

The temnospondyl amphibians from the Viséan of East Kirkton, West Lothian, Scotland

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ABSTRACT: A new temnospondyl amphibian *Balanerpeton woodi* gen. et sp. nov. is represented by over 30 complete or partial skeletons from the Viséan limestones, shales and tuffs in East Kirkton Quarry, Bathgate, near Edinburgh, Scotland. It is the commonest tetrapod represented in the East Kirkton assemblage and grew to about half a metre in length. Although superficially like the later *Dendrerpeton*, it is more advanced in possessing small premaxillaries each bearing a pronounced alary process, large external nares, large rounded interpterygoid vacuities, broadly bordered by the vomers anteriorly, a narrow vomer-pterygoid suture and a rod-like stapes. It is characterised by an unusual dental configuration in which each dentary bears a smaller number of larger teeth than the corresponding upper jaw ramus. A second probable temnospondyl is represented by two straight ribs of a much larger form.

The relationships of basal temnospondyls and other amphibian groups are discussed and it is proposed that the sister-group of the temnospondyls is the Microsauria and that neither colosteids nor *Caerorhachis* can be considered to be temnospondyls, as both fall outside the temnospondyl-microsaur clade. A preliminary study of character distribution across a selection of primitive temnospondyls, including *Balanerpeton*, suggests that it is more advanced than the long-snouted Edopoidea and the Dendrerpetontidae despite its Viséan age. This implies that by the Viséan, significant diversification of temnospondyls had taken place.

KEY WORDS: Carboniferous, Amphibia, anatomy, phylogeny, East Kirkton, Scotland.

The temnospondyl amphibians are the largest group of archaic amphibians represented in the fossil record from the Carboniferous to the early Cretaceous. Comprising about 40 families and 160 genera, they are more numerous than all the other early non-amniote tetrapod groups combined. They are now widely perceived as a grade of organisation between primitive tetrapods and some or all lissamphibians. There is general agreement that they form the stem-group of the Salientia (frogs) and an increasing consensus that they are also the stem-group of the Caudata (salamanders) (Milner 1988; Trueb & Cloutier 1991; Bolt 1991). The problem of the relationships of the Gymnophiona remains more controversial. Some workers perceive them as part of a natural group, the Lissamphibia, with the temnospondyls forming the lissamphibian stem (Milner 1988; Trueb & Cloutier 1991; Bolt 1991), while others perceive them as having a microsaur stem with their lissamphibian features being largely convergent (Carroll & Currie 1975). This dispute is beyond the scope of this paper and we shall treat temnospondyls as stem-lissamphibians in this work, without assuming that the position of gymnophionans has been definitively resolved. Several osteological characters of frogs and salamanders can be seen in temnospondyls and the origin of the temnospondyl amphibians represents the first steps towards the origin of the lissamphibians.

As noted by Milner (1990), the Temnospondyli has been variously defined, and our perception of early tetrapod taxa as basal temnospondyls has evolved steadily in recent years. In 1947, Romer defined the Temnospondyli on what we would now consider to be primitive tetrapod characters and, consequently, the group included such forms as ichthyostegids, loxommatids and colosteids. The description of the skull and part of the postcranial skeleton of *Ichthyostega* by Jarvik (1952, 1955) led to a general consensus that it was the

most primitive known tetrapod and that it represented a grade of organisation well below that of the Temnospondyli (e.g. Gaffney 1979). The loxommatids continued to be treated as temnospondyls until Panchen (1980) suggested that they might be more closely related to the anthracosaurs. Smithson (1982) and Panchen and Smithson (1988) have elaborated on this argument. Since Panchen's initial suggestion, no positive reasons have been put forward for retaining the loxommatids in the Temnospondyli.

Since the description of *Greererpeton* (Romer 1969; Smithson 1982; Godfrey 1989) and the reassessment of *Pholidogaster* by Panchen (1975), the colosteids have been recognized as a distinct family, having previously been associated with either ichthyostegalians or with trimerorhachoid temnospondyls. They have been argued by Godfrey *et al.* (1987) and Godfrey (1989) to be the most primitive temnospondyls. Colosteids occur from the late Viséan to the Westphalian D, and, if they were temnospondyls, would be the earliest members of the group. However, Milner *et al.* (1986) and Panchen and Smithson (1988) suggested briefly that they were less closely related to temnospondyls than were the microsaurs and thus could not be considered to be temnospondyls. This case is argued further by Milner (1993) and in the discussion of this paper.

Caerorhachis bairdi, probably from the Namurian of Scotland, was described by Holmes and Carroll (1977) as a primitive temnospondyl. Godfrey *et al.* (1987) concluded that it was the next most primitive temnospondyl to the colosteids. It has been reconstructed with small interpterygoid vacuities, but otherwise has no unequivocal temnospondyl features and has some characteristics, such as gastrocentrous vertebrae, which do not suggest a temnospondyl identity. It is considered further in the discussion of this paper.



Unequivocal temnospondyls (i.e. excluding colosteids and *Caerorhachis*) can be recognised by the following four characteristics. (1) Rounded interpterygoid vacuities at least half the width of the skull, primitively bordered only by the pterygoids (*Edops*) but, in most temnospondyls, bordered by the vomers and sometimes the palatines and ectopterygoids. The cultriform process of the parasphenoid is long and extends between the vomers. (2) Broad vomers widely separating the choanae. (3) Dorsolaterally orientated rod-like stapes associated with a large tympanic notch. (4) Short straight ribs.

The earliest described temnospondyls exhibiting some or all of this suite of temnospondyl characters are several specimens from the Westphalian A. They comprise *Dendrerpeton* and a cochleosaurid from Jarrow, Ireland (Milner 1980, Sequeira in press), the trimerorhachoid *Eugyrinus* from Trawden, Lancashire (Milner 1980) and a dendrerpetontid from Parrsboro, Nova Scotia (Milner 1982a). Such forms had not been found in pre-Westphalian beds, so the discovery of indisputable temnospondyls in the Viséan of East Kirkton is of great significance.

The tetrapod assemblage in the East Kirkton Limestone was discovered by Mr Stan Wood in 1984 (see Milner *et al.* 1986, p. 20 for details). The first specimen (now NMS G 1984.42.14) was an indeterminate tetrapod skull, but the second, collected in July 1984, was an almost complete temnospondyl skeleton which has been figured subsequently in several accounts of the East Kirkton assemblage (Wood *et al.* 1985; Milner *et al.* 1986; Rolfe *et al.* 1990). Since then, numerous specimens of this type of temnospondyl have been collected and it has proved to be the commonest tetrapod in the East Kirkton assemblage. Most specimens have been found in the spherulitic limestones, but they have also been collected from the black shales, the non-spherulitic limestones and the tuffs, although the latter are mostly fragments which can only be said to be attributable to the Temnospondyli. Almost all of the determinate specimens appear to belong to a single species which is described below. Many are poorly preserved and the new form is described from a small number of good specimens. Three isolated large ribs appear to belong to a second, much more massive, temnospondyl and they are described separately in the following account.

The following institutional abbreviations are used in this work:

BMNH	Department of Palaeontology, The Natural History Museum, London.
GLAHM	Hunterian Museum, Glasgow University, Glasgow.
GLAMG G	Geological Collections, Glasgow Museum and Art Gallery, Kelvingrove, Glasgow.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA.
NMS G	Department of Geology, National Museums of Scotland, Edinburgh.
SPW	Collection of Mr S. P. Wood, Edinburgh.
UMZC	University Museum of Zoology, Cambridge University, Cambridge, England.

1. Systematic palaeontology

Order TEMNOSPONDYLI Zittel, 1888

Family Incertae sedis

Balanerpeton gen. nov.

Type species. *Balanerpeton woodi* sp. nov.

Etymology. Greek *Balaneion*, a hot-spring or bath, and *herpeton*, a creeping animal; elided together in the interests of a more euphonious name.

Diagnosis. As for the only species.

Balanerpeton woodi sp. nov.

(Figs 1–18)

Synonymy.

- 1985 'fossil amphibian' Wood *et al.*, pp. 355–6
- 1985 'Temnospondyl' Milner, p. 321
- 1986 *Dendrerpeton*-like temnospondyl Milner *et al.*, p. 21; fig. 12
- 1988 'dendrerpetontid' Milner p. 89
- 1990 *Dendrerpeton*-like form Rolfe *et al.*, p. 20
- 1992 East Kirkton temnospondyl Milner & Sequeira, p. 44A

Holotype. GLAHM V2051 (previously SPW 2272), a complete skull and anterior axial skeleton in ventral aspect on a slab of black shale (Figs 1, 9, 11C)

Etymology. *woodi* for Stan Wood who discovered the East Kirkton locality and collected much of the material on which this work is based.

