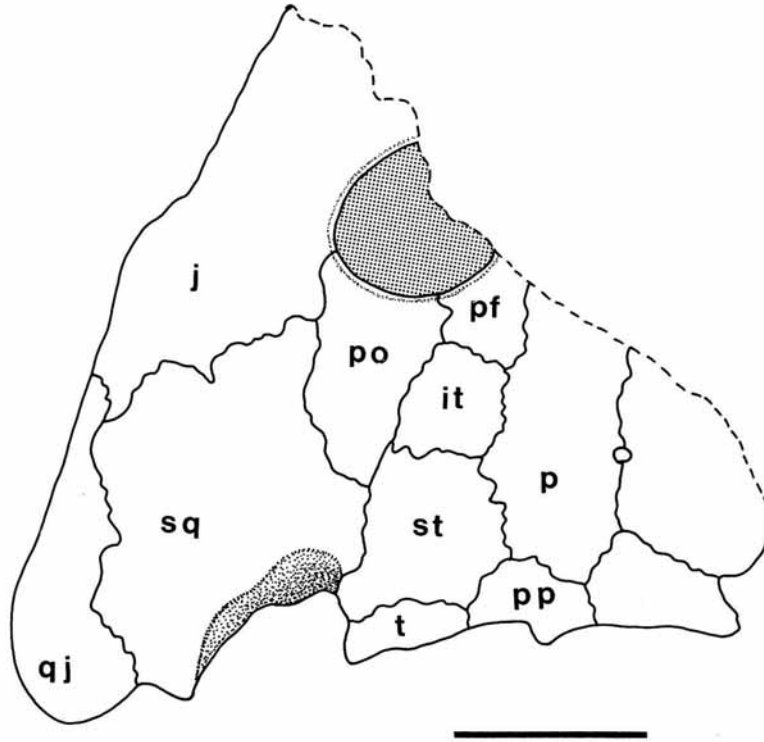


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SEQUEIRA and MILNER, *Capetus*



TEXT-FIG. 5. *Capetus palustris* Steen, 1938. MB Am.92. This specimen is now represented only by a bitumen cast, the location of the original being unknown. For list of abbreviations, see Text-fig. 2. Scale bar = 50 mm.

form a pair of parallel struts, which probably resisted part of the torsional stress generated between the anterior dentition and the jaw hinge during feeding.

The frontals make the greatest contribution to the interorbital width, which is not great in any specimen (*contra* Steen 1938). Steen described and reconstructed the holotype specimen of *Capetus* as possessing an interorbital width greater than the skull table length. This was based on a misinterpretation, in which the right frontal and postfrontal bones were amalgamated as a postfrontal. That error was then compounded in a mirror-image reconstruction with the midline suture misidentified (Text-fig. 3A). The resulting short skull table and *Edops*-like widely spaced orbits were both artefacts of this misinterpretation, but may well have influenced Romer and Witter (1942) when they associated *Capetus* with *Edops*. The skull of *Capetus* in fact bears a much closer resemblance to that of *Sclerocephalus* in general shape and Text-fig. 3B depicts it reconstructed correctly.

The lateral edges of the orbits are bordered by a jugal, which is different in shape from those of most other primitive temnospondyls. It intervenes broadly between the orbit and the maxillary and is as wide as, or wider than, the orbit for most of its length. Anterior to the level of the orbits, the jugal narrows to a point along its extensive common suture with the lacrimal. A similar condition pertains in *Edops*. The cheek margin is bordered largely by the relatively slender maxillary, which narrows posteriorly to a point contact with the quadratojugal, excluding the jugal from the skull margin (Text-figs 4, 6, 8). Cheek depth is never greater than interorbital width and increases to a maximum towards the jaw articulation.

The circumorbital series is conservative for temnospondyls and is unremarkable apart from the right postorbital in BMNH R4706 (Text-fig. 2). In this specimen, a pronounced lateral extension of this bone is wedged into the medial face of the jugal just below the posterior orbital edge; postorbitals in other *Capetus*

skulls are much less expanded at this point, so this may represent individual variation. The postorbitals of all specimens are primitively anteroposteriorly elongate, and are substantially longer than wide, wedging posteriorly between the supratemporal and squamosal.

The skull table structure is characteristic of primitive temnospondyls. A pair of intertemporals is present; their shape and size varies within the material studied. In BMNH R4706 and MB Am.92, they are about two-thirds of the area of the supratemporals, but in MB Am.84 they are relatively smaller. The parietals are large and anteroposteriorly elongated; a small pineal foramen is located two-thirds of the way back along the interparietal suture. The postparietals lack the lappets characteristic of *Cochleosaurus* and the unornamented posterior face of each postparietal is a narrow backward-sloping surface with little evidence even of thickenings associated with the underlying exoccipitals. The tabulars are anteroposteriorly narrow and grow posterolaterally with size increase to enhance the concave curvature of the occiput. Each otic notch is deeply ovoid and is bordered by the tabular, supratemporal and squamosal. A 2 mm wide margin of dense fine pitting lines the squamosal border of the notch in BMNH R4706, but is not present in the smaller MB Am.84.

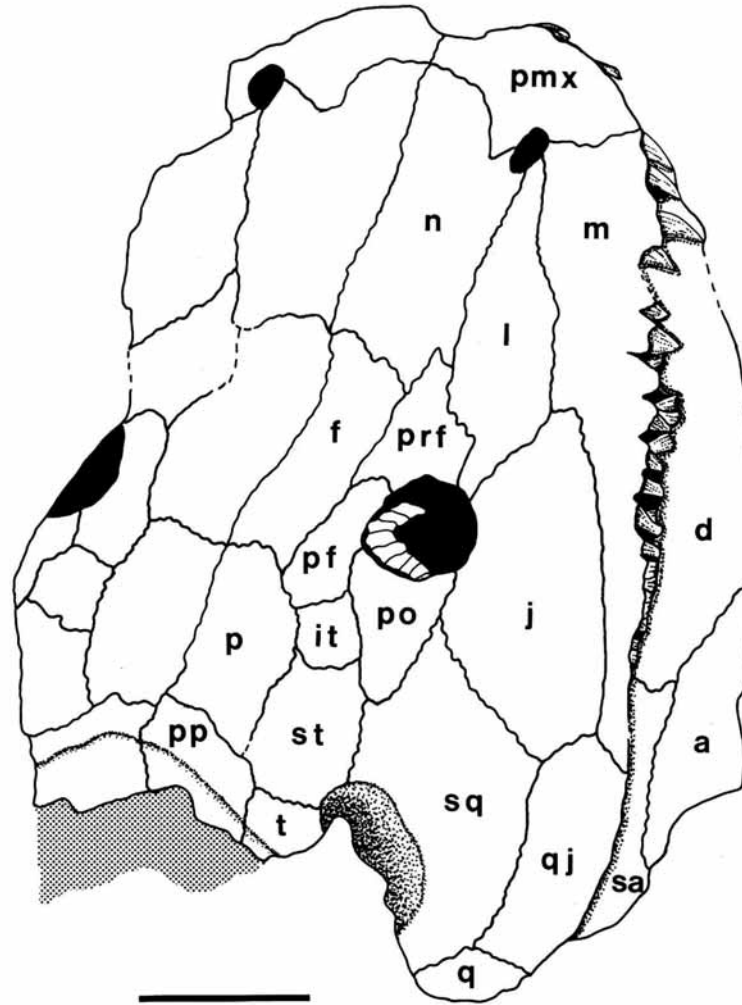
Sclerotic ring. A partial sclerotic ring is preserved in the right orbit of NMW 1898.X.51 (Text-fig. 6). Eight sclerotic plates appear to make up about one third of a ring, which suggests a normal temnospondyl sclerotic ring of about twenty-five elements (Milner 1982).