Locality. East Kirkton Quarry [O.S. Grid Ref. NS991690], near Bathgate, 27 km west of Edinburgh, Scotland.

Horizon. Black shale horizon, probably but not certainly Unit 82, East Kirkton Limestone, West Lothian Oil-Shale Formation, Strathclyde Group, Brigantian, Viséan, Dinantian.

Diagnosis. Unique feature (in context of temnospondyls) is: dentary ramus bearing 25–30 relatively large teeth + spaces, upper dentition comprising 40–42 smaller teeth + spaces. A second relatively unusual characteristic is the presence of large orbits and narrow interorbital distance. A third character of possible, but uncertain significance is that the dorsal vertebra with a reduced neural spine is the fifth, rather than the fourth, but this is of uncertain polarity. Derived characters shared with most later temnospondyls include: small premaxillary with large alary process interdigitating with anterior edge of nasal; vomers broadly entering anterior margins of large semicircular interpterygoid vacuities. Retained primitive characters include: intertemporals present, very reduced Meckelian fossae; intercentra showing traces of paired origin, entepicondylar foramen in the humerus.

1.1. Referred material

The following list comprises all of the determinate temnospondyl specimens from East Kirkton known to be in institutional collections. For most specimens, the general type of matrix is noted, and for those few NMS specimens found *in situ* in the quarry, the horizon of origin is noted. Most of the specimens were found in walls on neighbouring farmland or in spoil-heaps within the quarry and cannot yet be certainly attributed to specific horizons within the East Kirkton Limestone. It does appear that most associated tetrapod skeletons derive from Units 70–82 inclusive. During NMS excavations, *Balanerpeton* specimens or fragments have been collected from Units 52, 74, 79, 82 and 86 (Rolfe *et al.* this volume).

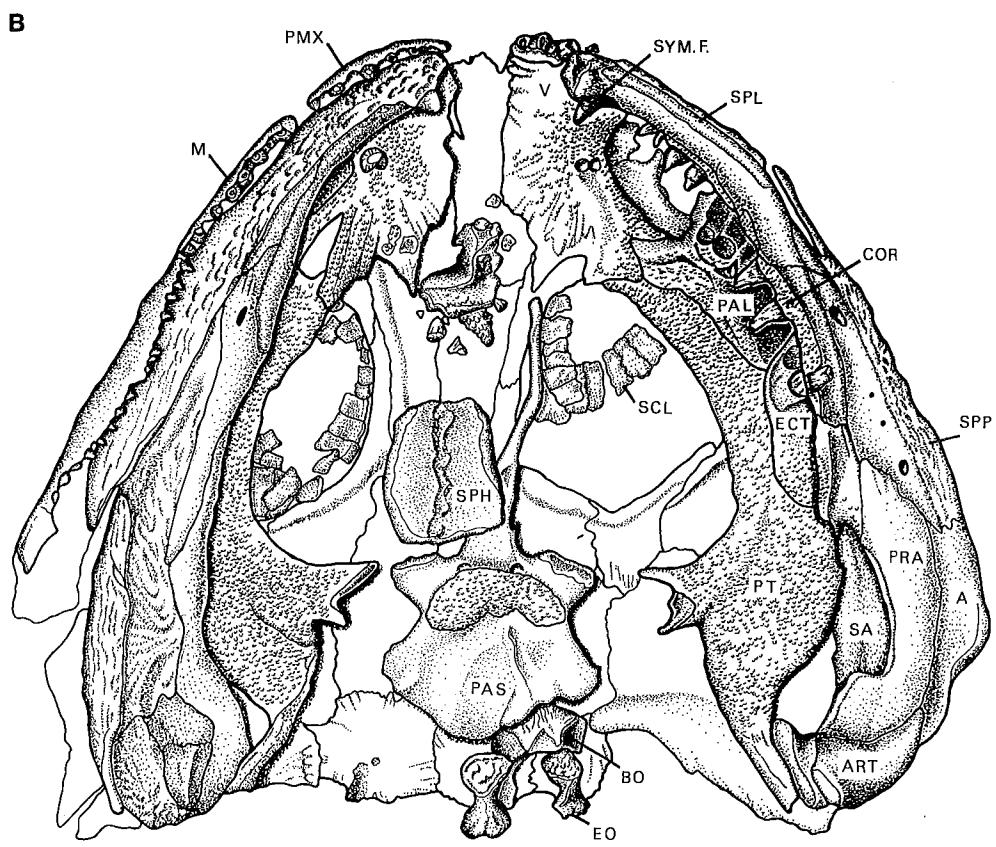
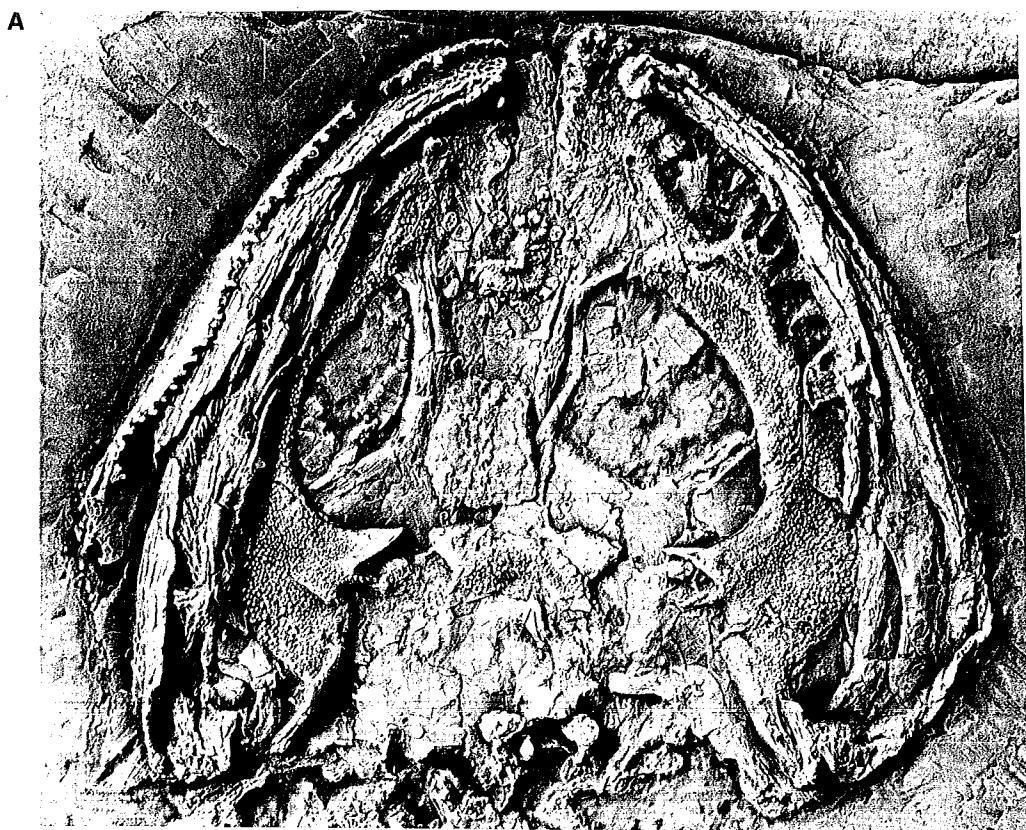


Figure 1 *Balanerpeton woodi* gen. et sp. nov., holotype, GLAHM V2051, East Kirkton, Bathgate; East Kirkton Limestone. (A) Skull and mandibles in ventral aspect, $\times 2.5$; (B) drawing of specimen, scale bar, 10 mm. For abbreviations to this and all other figures, see Section 5.

NMS G 1985.4.1 (=SPW 2042). Pt & cpt (Figs 7, 8, 11D, 12B-D, 14, 15B, D). Skull and almost complete postcranial skeleton including part of tail on limestone. Previously figured by Wood *et al.* 1985 fig. 3, Milner *et al.* 1986 fig. 12 & Plate I.

NMS G 1985.4.2 (=SPW 2049). Pt & cpt (Fig. 3). Skull roof and partial palate in ventral aspect on limestone. Figured by Wood *et al.* 1985 fig. 4.

NMS G 1985.4.6 (=SPW 2088). Pt & cpt. Partial skull in dorsal aspect and partial postcranial skeleton on limestone.

NMS G 1987.7.32 (=SPW 2210). Pt & cpt (Figs 2C, 6B, 10B, 11A). Partial skull in dorsal aspect and postcranial skeleton, including associated gastralia, on limestone.

NMS G 1987.7.33 (=SPW 2228). Pt & cpt (Figs 10C, 16B). Partial skull in ventral aspect and partial postcranial skeleton, including associated gastralia, on limestone.

NMS G 1987.7.35 (=SPW 2203). Pt & cpt. Skull in dorsal aspect and partial postcranial skeleton on limestone.

NMS G 1987.7.36 (=SPW 2135). Natural mould of ventral aspect of skull and palate on limestone, produced by weathering.

NMS G 1990.79.1. Pt & cpt. Crushed skull and humerus in limestone band in tuff. Collected *in situ* from Unit 74.

NMS G 1990.79.3. Pt & cpt in two fragments (Fig. 6C). Partial skull in ventral aspect and partial postcranial skeleton on limestone. Collected *in situ* from Unit 79.

NMS G 1990.79.4. Pt & cpt in five fragments (Fig. 6E). Partial skull in dorsal aspect, right stapes and partial postcranial skeleton on limestone.

NMS G 1991.47.2. Pt & cpt (Figs 6D, F). Partial braincase and both partial stapes in dorsal aspect on limestone.

NMS G 1992.14.2 (=SPW 2354). Pt & cpt on two blocks. Isolated skull in laminated limestone.

NMS G 1992.48.1. Poorly preserved left cheek on laminated limestone. Collected *in situ* from Unit 52.

NMS G 1992.48.2. Left region of skull table in counterpart. Collected *in situ* from Unit 86.

GLAHM V2052 (=SPW 2229) (Figs 10A, 13B, 15F, 16A). Partial postcranial skeleton, including associated gastralia, on black shale, possibly from Unit 82.

GLAMG G 1985.232.1 (=SPW 2069). pt & cpt (Fig. 13A). Pelvic girdle, hindlimbs and base of tail of a large specimen.

BMNH R10952 (=SPW 2114). Pt & cpt. Partial skull in ventral aspect and partial postcranial skeleton on limestone.

BMNH R10953 (=SPW 2050). Pt & cpt. Partial skull on limestone.

BMNH R10954 (=SPW 2097). Pt & cpt. Skull table in ventral aspect on limestone.

BMNH R10955 (=SPW 2047). Pt & cpt (Fig. 15E). Partial skull in dorsal aspect and partial postcranial skeleton on limestone.

BMNH R12014 (=SPW 2352). Pt & cpt (Fig. 4). Partial skull in dorsal aspect and partial postcranial skeleton on black shale, possibly from Unit 82.

BMNH R12015 (=SPW 2181). Pt & cpt (Fig. 6A). Associated vomers in dorsal aspect, right mandible and partial left mandible on limestone.

BMNH R12016 (=SPW 2355). Partial skull in ventral aspect on black shale, possibly from Unit 82.

UMZC T1261 (=SPW 2116). Pt & cpt. Partial skull in dorsoventral aspect and partial postcranial skeleton on limestone.

UMZC T1312 (=SPW 2322). Pt & cpt (Fig. 2). Partial skull in dorsal aspect on limestone.

UMZC T1313 (=SPW 2323). Pt & cpt (Fig. 12A, 15A, C, 17). Skull and partial postcranial skeleton of juvenile on black shale, possibly from Unit 82.

2. Description

Much of the following description is based on a relatively small number of specimens. The preservation of material in the black shale is considerably superior to that in the limestone and there is consequent emphasis on the few black shale specimens, particularly GLAHM V2051, selected as the holotype. Although incomplete, the holotype shows fine detail of the palate, mandibles, dentition and anterior axial skeleton, and is the only specimen to bear all the characters used to define the genus.

2.1. General features

2.1.1. General appearance. *Balanerpeton woodi* is one of the superficially salamandiform temnospondyls, like the dendrerpetontids, micromelerpetontids and amphibamids. It has a short-snouted skull with large, closely-set orbits, prominent tympanic notches and moderately large interpterygoid vacuities. The dermal bones of the skull are evenly pitted and no lateral-line sulci are present. No ossified branchial elements are present. The axial skeleton is that of a typical small temnospondyl and comprises about 24 rhachitomous presacral vertebrae, one sacral vertebra and an unknown number of caudal vertebrae. Trunk ribs are very short with narrow shafts lacking uncinate processes. The pectoral and pelvic girdles are robust structures with the exception of the pubis which was probably cartilaginous in all but the largest specimens. The limbs are of typical temnospondyl proportions and the forelimbs are approximately two-thirds the length of the hindlimbs. Most carpals and all tarsals were ossified in large individuals. A ventral integument, comprising rows of overlapping gastralia, is present.

2.1.2. Size range. Few specimens of *Balanerpeton* have a skull and presacral skeleton in articulation and none has a complete tail. Overall dimensions have had to be deduced from partial specimens, particularly skulls, which can be most certainly assigned to the genus. The skull:trunk ratio in *Balanerpeton* is 1:3 (e.g. NMS G 1985.4.1, see Fig. 7A). No specimen has a complete tail, but NMS G 1985.4.1 has some of the scale-bearing skin of the tail visible along one edge of the slab, the greater part of the tail being off the slab. In this specimen, the tail length can be seen to be at least twice the skull length, giving a skull:trunk:tail ratio of 1:3:2+. In apparently homeomorphic dissorophoid temnospondyls, such as branchiosaurids, with short (20–25) presacral columns and complete tails, the skull:trunk:tail ratio is 1:3:3 and these proportions are assumed for *Balanerpeton*.

In the available material, total mid-line skull lengths range between 25 mm (UMZC T1313) and 48 mm (UMZC T1312). If isometric growth is assumed in *Balanerpeton*, then total lengths for these individuals may be estimated as ranging from 175 mm to 336 mm. However, the largest individual of *Balanerpeton*, GLAMG G 1985.232.1, is known only from the posterior postcranial region including a femur 35.3 mm long. Scaling this specimen against the femur of NMS G 1985.4.1 and assuming isometric growth, the resulting total length for GLAMG G 1985.232.1 is estimated as 434 mm.

2.2. Skull

2.2.1. Skull roof (Figs 2, 3A, 3C, 4, 5A–B, 17). The skull roof of *Balanerpeton woodi* is a mosaic of primitive and derived features. An abbreviated snout is bordered anteriorly by a narrow premaxillary (Figs 2A–B, 4). The posterior margin of each premaxillary bears a pronounced

alary process or pars dorsalis, which does not directly border the external nares but is inset towards the midline. These 'free' alary processes extend backwards to lie almost level with the posterior margin of the external nares; they are well developed even in the juvenile specimen UMZCT1313 (Fig. 17). Most of the snout area is occupied by slightly anteriorly expanded nasals, which are bordered laterally by the lacrimals along an extensive common suture. The lacrimal shows no tendency to reduction and enters both the narial and orbital margins, making a substantial contribution to the latter. Although withdrawal of the lacrimal from the margins of both naris and orbit occurs in larger, longer-snouted temnospondyls and may thus be partly a size-linked character, it is not restricted to them since similar lacrimal withdrawal also occurs in post-metamorphic individuals of *Sclerocephalus* before significant snout elongation (Boy 1988). A slender maxillary extends posteriorly from the external naris to suture at almost a point contact with the quadratojugal; this configuration excludes the jugal from the cheek margin (Figs 2A, 4).

Large external nares are located on the anterolateral edge of the snout and are bordered by the premaxillaries, maxillaries, nasals and lacrimals. No septomaxillaries have

been detected in any specimens, although none has a well-preserved snout and such a small bone may have been subject to postmortem loss.

A striking feature of *Balanerpeton woodi* is the extreme narrowness of the interorbital region which separates very wide, dorsolaterally directed orbits. Frontal bones are consistently very slender, even in the largest animals, and there is only slight evidence of negative allometry of orbits which is commonly associated with ontogenetic development, there being change in ratio of orbital diameter:total skull length of 1:2.55 in the juvenile to 1:3.10 in the largest skull, UMZCT1312. With the exception of the jugal, the configuration of the circumorbital bones is conservative and plesiomorphic for temnospondyls. Prefrontals and postfrontals of approximately equal size meet halfway along the medial orbital edge via a very short suture. The posterior orbit margin is bordered by an elongate, triangular postorbital which reaches over halfway to the otic notch. A triangular jugal narrows to an anterior point contact with the lacrimal near the anterior orbital edge.