Palate. Significant regions of the palate are visible only in NMW 1898.X.51 (Text-fig. 7) among the surviving specimens, and even in this skull, much of the left side has been obscured by overlying jaw elements. General palatal structure in *Capetus* is that of a primitive temnospondyl. The interpterygoid vacuities are small; in comparison with the snout-quadrate length, they are a quarter as long and a sixth as wide. Pronounced anterior narrowing of each vacuity to a point occurs as the pterygoid curves towards its median articulation with the cultriform process of the parasphenoid.

The shape of the vomers is of considerable importance in determining the phylogenetic position of *Capetus*. In NMW 1898.X.51, the vomers are not well preserved but their general shape is clear. They are not very elongate anteroposteriorly; most notably, they lack the extreme elongation anterior to the leading edge of the choanae which is characteristic of cochleosaurs. This area is poorly preserved but there is no space for such an anterior extension. One of the specimens figured by Broili (1908, pl. 1, fig. 3) is an anterior snout region in palatal aspect and also appears to bear a pair of squarish vomers, each apparently with an anterior pit or depression, probably for the reception of parasymphyseal fangs. No such pits are visible in NMW 1898.X.51 however, so their existence must be treated with caution. In NMW 1898.X.51, each vomer contacts the pterygoid along an extensive common suture running at an angle of 45° from the anterior choanal edge towards the midline. Because the vomer and the pterygoid are overlain by the displaced left mandible immediately anterior to the interpterygoid vacuity, their configuration in this region can only be guessed at by extrapolating the common suture back to the midline. This suggests that the vomer was completely excluded from the vacuity and, if so, this represents a primitive character-state shared with *Edops* and *Chenoprosopus*. The portion of the vomer level with the choanae is less elongated than that found in cochleosaurs. In NMW 1898.X.51, there appears to be a small and uninformative exposure of the right palatine between the right mandible and the pterygoid (Text-fig. 7). No ectopterygoid is visible in any of the available specimens.

The broad pterygoid expands posterolaterally into a wide flange at the level of its articulation with the braincase. In NMW 1898.X.51, elements of the single circular occipital condyle are preserved posterior to the crushed braincase. In MB Am.84, a series of crushed elements are superimposed on the left tabular and vicinity. They are too damaged to merit description or to be figured in detail, but appear to represent a displaced part of the braincase and occiput. Rod-like elements associated with this crushed material may represent the paroccipital processes.

Mandible. Incomplete mandibles are preserved in NMW 1898.X.51 (Text-figs 6–7), a portion of the left dentary is present in MB Am.84 (Text-fig. 4), the anterior of the left mandible is preserved in NMW 1895.2366 (Text-fig. 8B) and the external face of the posterior region of the right mandible is represented in UMZC T.144 (Text-fig. 8A). The mandibular rami are robust and deep, reaching a maximum vertical depth midway along the extensive angular. In this region, mandible depth equals, and may exceed, cheek depth. The relationship of the elements on the external face of the mandible (Text-fig. 9C) resembles that in *Sclerocephalus* (Boy 1988, fig. 6A) and *Eryops* (Sawin 1941, pl. 5). The angular has a sharply curved ventral margin, like those in the above deep-jawed genera but unlike many temnospondyls with flatter mandibular rami where the ventral margin is relatively straight. Part of the medial face of the right mandible is exposed in NMW 1898.X.51 but little sutural detail is visible.



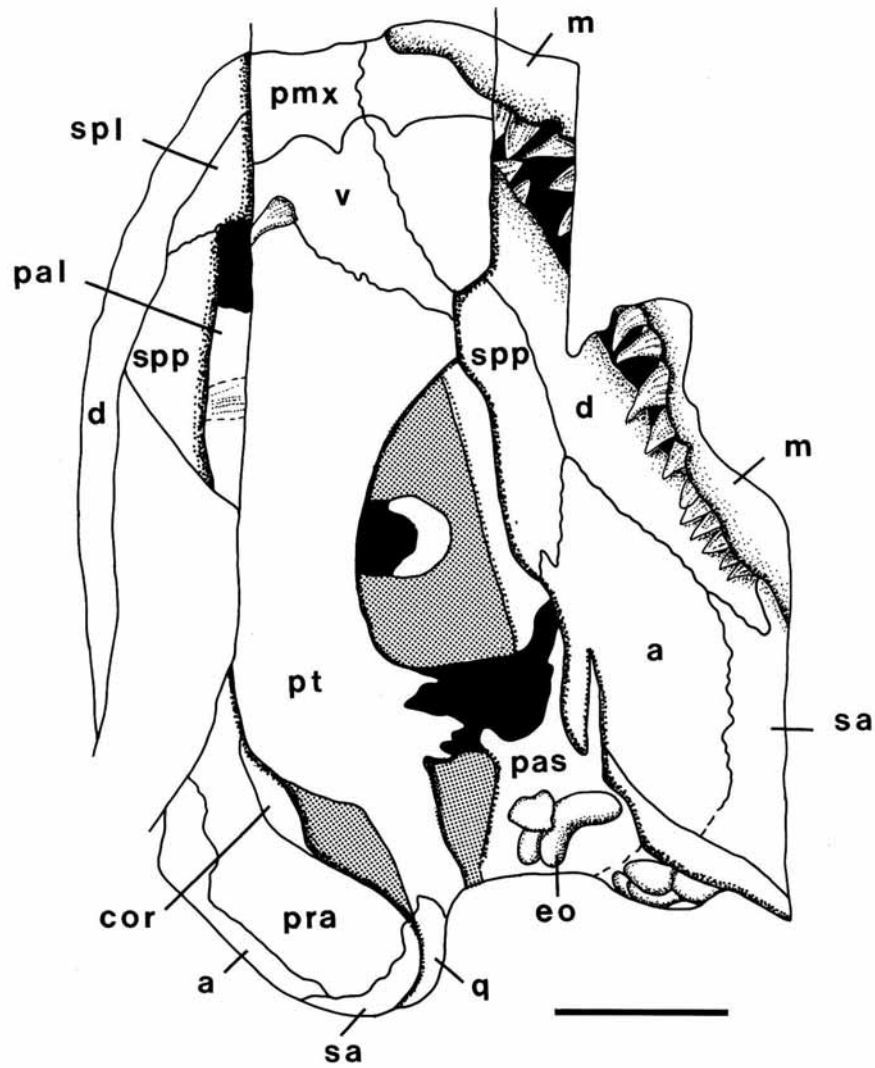
TEXT-FIG. 6. *Capetus palustris* Steen, 1938. NMW 1898.X.51 part. Stippled area behind skull table represents a patch of ossicle-bearing skin (see Text-fig. 8c). For list of abbreviations, see Text-fig. 2. Scale bar = 50 mm.