The skull table is approximately the same length (measured from the pineal to posterior edge) as the snout. A large pineal foramen is located on the anterior third of

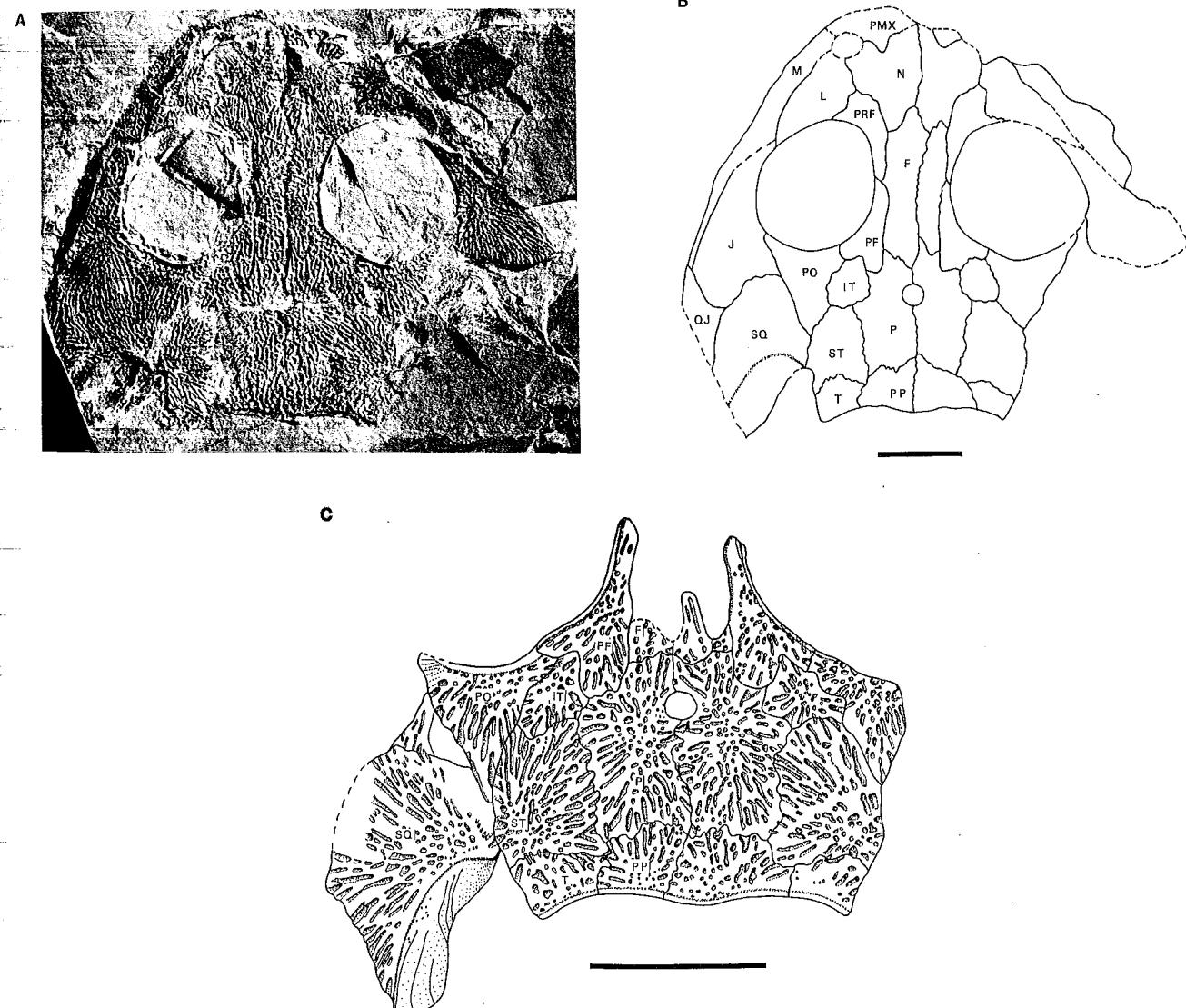


Figure 2 *Balanerpeton woodi* gen. et sp. nov., skull roofs. (A, B) UMZCT1312. (A) Natural mould of dorsal surface of skull, photograph reversed to simulate positive relief of original bone, $\times 1.25$; (B) interpretive drawing of same specimen, also reversed; (C) NMS G 1987.7.32, drawing of dorsal surface of skull table and left cheek. Scale bars, 10 mm.

the common parietal suture and persists in large specimens. Paired, rhomboidal intertemporals, of approximately the same dimensions as the tabulars, abut the anterolateral margins of the parietals and extend forwards to indent the posterior margins of the postfrontals. The gently concave posterior skull-table margin is composed of shallow postparietals and slightly smaller tabulars. The latter show no tendency to posterolateral elongation as 'horns'. The margin of the tympanic embayment is formed by the tabular, supratemporal and squamosal.

2.2.2. Palate and braincase (Figs 1, 3B, D, 5B, 6A–D). The palate of *Balanerpeton* possesses several features characteristic of advanced temnospondyls. Enlarged, anteriorly rounded palatal vacuities, of combined width approximately half the skull width, are anteriorly bordered by substantial vomers. The vomers completely exclude the pterygoids

from the anterior margin of the vacuity and short posterior vomerine extensions enclose the narrow anterior termination of the cultriform process. The remaining palatal vacuity is bordered by slender palatine rami of the pterygoids. The pterygoids differentiate posterolaterally into small quadrate rami. The entire ventral surface of the pterygoids is covered in a shagreen of denticles. Such size reduction of the triradiate pterygoid is considered to be a derived character.

The palatines and ectopterygoids are of similar dimensions and retain the plesiomorphic condition in which there is no substantial reduction of either bone, and the ectopterygoid enters the anterior margin of the subtemporal fossa (a primitive feature). In some temnospondyl clades, including the otherwise primitive Cochleosauridae, the ectopterygoid is excluded from the fossa margin by outgrowths of the jugal and/or pterygoid. The subtemporal

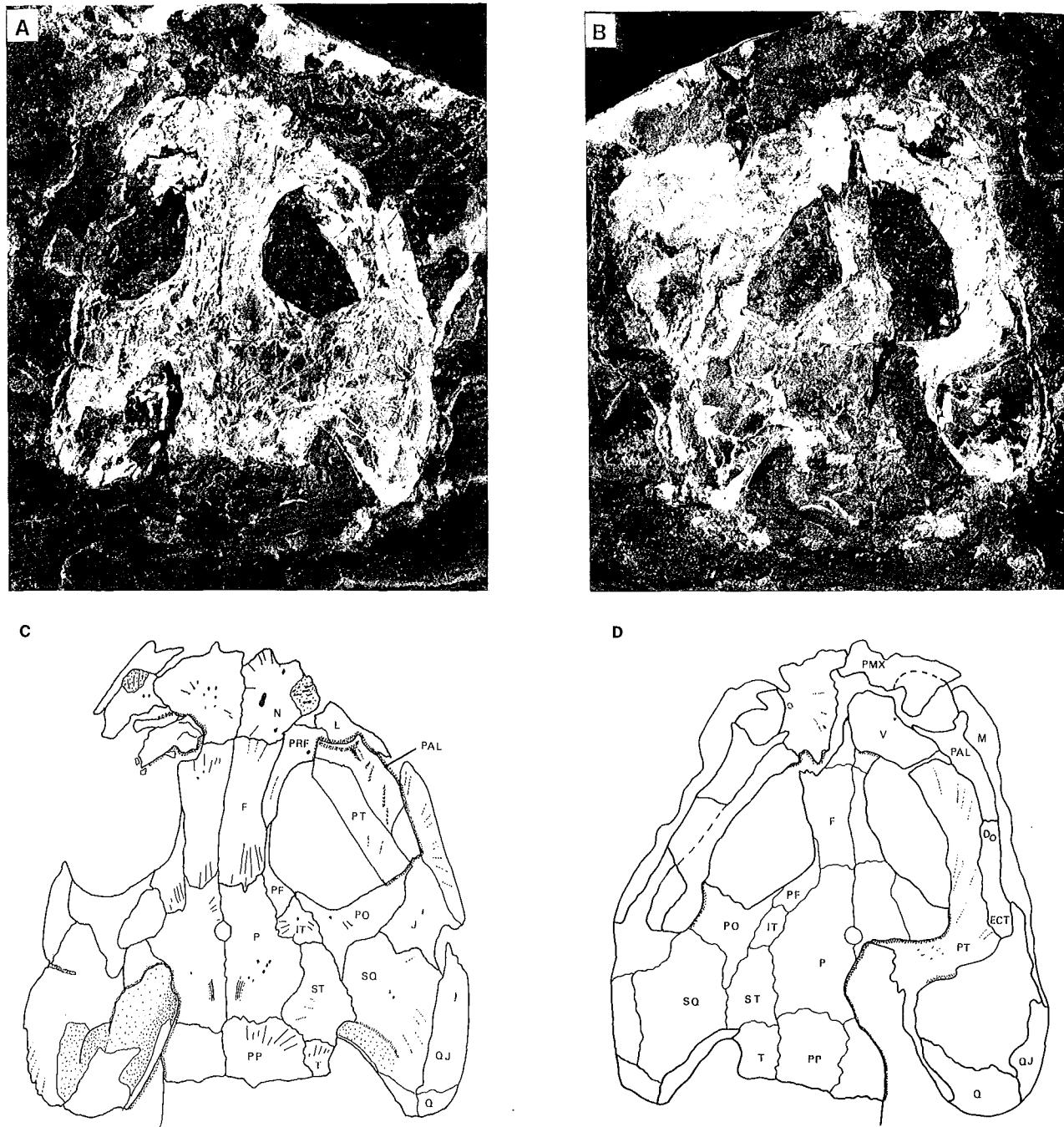


Figure 3 *Balanerpeton woodi* gen. et sp. nov., NMS G 1985.4.2, skull in counterpart. (A) Internal face of skull roof, $\times 1.5$; (B) dorsal surface of palate, $\times 1.5$; (C) drawing of A; (D) drawing of B. Scale bar, 10 mm.

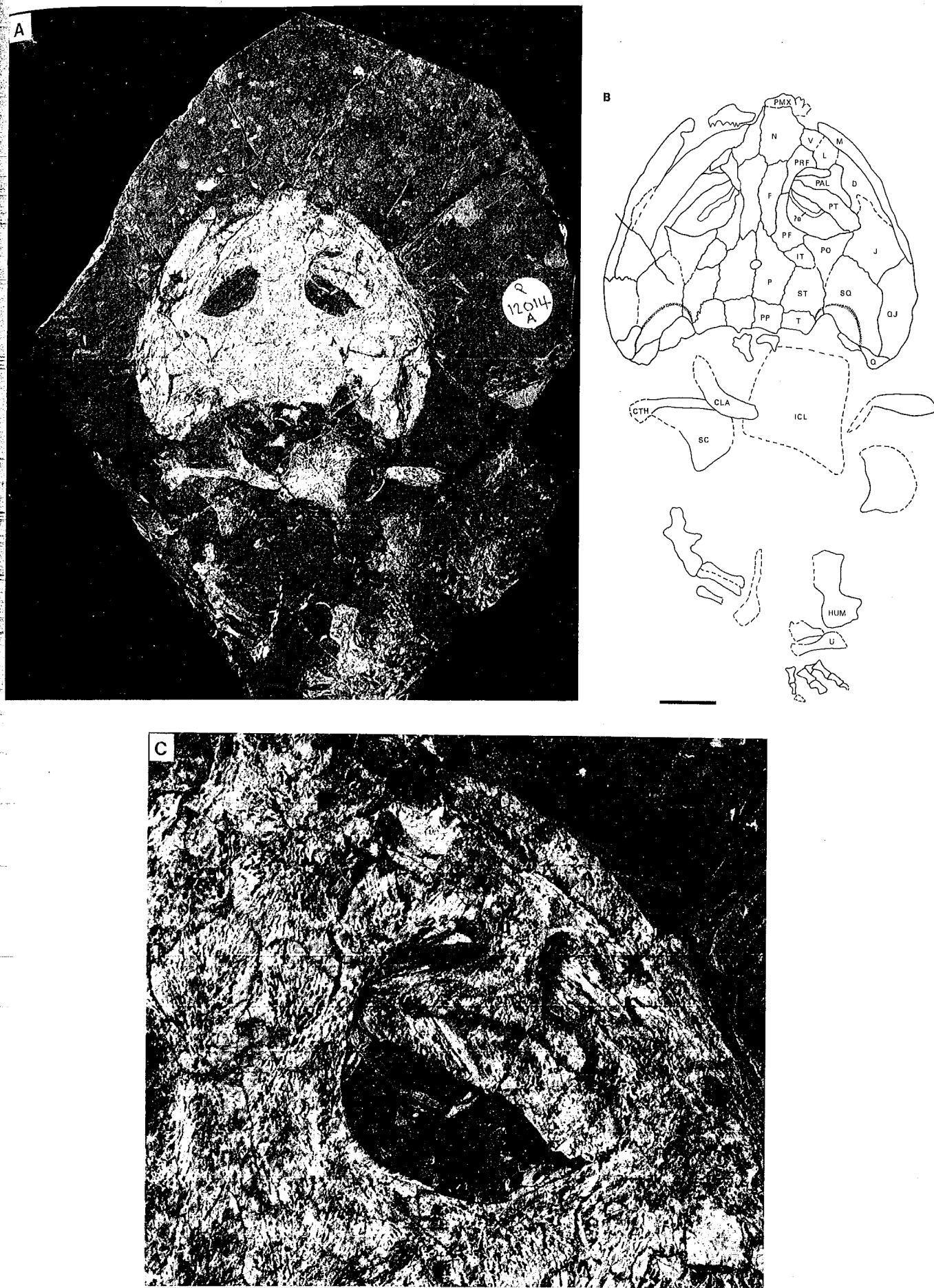


Figure 4 *Balanerpeton woodi* gen. et sp. nov., BMNH R12014. (A) Entire specimen $\times 1$; (B) interpretive drawing of A.; (C) striations in orbit, possibly representing an eyelid, $\times 4$, scale bar, 10 mm.

fossa of *Balanerpeton* is of moderate size and extends approximately one-third the length of the skull. In the anterior portion of the palate, elongate, elliptical choanae are enclosed by the vomers, palatines, and maxillaries; the posterior pars palatina of the premaxillary just fails to contact the anteriormost choanal margin. The posterior margins of the choanae lie level with the anterior edge of the palatal vacuity; choanal length is equal to palatine length. There is no evidence of palatal kinesis; the pterygoid appears to have sutured rigidly along its lateral edge and was, similarly, firmly articulated to the braincase.

The ventral surface of the braincase comprises a broad parasphenoid which is co-ossified to the overlying basisphenoid. Two carotid arterial foramina are present in front of the denticulated region; their path converges as they enter the slender cultriform process. A well-ossified, parallel-sided sphenethmoid is centrally placed on the dorsal surface of the process. It is present, though slightly displaced, in GLAHM V2051 (Fig. 1B) and NMS G 1990.79.3 (Fig. 6C). Other internal elements of the braincase are occasionally visible in specimens in which the skull is disarticulated or compressed producing lateral displacement of the braincase elements. In NMS G 1987.7.32, a pair of elements lying in parallel next to the parasphenoid appear to be the epityrgoids (Fig. 6B). If this interpretation is correct, each has a slender dorsal process fanning out to a slightly expanded ventral blade. In

GLAHM V2051, a bent rectangular element with a prominent foramen lies next to the atlas neural arches behind the skull table (Fig. 9). This does not correspond to a cervical element, nor can it be an exoccipital or basioccipital as these are *in situ*. It appears to be a pro-otic.

2.2.3. Occiput (Fig. 1). Parts of the occiput have been preserved in several specimens but the main elements are best seen in the holotype, GLAHM V2051. The basioccipital is a robust block of bone and appears to form most of the occipital condyle, as in *Edops*. Stout-waisted exoccipitals suture broadly with it (Fig. 1B), the sutural surfaces being exposed in GLAHM V2051. No ossified opisthotics are visible, but were presumably present between the exoccipitals and the underside of the skull roof, as in most other Palaeozoic temnospondyls.

2.2.4. Mandible (Figs 1, 5C–D, 6A). Mandibular structure is most clearly determined from the holotype specimen. The parabolic lower jaws are of conventional temnospondyl configuration with the exception of their unusual pattern of dentition, which is discussed separately. A robust articular condyle surmounts the posterior margin of the moderately enlarged adductor fossa; there is no retro-articular process. The dorsal edges of the surangular and posterior coronoid are differentiated into a relatively high surangular process which is particularly apparent in UMZCT1261. All three coronoids are densely denticulate.