EXPLANATION OF PLATE 2

Capetus palustris Steen, 1938. NMW 1898.X.51, silicone-rubber cast of main part $\times 0.66$. For interpretation, see Text-figure 6.



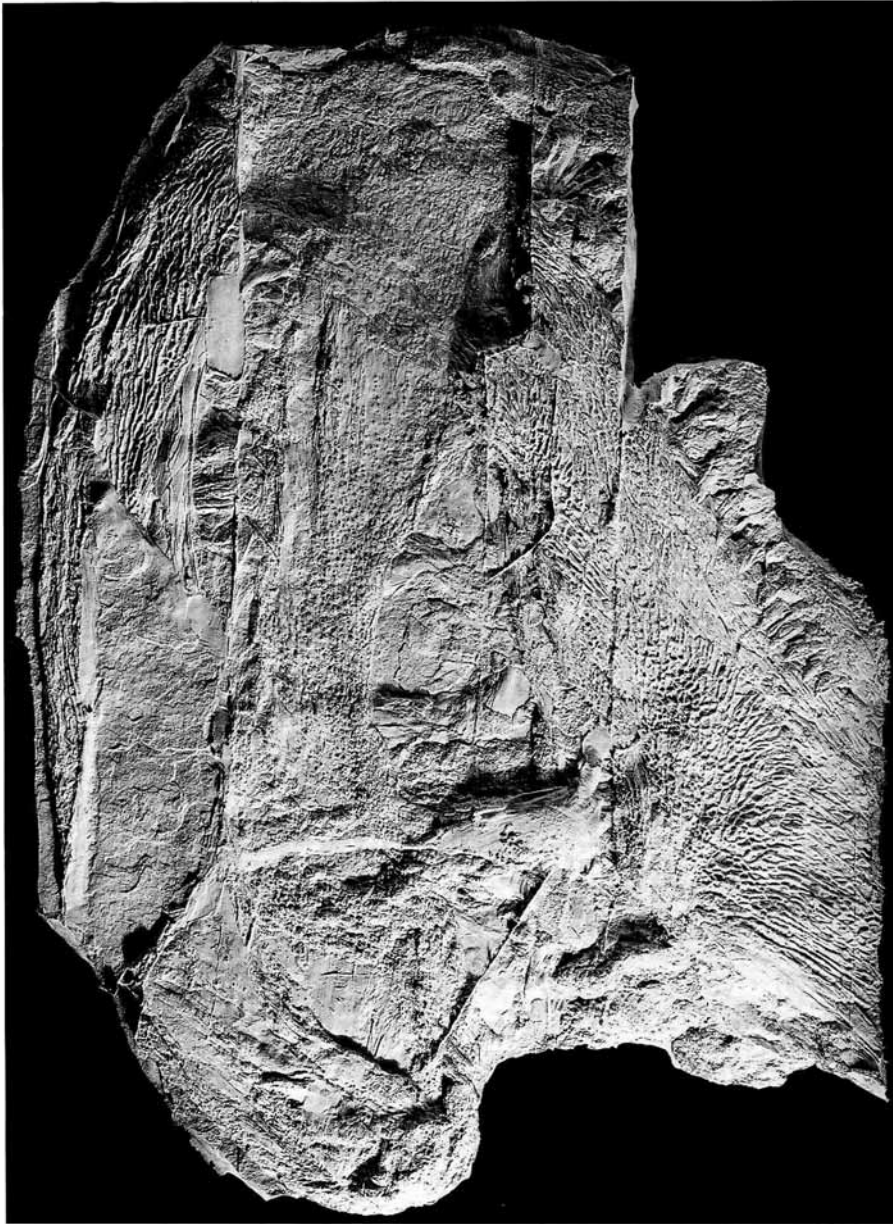
SEQUEIRA and MILNER, *Capetus*



TEXT-FIG. 7. *Capetus palustris* Steen, 1938. NMW 1898.X.51 counterpart. Stippled area is internal surface of skull roof. For list of abbreviations, see Text-fig. 2. Scale bar = 50 mm.

EXPLANATION OF PLATE 3

Capetus palustris Steen, 1938. NMW 1898.X.51, silicone-rubber cast of counterpart $\times 0.66$. For interpretation, see Text-figure 7.



SEQUEIRA and MILNER, *Capetus*

Dentition. Marginal teeth, palatal fangs and denticles are visible in MB Am.84, NMW 1895.2366, NMW 1898.X.51, UMZC T.144 and the two specimens figured by Broili. The teeth and fangs are simple sharp-pointed cones of typical labyrinthodont appearance. They are dagger-like with no suggestion of curvature, although the posterior teeth may be slightly backwardly-directed. In the large NMW 1895.2366, the anterior dentary teeth appear to be genuinely flattened bilaterally and may have had a slight keel.

In MB Am.84 there is space for about fifty marginal teeth on the left upper jaw ramus. There appears to have been space for about twelve premaxillary teeth and thirty-eight maxillary teeth, the latter growing to a height of 15 mm in NMW 1898.X.51. A precise dentary tooth count is not possible, and the presence or absence of coronoid teeth cannot be ascertained. NMW 1898.X.51 shows some evidence of pseudocanine peaking with two or three enlarged teeth around the premaxillary-maxillary junction. NMW 1895.2366 appears to have some enlarged teeth at the very anterior end of the dentary (Text-fig. 8b), but these may be symphyseal fangs crushed into the same plane as the marginal dentition.

In NMW 1898.X.51, one or two vomerine fangs border the anteromedial edge of each choana. These fangs are no larger than the marginal teeth. A poorly-defined structure which might be a much larger fang lies displaced across the right palatine. The presence of relatively large palatine fangs is a feature of some primitive temnospondyls. The presence or absence of palatine tooth-rows and ectopterygoid fangs or teeth cannot be established.

In NMW 1898.X.51, a thin scatter of denticles covers the palatal surfaces of the vomer and pterygoid, becoming most concentrated towards the medial edge of the latter. There are also patches of denticulate bone in the interpterygoid region, but it is not clear whether these are part of the parasphenoid or isolated denticle-bearing plates covering the interpterygoid region.

Stapes. A small bone fragment abutting the left otic notch in MB Am.84 (Text-fig. 4) may represent a portion of the shaft of the left stapes.

Interclavicle. A large rhomboidal interclavicle with a length:width ratio of 1.47:1 is preserved in MB Am.84 (Text-fig. 4). It has been turned over relative to the skull, and also anteroposteriorly reversed by rotation through 180°. The pattern of dermal ornament on its ventral face resembles that of postmetamorphic specimens of *Sclerocephalus* (Boy 1988, fig. 9) with pitting over the centre of ossification grading into radial grooves along the margins. Large articular surfaces for the clavicles lie posterolateral to the strongly fimbriated anteromedial edge of the interclavicle. Facet outlines suggest that the clavicles must have been broad-bladed structures.

Dermal ossicles. A flap of ossicle-bearing skin appears to have been preserved immediately behind the skull table of NMW 1898.X.51. This can be seen as a series of fine ridges and folds in the surface of the cast immediately behind the postparietals (Pl. 2). In places, these folds can be seen to incorporate small disc-like structures which may be interpreted as osteoderms in the skin of the back (Text-fig. 8c). They are oval and bear a pattern of fine concentric rings. They are only 4–5 mm in diameter but otherwise resemble the 10 mm osteoderms described in a specimen of *Eryops* by Romer and Witter (1943).

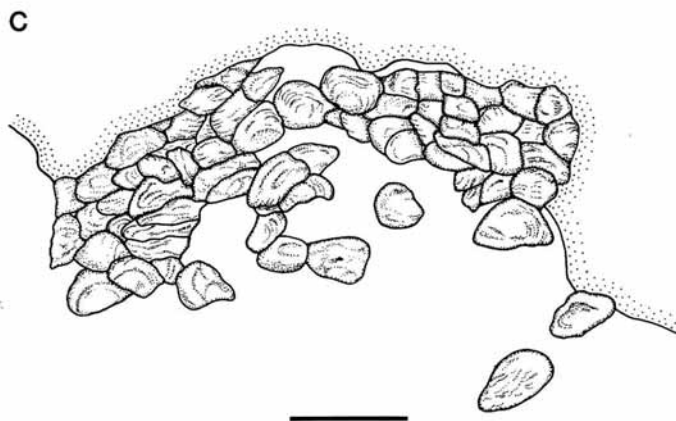
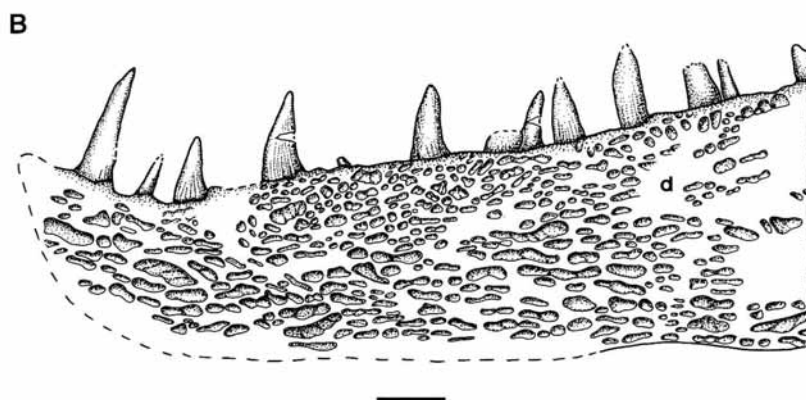
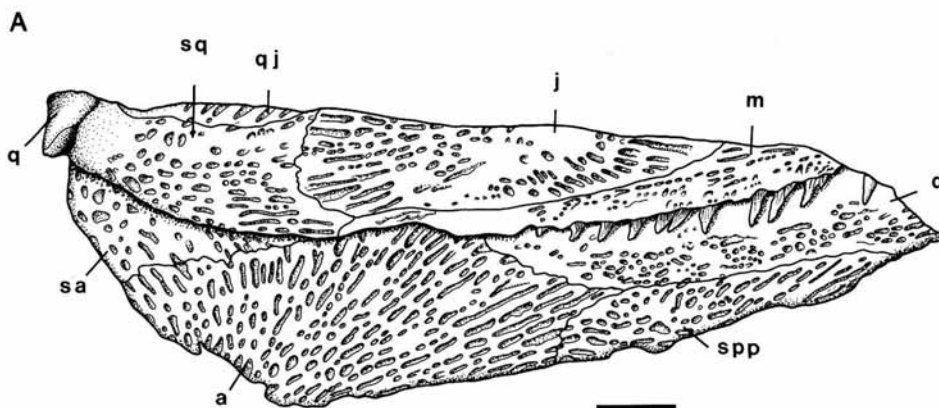
Reconstruction. The reconstructions of the cranium and mandible in Text-figure 9 are composite and are based on the general configuration and palate of NMW 1898.X.51, augmented with skull roof details from BMNH R4706 and mandibular detail from UMZC T.144 and NMW 1895.2366. The reconstruction of the smaller skull roof in Text-figure 10 is based solely on MB Am.84. These reconstructions differ in several details from the provisional reconstructions previously produced by Milner and Sequeira (in press) and supersede them. The general shape and depth of the skull is most similar to the slightly later *Sclerocephalus* from the Lower Permian of Germany (Boy 1988).

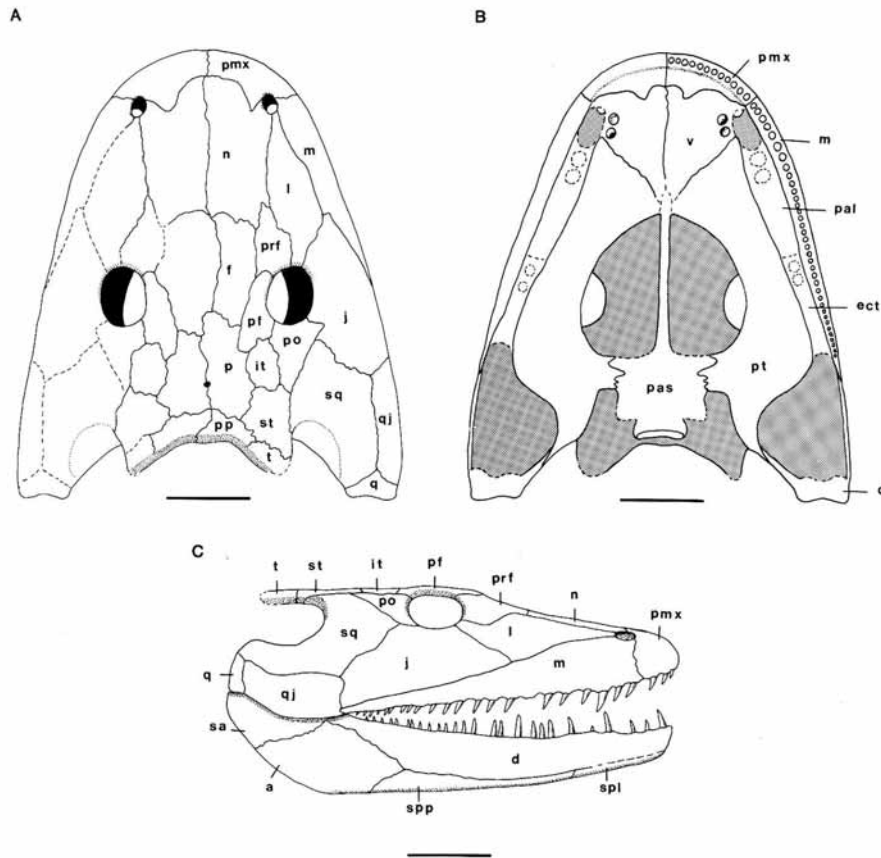
DISCUSSION

Relationship of Capetus to other primitive temnospondyls

The following discussion of characters and character-states has the limited aim of comparing the