Two small Meckelian fossae and, between them, two

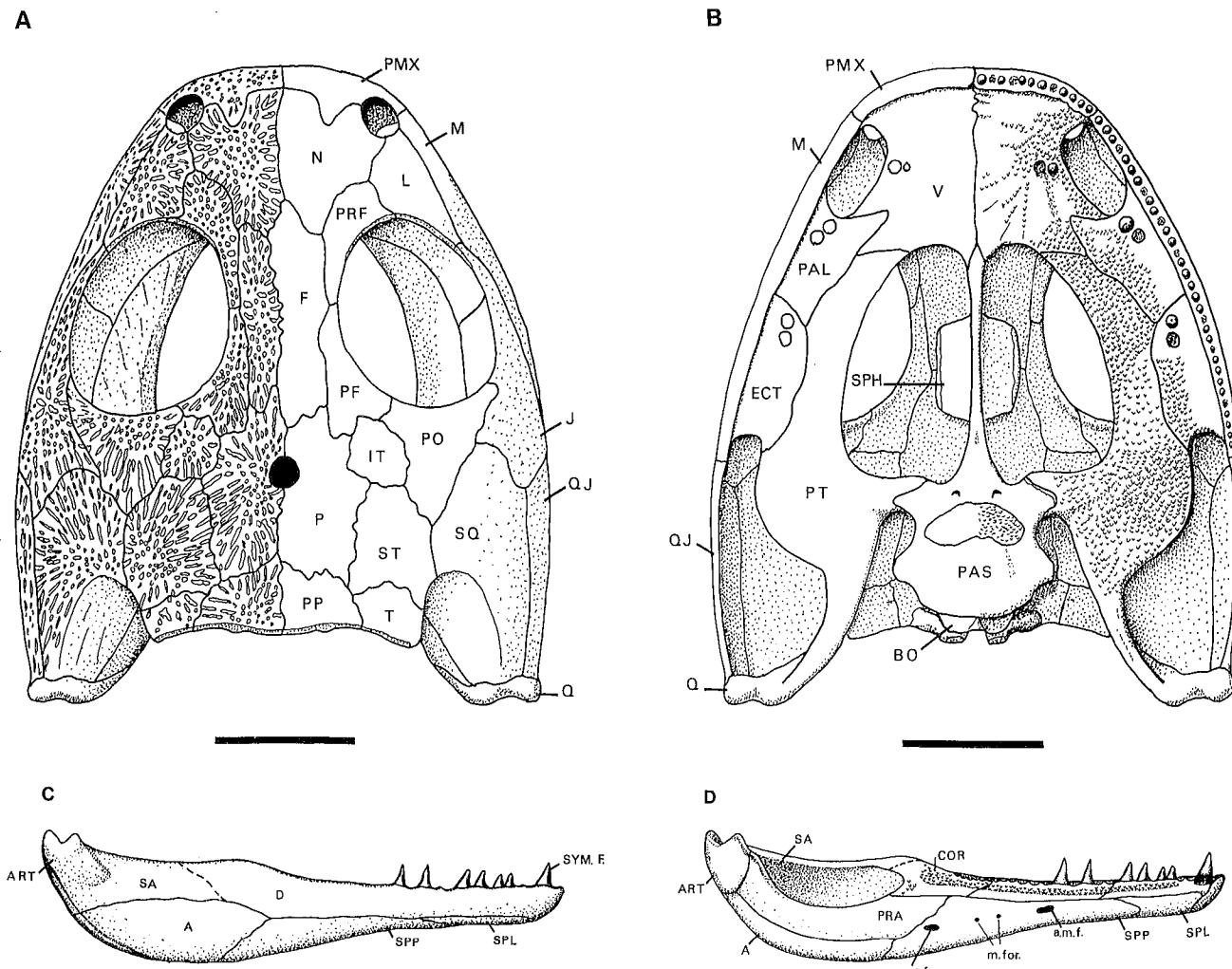


Figure 5 *Balanerpeton woodi* gen. et sp. nov., reconstructions of skull and mandible. (A) Skull in dorsal aspect; (B) palate in ventral aspect; (C) mandible in lateral aspect based on several specimens; (D) medial aspect based on GLAHM V2051. Scale bars, 10 mm.

foramina are present along the medial surface of the postsplenial; there is no indication of a para-articular foramen at the prearticular-articular junction. The two foramina in the middle of the postsplenial may be the rudiment of a second anterior Meckelian fossa such as occurs in *Caerorhachis*. Both anterior and posterior Meckelian fossae are tiny compared with those of most temnospondyls. Unusually, the posterior fossa seems to lie anterior to the angular-postsplenial suture. The presplenial appears to have been excluded from the short, vertically-orientated jaw symphysis which expands slightly into a small buttress on its posteroventral edge. Most of the mandible lies within the vertical plane with only slight torsion occurring near the adductor fossa.

2.2.5. Dentition (Figs 1, 5C–D). The following details derive from specimens GLAHM V2051, UMZC T1261 and NMS G 1987.7.32. The upper and lower marginal teeth are of similar conical shape, being sharply pointed and slightly recurved. However, the marginal teeth in the mandible of the holotype specimen are far larger and more robust than the maxillary complement. Each tooth bears longitudinal striations ascending from the base and grading into smooth enamel towards the pointed apex. The tooth bases are subcircular in outline; their transverse impressions reveal labyrinthine infolding of enamel towards the central tooth core.

Upper marginal teeth. The full complement of marginal teeth is estimated to be 40–42 in each ramus of the upper jaw. There is space for 12 teeth on each premaxillary of the holotype. All upper marginal teeth appear to have been of similar small size and no pseudocanine peaking is apparent.

Lower marginal teeth. In the holotype specimen, the teeth on the mandibular rami are approximately three times the linear dimensions of those of the upper jaw. There is a consequent reduction in the total number of teeth present on the lower jaw, with room for an estimated maximum of 25 teeth on each dentary of GLAHM V2051. However, NMS G 1987.7.32 and UMZC T1261, which are of similar or slightly larger skull size, appear to possess 30–35 teeth per dentary. Absolute tooth numbers may have been individually variable and may also have been size linked; insufficiency of data precludes an accurate assessment for this sample.

In GLAHM V2051, the morphological left dentary can be seen to bear a recurved symphyseal fang, which is not significantly larger than other dentary teeth, but is set slightly more medially, in line with the coronoid denticles. Some specimens (NMS G 1987.7.32, UMZC T1261) show evidence of size-differentiated tooth clusters in the remaining mandibular dentition. A dense, even shagreen of coronoid denticles is present on a raised plate on the dorsal surface of each coronoid; these elongate denticle-bearing plates lie along the mesial edge of the marginal dentition. Although most denticles on the posterior coronoid of the holotype are located on the plate, there is also a small denticle cluster just ahead of the anterior margin of the adductor fossa.

Palatal dentition (Figs 1, 5B, 6A–B). Fang-pairs are present on the vomers, palatines and ectopterygoids and the entire remaining bone surface of the palate is abundantly covered with denticles. The vomerine fang-pair is located at the anteromedial edge of the choana, about half way along the anteroposterior length of each vomer. They are the smallest palatal fangs and each pair is orientated at right angles to the mid-line suture; the remaining fang-pairs are aligned parallel to the nearest marginal dentition. Denticle

ridges radiate posterolaterally towards the vomerine margin and choanal edge from these fangs; fewer denticles are present on the anterior vomer. The larger palatine fangs are accommodated on a small, raised shelf at the anterolateral end of the Y-shaped palatine; there are of similar size to those on the ectopterygoid. The ectopterygoid pair do not appear to have developed on such a shelf, but their configuration is partially obscured in the holotype.

A shagreen of denticles covers most of the palatines, ectopterygoids and pterygoids and reaches along the quadrate ramus of the latter bone. The lateral regions of the palatines and ectopterygoids are not exposed on any specimen and the presence of denticles in this region cannot be confirmed. On the parasphenoid, denticles are restricted to a crescent-shaped region which lies just posterior to the basipterygoid articulation and stretches across the waisted portion of the basal plate. Small, isolated denticulate plates lying anterior to the sphenethmoid in GLAHM V2051 were probably dislodged from the skin that covered the interpterygoid vacuities.

2.2.6. Stapes and hyobranchial skeleton (Fig. 6E–F). Stapes are visible in two specimens, NMS G 1990.79.4 and NMS G 1991.47.2. One left stapes and two right stapes are represented in these specimens; none is complete and most detail derives from the right stapes of NMS G 1990.79.4 which is obliquely sectioned and exposed in anterior aspect. The element possesses advanced structural modifications associated with reception and transmission of high-frequency sound waves; it is morphologically most similar to the stapes of the Lower Permian temnospondyl *Doleserpeton*.

The stapes of NMS G 1990.79.4 is 5·6 mm long, measured from the base of the footplate to the unfinished distal tip of the shaft; the stapes of NMS G 1991.47.2 is slightly smaller being of length approximately 5·0 mm. The footplate of NMS G 1990.79.4 is 3·0 mm high and thus the ratio of stapes height to length is 1:1·86. The relative increase in shaft length together with its slender shape implies that its original functional role as a supporting element in the palate has been superceded by its role as an impedance-matching ossicle for reception of high-frequency sound. This is the earliest example of such a stapes in the fossil record and predates that of *Doleserpeton* by 60 Ma.

A well defined stapedial groove is present on the dorsal shaft surface and is continuous with the large, ventrally located stapedial foramen. The squared distal end of the shaft in NMS G 1991.47.2 implies that it may have possessed a cartilaginous extracolumellar process linked to the tympanum. The stapedial footplate is undivided and consists of a single proximal head.

No ossified hyobranchial elements have been identified in any specimens, nor is there any trace of gill rakers in the smallest specimen (UMZC T1313).

2.2.7. Sclerotic ring and possible eyelid (Figs 1, 4C). Partial articulated series of ossified sclerotic plates are preserved in both orbits of the holotype (Fig. 1). Seventeen plates occupy just over half the circumference of the right orbit margin, suggesting a typical temnospondyl condition of about 30 plates per sclerotic ring (Milner 1982b). Each plate is slightly under 2 mm in radial length.