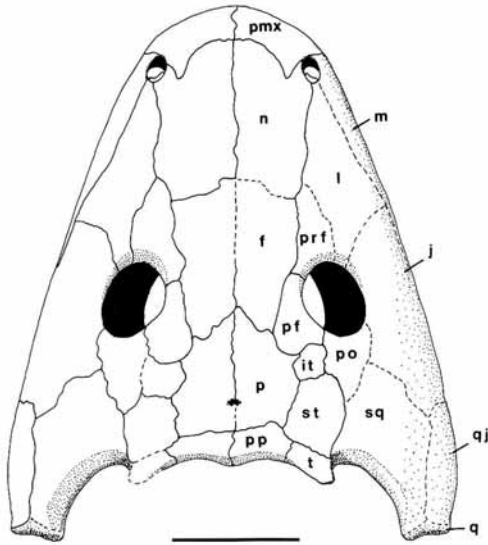
TEXT-FIG. 8. *Capetus palustris* Steen, 1938. a, UMZC T.144, posterior end of right mandible. b, NMW 1895.2366, anterior end of left mandible. c, NMW 1898.X.51, dermal ossicles immediately behind skull table. This figure represents the best-preserved part of the stippled area depicted in Text-figure 6. For list of abbreviations, see Text-fig. 2. Scale bars = 10 mm.





TEXT-FIG. 9. *Capetus palustris* Steen, 1938. Whole skull reconstruction of large specimen, in A dorsal aspect, B palatal aspect, and C right lateral aspect with mandible. Based on NMW 1898.X.51, BMNH R4706 and UMZC T.144. For list of abbreviations, see Text-fig. 2. Scale bar = 50 mm.

characteristics of a small range of primitive temnospondyls, mostly superficially crocodile-like forms, in order to establish their relationships. The genera involved (with sources in parenthesis) are *Capetus* (redescribed here), *Edops* (Romer and Witter 1942 and authors' personal observations), *Cochleosaurus* (Rieppel 1980, Godfrey and Holmes in press, and authors' personal observations), *Chenoprosopus* (Langston 1953), *Trimerorhachis* (Case 1935 and authors' personal observations), *Sclerocephalus* (Boy 1988) and *Onchiodon* (Boy 1990). Outgroup comparison is made with the loxommatids (Beaumont 1977). Comparison is not made with either *Caerorhachis* or *Dendroperon* as the only skull of the former is both small and poorly preserved, while unpublished work on the latter genus by the authors suggests that it is composed of at least two distinct taxa, which precludes it from being a suitable outgroup at present. Unlike Boy (1990), we have not used either trimerorhachoids or dissorophoids as outgroups, as both are believed to be more derived temnospondyls than the edopoids, and dissorophoids are believed to be more derived than both



TEXT-FIG. 10. *Capetus palustris* Steen, 1938. Whole skull reconstruction of medium specimen in dorsal aspect, based on MB Am.84. Scale bar = 50 mm.

edopoids and eryopoids (Milner 1990a, 1990b). The character number prefixes relate to the cladogram in Text-figure 11.

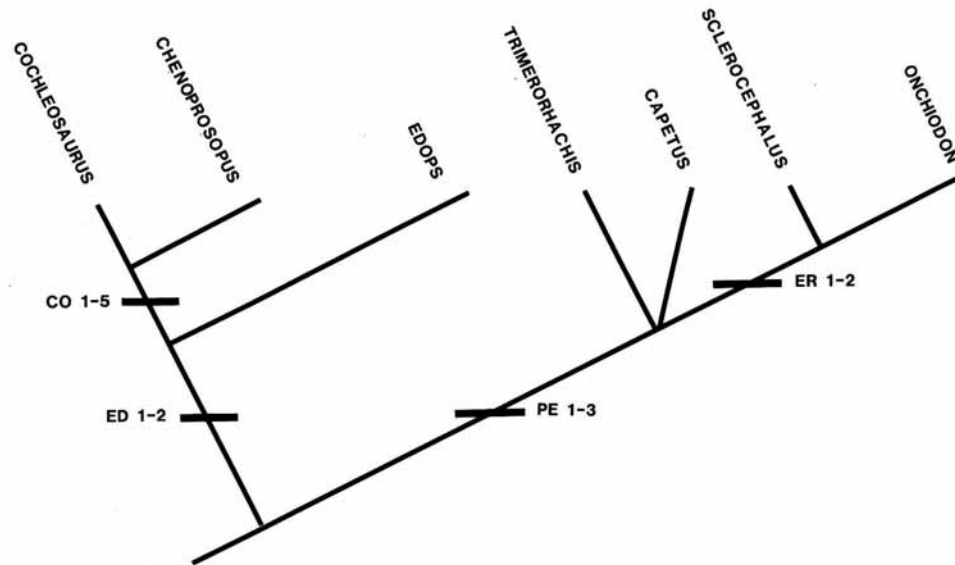
Edopoid characteristics

The Superfamily Edopoidea is a primitive clade of temnospondyls (Milner 1990b) consisting of two families: the Cochleosauridae, comprising *Cochleosaurus* and *Chenoprosopus* and defined below; and the Edopidae, a monotypic family based on *Edops craigi* from the Lower Permian of Texas (Romer and Witter 1942).

Edops shares the following with the Cochleosauridae.

- ED.1. Enlarged premaxillaries with a long common median suture and extending well back along the jaw margin behind the level of the common suture. Small naris set well back along snout (Milner 1990b). The small size of the naris is probably primitive, and its position is a manifestation of the premaxillary shape. The pattern of enlargement of the snout by expansion of the premaxillaries occurs elsewhere among primitive tetrapods only in some urocordylid neotrideans where it is clearly a convergence (e.g. *Sauroplorea*).
- ED.2. Jugal-prefrontal contact excluding lacrimal from the orbit margin (Milner 1980a, 1990b). This appears to be a derived character occurring in most but not all long-snouted temnospondyls. It defines the Edopoidea against many other temnospondyls including *Dendroperon*, *Trimerorhachis*, the East Kirkton temnospondyl, the Dissorophoidea and the Zatrachydidae. However, it also occurs in the Eryopoidea and Parioxyidae, and in the Actinodontidae and all its stereospondyl relatives.