In BMNH R12014, the dorsomedial region of each orbit bears a faintly mineralised series of fold-like structures paralleling the curved dorsomedial margin (Fig. 4C). There are no discrete palpebral ossifications, but the position and nature of these structures suggests that eyelids with a slightly mineralized integument were present.

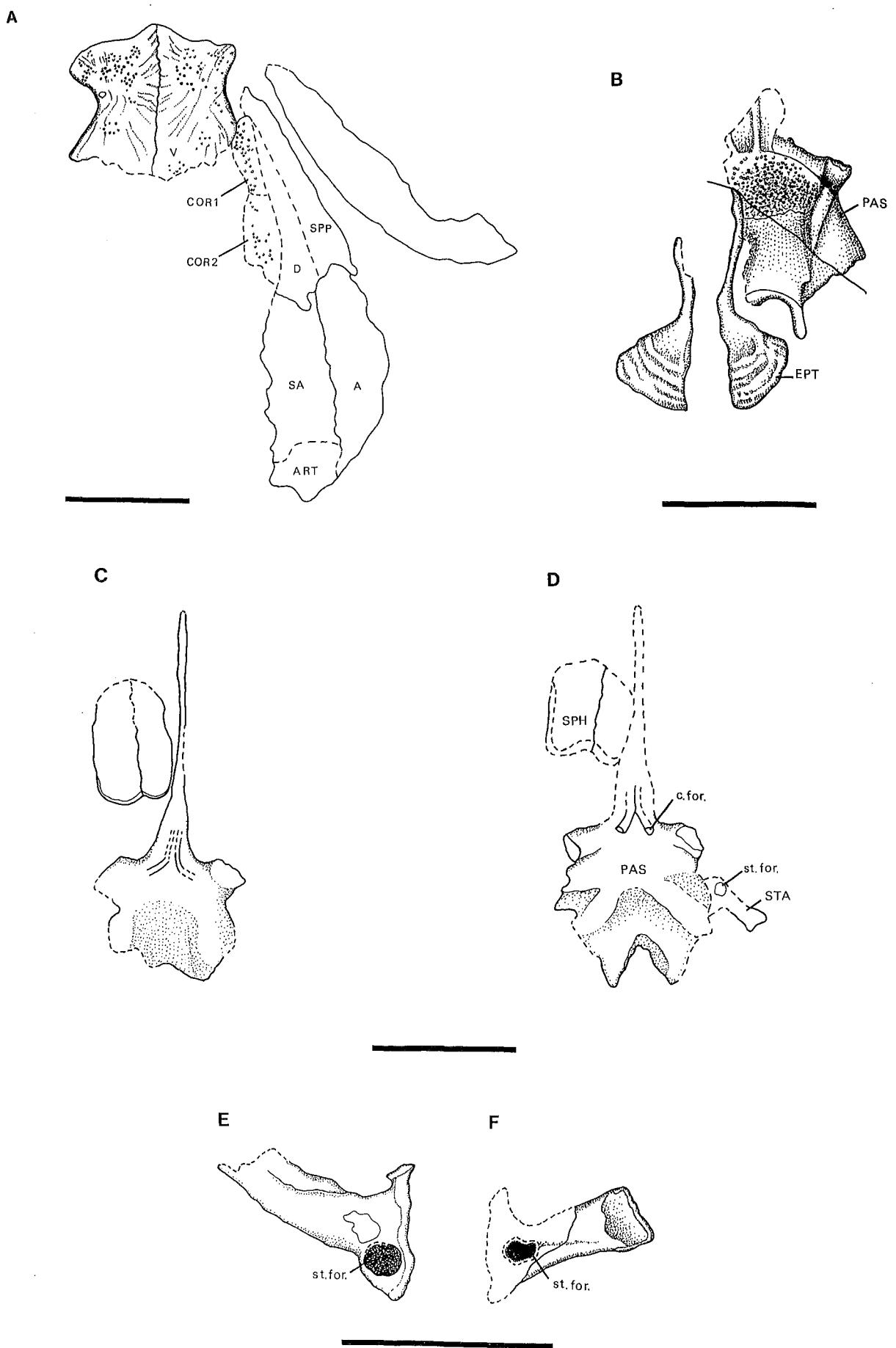


Figure 6 *Balanerpeton woodi* gen. et sp. nov., palate and braincase. (A) BMNH R12015, drawing of vomers in ventral aspect, and mandible in lateral aspect; (B) NMS G 1987.7.32, drawing of epipterygoids and parasphenoid; (C, D) Paraphenoids and sphenethmoids, (C) NMS G 1990.79.3, (D) NMS G 1991.47.2, (E, F) Stapes (E) NMS G 1990.79.4, (F) NMS G 1991.47.2. Scale bars, 10 mm (A–D), 5 mm (E, F).

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2.3. Axial skeleton

2.3.1. Proatlas-atlas-axis complex (Fig. 9). This is most clearly observed in the holotype. The atlas complex has been disrupted and isolated components abut the posterior skull-table margin; the axis remains articulated in the vertebral column. A small bone wedged between the anterior facet of the axis and the skull-table margin probably represents a proatlas in lateral aspect; paired slender elongate neural arches which comprise the atlas overlap further along the skull-table edge. None is completely exposed but one presents a wide, recurved flange which is interpreted as the dorsolateral portion of the neural arch. There is no clearly associated intercentrum nor pleurocentra.

The robust axis is the largest vertebra; it consists of massive, paired and apparently fused neural arches. The high, broad neural spine has an undulating but unstriated lateral surface providing a wide area for muscle attachment. A thickened ridge along the anterolateral margin of the spine is probably a crushed prezygapophysis; the posterior portion of the vertebral element is obscured by the prezygapophyses of the following vertebra. Again, no central elements remain firmly associated with this complex.

2.3.2. Dorsal vertebrae (Figs 7–10B). The 22 postaxial dorsal vertebrae are roughly similar in size, but their total length gradually increases to maximum dimensions at the sacrum (NMS G 1985.4.1, GLAHM V2052, UMZC T1261). Each vertebra consists of paired neural arches, which are not co-ossified and which are associated with one anterior intercentrum and two smaller posterior pleurocentra; strongly developed zygapophyses provide large articular surfaces resulting in increased column strength. Dimensions of the neural spines and neural arches are almost equal with the exception of dorsal vertebra 5 in the holotype. The visible left half of the neural spine in this specimen is significantly reduced in height and is semicircular in lateral outline. Height reduction in an anterior dorsal vertebra is a widespread phenomenon in temnospondyls, but it usually occurs in vertebra 4 instead. This condition has been described for *Eryops* and *Sclerocephalus haeuseri* (Moulton 1974; Boy 1988) and appears also to be present in *Trimerorhachis sandovalensis* (Berman & Reisz 1980). In all these cases, vertebra 4 has the reduced neural spine, suggesting perhaps, that the modification is phenotypically plastic. Pronounced abridgement of an anterior neural spine also occurs in the Devonian osteolepiform *Eusthenopteron foordi*, where it is associated with the second dorsal vertebra and results from accommodation of the overlying large supraneural spine (Jarvik 1980). The unfinished nature of similarly reduced neural spines in temnospondyls suggests that the blades were capped with cartilage.

Intercentra and pleurocentra are well ossified except in the juvenile, UMZC T1313. The larger intercentra are stout elements which are wedge-shaped in lateral aspect and crescentic and unfused in anteroposterior view. However, almost all have been flattened and their exposed inner surfaces reveal the elements to be structurally bipartite. A sagittally directed suture traverses the broad base of each intercentrum; it marks the zone of fusion of the contralateral intercentral components. The posterodorsal edge of the intercentrum is slightly expanded where it contacts the rib head. Two specimens (NMS G 1985.4.1, NMS G 1987.7.32) possess a series of five or six more heavily ossified intercentra just anterior to the sacrum. This implies that the entire sacral region was specifically modified as a load-bearing complex and provides further evidence of terrestriality in *Balanerpeton*. The paired pleurocentra are

lozenge-shaped and slender in lateral outline; each consists of only one unfused element. Their maximum linear dimensions are 80% of those of the flattened intercentra and they abut the posterior edge of each haemal arch.

2.3.3. Sacral and caudal vertebrae (Figs 10, 14A). A morphologically distinct sacral vertebra has not been identified in any of the available material, but a single pair of sacral ribs in some specimens suggests that only one is present. The conservative structure of the preceding vertebral elements suggests that the major modification of the sacral vertebra will simply be an increase in robustness to provide a firm articular region for the large sacral ribs and pelvis (Fig. 14A).