One character used incorrectly to define the Edopoidea by Milner (1980a) followed by Godfrey *et al.* (1987) was the presence of sculptured triangular septomaxillary sutured into the dermal roof of the snout behind the external naris. This has proved to be more widely distributed among temnospondyls, though seldom figured, and may characterize all except the eryopid-dissorophoid-lissamphibian clade, where it is replaced by a free septomaxillary in the naris.



TEXT-FIG. 11. Cladogram of relationships of the temnospondyl genera discussed in the text. Numbers denote characters as used in the text.

Cochleosaurid characteristics

Recent workers (Milner 1990b; Godfrey and Holmes in press) have considered the Cochleosauridae to be restricted to two genera and three species, namely *Cochleosaurus bohemicus*, *C. florensis* and *Chenoprosopus milleri*. The following list of derived characters defining the family is modified from that provided by Godfrey and Holmes (in press).

- CO.1. Closure of the pineal foramen in adults (Steen 1938; Langston 1953; Godfrey and Holmes Character 1).
- CO.2. Possession of depressed areas on the skull roof that exhibit subdued sculpturing (Rieppel 1980; Godfrey and Holmes Character 2).
- CO.3. Elongate anterior region of the palate produced by elongation of both the vomers and the internal narial openings, resulting in the relatively posterior position of the anterior border of the interpterygoid vacuities (Godfrey and Holmes Character 3 modified; Godfrey and Holmes also cited the extremely large premaxillaries on the dorsal surface of the skull as part of this character but these also occur in *Edops* – see below).
- CO.4. Ectopterygoid and maxillary excluded from the subtemporal fossa by a pterygoid-jugal suture (Godfrey and Holmes Character 4). An inevitable correlate of this character is that the jugal also separates the maxillary and the quadratojugal on the cheek. Milner (1980a) attributed the latter character to all the long-snouted edopoids but there is a contact between maxillary and quadratojugal in *Edops*, albeit a point contact.
- CO.5. Choanae wider anteriorly than posteriorly (Godfrey and Holmes Character 6).

Two other derived characters used by Godfrey and Holmes are of value only in defining the Cochleosauridae within the Edopoidea, as they occur widely elsewhere within the Temnospondyli. Transverse width of the skull through the mid-orbital region is less than the antorbital length (Godfrey and Holmes Character 5).

Squamosal embayment (= otic notch or temporal notch) with substantial participation of supratermporal along its dorsal rim (Godfrey and Holmes Character 7).

Post-edopoid characteristics

The following characteristics define the trimerorhachoid and eryopoid grades of temnospondyls, and their descendent clades: the Brachyopoidea, Stereospondyli, Dissorophoidea and Lissamphibia.

- PE.1. Interpterygoid vacuities wide and anteriorly rounded.
 PE.2. Palatine rami of the pterygoids so reduced that the vomers enter the margin of the vacuities.
 PE.3. Prominent alary process (pars dorsalis) on the premaxillary which is a relatively narrow bone bordering a large naris. Edopoids retain a simple massive premaxillary with a straight posterior edge like that of loxommatids. Post-edopoid temnospondyls have relatively larger nares and smaller premaxillaries. They include the East Kirkton temnospondyl, trimerorhachoids (not figured by Case 1935 but found in first-hand study by the authors) and all eryopids, dissorophoids and stereospondyls. Milner (1990b) suggested that this derived character defined all temnospondyls with the situation in edopoids being a reversal, but it appears to operate without contradiction at this higher node with the edopoid condition regarded as primitive by outgroup comparison with loxommatids.

Eryopoid characteristics

The Eryopoidea is here taken as a grade of temnospondyl at the base of both the clade Stereospondyli and the dissorophoid–lissamphibian clade (Milner 1990a, 1990b). This grade includes the stem-stereospondyl families Actinodontidae, Intasuchidae and Archegosauridae; and the stem-dissorophoid families Zatrachydidae, Eryopidae and Parioxyidae. The defining characters for the Eryopoidea define a node including all the descendent taxa.

- ER.1. Intertemporals absent (Milner 1990a). The loss of the intertemporals has demonstrably occurred within several early tetrapod groups (e.g. Loxommatidae, Colosteidae) but is here taken as a valid character in the absence of contradictory characters.
 ER.2. Exoccipitals enlarged to give bilobed occipital condyle.

Edopoid–eryopoid relationships

Boy (1990) proposed a set of relationships for the edopoid and eryopoid temnospondyls in which *Edops* is the sister-taxon to a clade of the Eryopidae, Parioxyidae and Zatrachydidae (hereafter the E-P-Z group) while *Chenoprosopus* (and by implication *Cochleosaurus*) is the sister-taxon to the Actinodontidae and Archegosauridae (hereafter A-A group). Boy's E-P-Z grouping corresponds to those 'eryopoid' families which Milner (1990a, 1990b) placed at the base of the dissorophoid–lissamphibian clade, and their unity is not disputed. Likewise the A-A group were placed by Milner (1990a, 1990b) at the base of the Stereospondyli and their unity is also supported. However Boy's suggestion that the Edopoidea and eryopoid-grade temnospondyls are both diphyletic is not supported, for the following reasons.

1. It uses as outgroups, the Dissorophoidea, which Godfrey *et al.* (1987) and Milner (1990a, 1990b) have argued to be more derived than the Edopoidea within the Temnospondyli, and the Trimerorhachoida which Godfrey *et al.* (1987) argued to be the sister-group of the Edopoidea, and Milner (1990b) argued to be more derived than the Edopoidea.
2. Boy (1990, p. 306, character 25) associated *Chenoprosopus* with the A-A group on the presence of a nasal-maxillary contact excluding the lacrimal from the septomaxillary or naris margin. However, the lacrimal does reach the septomaxillary in *Cochleosaurus florensis* (Godfrey and Holmes in press), in *Cochleosaurus bohemicus* and in an undescribed cochleosaurid from Linton. As the unity of these forms with *Chenoprosopus* in the Cochleosauridae is well demonstrated, we conclude that the nasal-maxillary contact in *Chenoprosopus* must be convergent with that in the Actinodontidae and the Archegosauridae, probably associated with snout elongation within each group.

3. Boy (1990, p. 306, characters 4 and 26) associated *Chenoprosopus* with the A-A group on the presence of an elongate prefrontal which is anteriorly constricted, whereas *Edops* was associated with the E-P-Z group on the presence of an elongate prefrontal which is anteriorly expanded. Clearly the elongate nature of the prefrontal cannot define either group and the constricted and expanded alternatives cannot both be derived, so that at best only one of Boy's two groupings might be supported by this character. The character is correlated with general snout width and one can argue on ontogenetic grounds that the narrow prefrontal found in juveniles is more likely to represent the primitive condition, in which case only the character-state of anteriorly broad prefrontal could be used to unite *Edops* and the E-P-Z group. It may be noted that other unrelated broad-snouted temnospondyls also possess anteriorly broad prefrontals (e.g. *Parotosuchus* and *Cyclotosaurus* (see Welles and Cosgriff 1965, figs 16, 20, 27) and this character could be argued to be a convergent feature of broad-snouted temnospondyls.

4. Boy (1990, character 5) also united *Edops* and the E-P-Z group on the presence of a vertically orientated ilium with an expanded dorsal region, but noted that this also occurs convergently in some dissorophoids. It is thus a convergent feature of large terrestrial temnospondyls, and not a particularly compelling character.

Thus the characters used by Boy to unite *Chenoprosopus* with the A-A group are argued not to be valid, but the characters used to unite *Edops* with the E-P-Z group may be valid although one occurs convergently elsewhere.

The two characters used by Boy to unite *Edops* with the E-P-Z group must be set against the five characters listed here to unite post-edopoid temnospondyls, namely PE.1-3 and ER.1-2.

The position of Capetus

Capetus palustris cannot be placed within the Cochleosauridae as it lacks characters CO.1-5 listed above as defining that family. The pineal foramen is retained, there are no areas of subdued ornament, the vomers are not elongate, the jugal does not extend onto the cheek edge or palate and the choanae are not of cochleosaurid shape. *Capetus* cannot be placed within the Edopoidea as it lacks the characters ED.1-2 defining that superfamily. The premaxilla is not enlarged and the lacrimal is not excluded from the orbit margin by a jugal-prefrontal contact. *Capetus* does appear to exhibit pseudocanine peaking, a character which it shares with *Edops* but this is contradicted by the absence of other edopoid characters, and is a homeoplastic feature found in several large temnospondyls. At most, *Capetus* could be a stem-edopoid (i.e. an earlier offshoot of the superfamily than *Edops*) but we can find no derived character to support such a position. *Capetus* cannot be placed in the Superfamily Edopoidea where it has previously resided.

Capetus certainly lacks PE.1 and ER.1, probably lacks PE.2 (ER.2 is unknown) and cannot be associated with the Eryopoidea. However, it does possess PE.3 - the narrow premaxillaries each with a large alary process. This derived character suggests a position on the post-edopoid side of the edopoid-post-edopoid dichotomy. It also occurs in the Trimerorhachidae and the undescribed temnospondyls from East Kirkton, which would thus also be on the post-edopoid branch. In this position, *Capetus* could not be placed readily in any pre-existing family, and to create a family for *Capetus* alone would be to create a redundant taxon. Our solution is to treat *Capetus* as a plesion *sensu* Patterson and Rosen 1977, i.e. an extinct holophyletic taxon of any size which is the sister-taxon to a clade incorporating living taxa. *Capetus* would stand as a plesion on the stem of the Lissamphibia, ranked after the Edopoidea but before the Stereospondyli.

However, one other distinctive feature of *Capetus* may contradict this position. *Capetus* is unusual among long-snouted temnospondyls in retaining the character-state of the lacrimal entering the orbit margin. In both edopoids and 'eryopoid'-grade temnospondyls, the jugal and prefrontal meet to exclude the lacrimal. It might be argued that this is a shared derived character for the Edopoidea and Eryopoidea, and that *Capetus* must therefore represent a more primitive side-branch prior to the edopoid-eryopoid dichotomy. This, however, is an artefact of the restricted range of taxa used in this comparison, in the interests of comparing homoeomorphic forms. The

lacrimal enters the orbit margin in *Trimerorhachis* (Case 1935), the East Kirkton temnospondyl, the zatrachydids and the dissorophoids, all of which are post-edopoid temnospondyls. Clearly some convergence or reversal of this character has occurred. One possibility is that the edopoids and eryopoids have separately excluded the lacrimal from the orbit margin, with the zatrachydids and dissorophoids reversing the character. An alternative is that edopoids, stereospondyls and eryopoids have separately excluded the lacrimal from the orbit margin and that other groups retain the primitive condition.

Conclusion

Capetus palustris is a primitive temnospondyl which cannot be placed readily in any pre-existing family or superfamily. It is clearly not a member of the clade Edopoidea, but may be a very primitive relative of the temnospondyls of the eryopoid grade of organization. Pending more comprehensive character analysis of all primitive temnospondyls, which the authors plan to undertake, it is considered to be a plesion within the ranked series of temnospondyl plesions leading to the Lissamphibia.

SYSTEMATIC POSITION OF *GAUDRYA LATISTOMA*

Fritsch (1885, p. 31) created the taxon *Gaudrya latistoma* for a large anterior palate in the private collection of Hr Cajetan Bayer of Plzeň. Fritsch made plaster casts of the specimen; one is in his original collection (NMP Fritsch Gypskopie 304) and others are widely distributed in museums. The current location of the original specimen is not known to the authors; it does not appear to be in the collection at the Národní Muzeum, Prague or the Zapadočeske Muzeum at Plzeň. The systematic position of *Gaudrya latistoma* must therefore be determined from the cast and from Fritsch's illustrations (1885, pl. 61, fig. 1 (the specimen), figs 2–3 (sections of the teeth)).

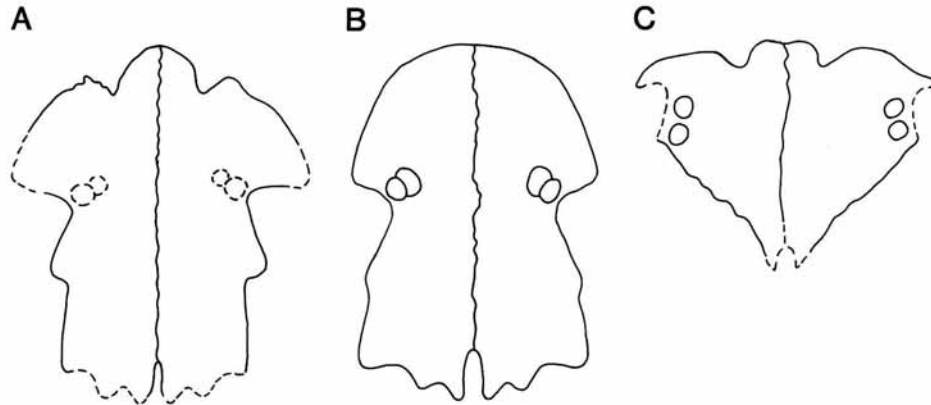
The specimen comprises paired vomers in dorsal aspect bordered by the palatal component of the premaxillaries including the premaxillary dentition in transverse section. In parts, the vomerine bone is missing, revealing a natural mould of the ventral surface of the vomers. Each premaxillary was anteroposteriorly elongate along the jaw margin and had space for 19 to 20 teeth. The small elements figured by Fritsch as vomers appear to be palatal shelves (pars palatina) of the premaxillaries. The large elements labelled palatines by Fritsch are the vomers (Text-fig. 12A). They are unusually elongate from the level of the leading edge of the choana backwards, a condition shared with *Cochleosaurus* and *Chenoprosopus*. The palatal surface is covered in tiny denticles. The choana has a straight anterior margin perpendicular to the long axis of the skull. The anteromedial margin curves sharply through about 120° to a straight, posterolaterally directed medial margin extending back to the palatine. There is no evidence of intervomerine vacuities or depressions. Scaled against the vomers of several specimens of *Cochleosaurus*, the *Gaudrya* vomers appear to have belonged to a skull of between 185 and 210 mm total midline length.

Subsequently, the specimen was treated as indeterminate by Steen (1938, p. 261) and was ignored by Romer and Witter (1942) in their discussion of Nýřany edopoids. However, Romer (1947, p. 104) associated all large Nýřany temnospondyl specimens, not already in *Cochleosaurus*, under the binomen *Gaudrya latistoma* as the senior binomen. Subsequent authors have accepted this synonymy (e.g. Langston 1953; Milner 1980b). No further species have been incorporated in the genus.

Comparison of the cast of the holotype of *Gaudrya* with specimens of *Cochleosaurus* and the new material of *Capetus* leads to the following three observations.

1. In the holotype of *Gaudrya latistoma*, the premaxillary ventral margin and tooth row extend well back and imply the presence of anteroposteriorly elongate premaxillaries. This is character ED.1 described above and occurs in *Cochleosaurus* at Nýřany, and also in edopoids such as *Edops* and *Chenoprosopus* but does not occur in *Capetus* as can be seen in MB Am.84 and NMW 1898.X.51.

2. In the same holotype, the vomers are very elongate behind the level of the anterior edge of the



TEXT-FIG. 12. Restored vomers of large long-snouted temnospondyls in the Nýřany assemblage. A, holotype of *Gaudrya latistoma* Fritsch, 1885 (based on his plate 61, fig. 1). B, *Cochleosaurus bohemicus* Fritsch, 1885 (original figure based on NMW 1898.X.41). C, *Capetus palustris* Steen, 1938 (original figure based on NMW 1898.X.51).

choana (Text-fig. 12A). Such elongation in the posterior region of the vomer is unusual in temnospondyls. It is character CO.3 listed above for the Cochleosauridae and occurs in *Cochleosaurus* (Text-fig. 12B) at Nýřany, and also in *Chenoprosopus* but does not occur in *Capetus* as can be seen in NMW 1898.X.51 (Text-figs 7–8, 12C).

3. If *Edops*-like palatal proportions are assumed, the *Gaudrya* snout-tip would have belonged to a skull of at least 400–500 mm midline length and this large size may have influenced Romer to associate it with the large *Capetus*, as none of the then-described *Cochleosaurus* skulls exceeded 250 mm in length. However, given that the elongate shape of the *Gaudrya* vomers corresponds to those of *Cochleosaurus* in which they are proportionately large, the *Gaudrya* specimen could have belonged to a *Cochleosaurus* skull of 185–210 mm length as noted above. The largest *Cochleosaurus* specimen seen by the authors is MB Am.85, a skull table with the diagnostic postparietal lappets. This specimen, scaled against the skull tables of more complete skulls, appears to have belonged to a skull of about 260 mm midline length. Thus the size of the *Gaudrya* holotype falls within the known range for *Cochleosaurus*.

These features combine to suggest that the holotype of *Gaudrya latistoma* is simply a fragment of a large specimen of *Cochleosaurus bohemicus* from the same locality. It is formally proposed that *Gaudrya latistoma* be treated as a junior subjective synonym of *Cochleosaurus bohemicus*.

CAPETUS AND THE NÝŘANY ASSEMBLAGE

At least eight specimens of *Capetus* were collected, although the two at Munich were apparently destroyed in 1944 and one in Berlin is represented only by a cast. These eight specimens form part of an assemblage of at least 700 tetrapod specimens (Milner 1987). *Capetus* thus constitutes a numerically small component (about one per cent) of the preserved tetrapod assemblage, although it is more common than most other vertebrates of comparable size. The largest specimens had a skull length of about 400 mm, suggesting an animal of about 1.5 m total length. *Capetus* would thus have been one of the largest tetrapods in the Nýřany assemblage, and a few individuals would have represented a significant fraction of the tetrapod biomass at any one time.

There are four tetrapods with superficially crocodile-like skulls in the Nýřany assemblage, namely the temnospondyls *Cochleosaurus* and *Capetus*, and the loxommatids *Baphetes* and *Megalocephalus*.

This diversity presents an interesting problem in understanding the niches which these forms might have filled. Of the four genera, the two loxommatids are each represented by a single determinate specimen (the *Megalocephalus* specimen is undescribed) and are clearly exotic elements in the Nýřany assemblage. As suggested by Milner (1980b, 1987) they were both small individuals in comparison with representatives of these genera in the British Coal Measures, and it is reasonable to assume that they were juveniles which had strayed from their typical habitat. The British loxommatid material tends to be associated with fish-rich assemblages from large abandoned channels, and it may be that the Nýřany loxommatids also typically lived in such a habitat. *Baphetes* was broad-snouted and *Megalocephalus* had a longer narrower snout, and they may thus have been the counterparts to alligators and crocodiles respectively in larger water bodies in the Late Carboniferous.

Of the temnospondyls, *Cochleosaurus* is represented by nearly 100 out of a sample of 700 tetrapod specimens, whereas *Capetus* is represented by eight. However, of the 100 or so specimens of *Cochleosaurus*, only about ten are of individuals of comparable size to the *Capetus* remains, the rest being smaller. Very small *Cochleosaurus* with 25 mm skulls may still be recognized by the large premaxillaries and by the swellings on the postparietals marking the early ontogenetic stage of the postparietal lappets which characterize the adults. This *Cochleosaurus* material is currently being studied by the senior author, and no small *Capetus* specimens have been found in it. Consequently, the assemblage contains a small number of presumed adults of each genus, together with a much larger number of larvae and juveniles of *Cochleosaurus* but no juveniles of *Capetus*. Clearly *Cochleosaurus* was reproducing in the Nýřany water-body and passing much of its early life-history there, the varying sizes of juvenile suggesting that several age-classes were represented. The absence of *Capetus* juveniles of any size indicates that it was not using this water-body as a breeding site.

Large individuals of *Cochleosaurus* and *Capetus* had skulls of different shape, the largest *Cochleosaurus* having a narrow elongate snout, whereas that of *Capetus* was much broader and slightly shorter. If, as with the loxommatids, the analogy with modern crocodylians is pursued, then *Capetus* would have been a more alligator-like form feeding on aquatic and terrestrial slow-moving tetrapods, while *Cochleosaurus* was more crocodile-like, perhaps specializing in predation on swimming tetrapods.

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