No specimen has a complete articulated tail and the number of caudal vertebrae is unknown. The base of the tail is visible on a few specimens and nine caudal vertebrae and associated haemal spines are preserved in NMS G 1987.7.33. These vertebrae are poorly preserved and are present mainly as impressions on the matrix. Consequently few details are discernible, but there is a considerable size decrease down the series. A faint impression of the soft tissue of the tail remains on the part of NMS G 1985.4.1.

2.3.4. Ribs and haemal arches (Figs 7–10A, 10C). The following data derive mainly from specimens GLAHM V2051, GLAHM V2052, NMS G 1985.4.1 and UMZC T1261. All trunk ribs are short and straight and of a similar construction, with a central narrow shaft expanded proximally into the articular head. Uncinate processes are never present. The anterior seven-eight pairs of thoracic ribs level with, and immediately posterior to, the pectoral girdle are stout and bear an enlarged spatulate articular head which is not conspicuously bicipital. This is separated from the expanded distal portion of the rib by the narrow, short shaft. The remaining dorsal ribs are not enlarged distally and the shaft remains straight and narrow. Trunk rib length gradually decreases towards the sacral region.

Paired sacral ribs, well preserved in NMS G 1985.4.1, are short, stout and are distinguished by their obviously bicipital heads. By inference, the sacral vertebra would have had well-developed articular surfaces on the intercentrum and neural arch for reception of these ribs. Only a few caudal ribs remain in NMS G 1985.4.1; their proximal heads are very reduced and the narrow shafts are recurved. Haemal chevron impressions remain in the matrix on UMZC T1261, they are triangular and equivalent in length to the caudal vertebrae.

2.4. Appendicular skeleton

2.4.1. Pectoral girdle (Figs 4A–B, 11). The following derives mainly from specimens GLAHM V2051, NMS G 1985.4.1, NMS G 1987.7.32, UMZC T1313 and BMNH R12014. The pectoral girdle elements comprise the median interclavicle together with paired clavicles, scapulocoracoids and cleithra. All elements are ossified even in the juvenile UMZC T1313. The interclavicle is a relatively small, rhomboidal bone varying from 1.5 to 1.1 times longer than wide (see Section 2.6 Ontogeny). Its centre of ossification is defined by a cluster of dermal pits which grade into grooves radiating towards the bone margin. Articular facets for the clavicles are small and occupy approximately one-third of the interclavicular surface area. Clavicles are only incompletely represented. Each has a relatively narrow ventral blade which grades into posterodorsally oriented, slender, unornamented dorsal shaft. The scapulocoracoids are substantial kidney-shaped bones of maximum linear dimensions just less than the humeri. Imperfect preservation precludes identification of the glenoid and supracoracoid



Figure 7 *Balanerpeton woodi* gen. et sp. nov., NMS G 1985.4.1. (A) Nearly complete specimen, $\times 1$; (B) Interpretative drawing, Scale bar, 10 mm.

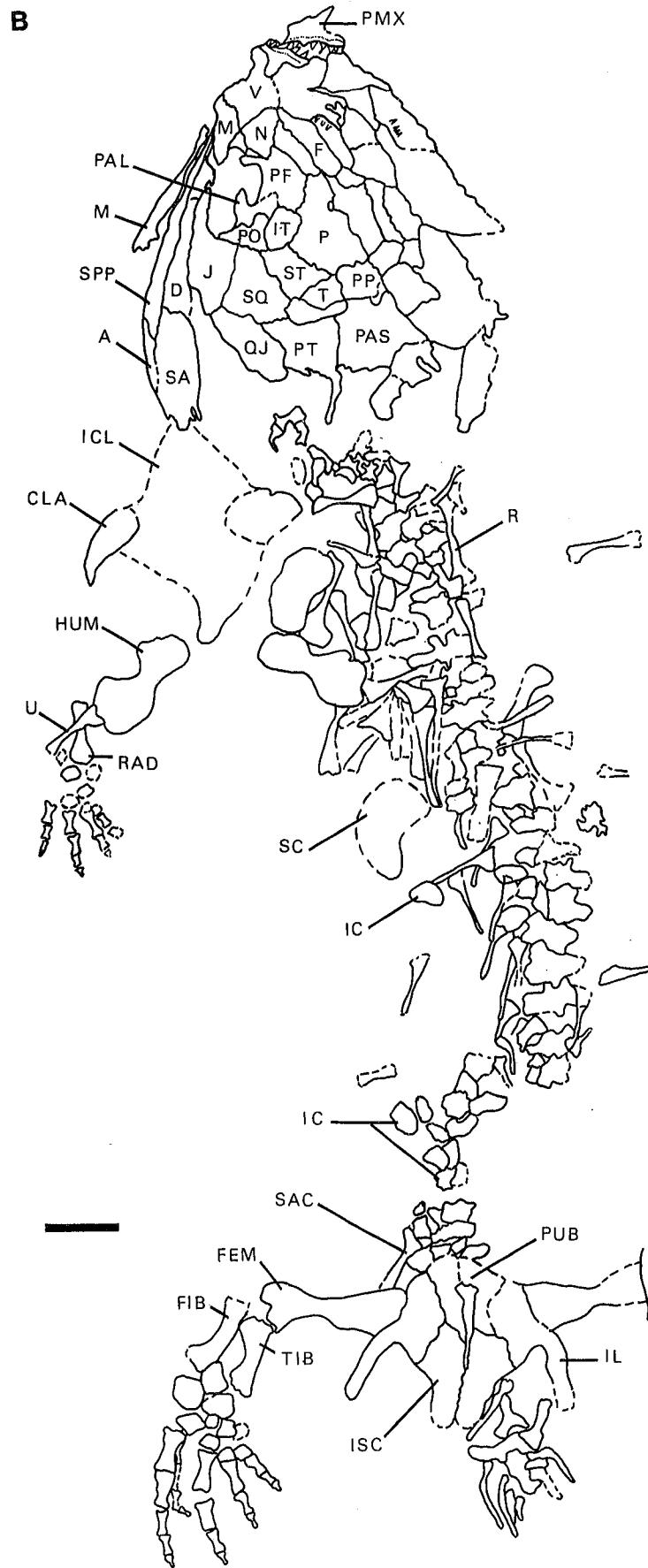


Figure 7 (continued)



Figure 8 *Balanerpeton woodi* gen. et sp. nov., NMS G 1985.4.1, counterpart, $\times 1$.

foramina in any specimens. The cleithrum is a rod-like, slender-shafted element which bears a small, expanded dorsal blade.

2.4.2. Pelvic girdle (Figs 13, 14A, 15A–B). Pelvic girdle structure in *Balanerpeton woodi* is undoubtedly that of a terrestrial temnospondyl. With the exception of the pubis, all elements are well ossified, even in the juvenile UMZCT1313. The ilia and ischia are firmly sutured along the posterior half of the iliac bases. Less well-ossified pubes articulate with the anterior portion of the ilia to complete the central pelvic region. An elongated, posterodorsally directed iliac blade, which lacks a dorsal process, arises from the broadly triangular base. Relative iliac blade length is ontogenetically variable; it represents 65% of the total ilium height in the juvenile UMZCT1313, but only about 50% in larger specimens (NMS G 1985.4.1, GLAHM V2052, UMZCT1261). The medial face of the iliac baseplate possesses a prominent central ridge which is continuous with the iliac blade. Because the sides of the pelvis tend to splay out during compression, the ilia tend to be preserved with the lateral faces downwards in the matrix, and consequently, details of the lateral surface are entirely lacking in the sample.

The ischial plates are the largest pelvic elements. Their overall shape is somewhat variable, but they are essentially cornuate, fanning outwards along their anterior suture.

Ischia are rather more kidney-shaped in the juvenile UMZCT1313 and larger specimen GLAHM V2052.

Ossified pubes are present only in NMS G 1985.4.1 and GLAMG G 1985.232.1 and are incompletely preserved in these relatively large specimens. They clearly ossified late in ontogeny. The obturator foramen is not visible on the preserved bone.

2.4.3. Forelimb (Fig. 12). The forelimb is poorly represented in the available material and is incomplete in all specimens. The following data derives mainly from NMS G 1985.4.1, BMNH R.12014 and UMZCT1313. In these three specimens, most elements are represented and their ossified condition confirms the terrestrial status of *Balanerpeton woodi*. The humeri are robust and broadly expanded at their proximal and distal ends; the intervening shaft is short and relatively broad. A pronounced deltopectoral crest runs along the anterior surface of the bone, diminishing in height towards the distal end. Primitively, a large entepicondylar foramen pierces the broad mesial surface of the entepicondyle just below the waisted central portion of the shaft. Articular condyles for reception of the radius and ulna are located on the distal end of the bone. The proximal end of the humerus is unfinished in the juvenile UMZCT1313 and was probably capped by cartilage.

The radius and ulna are about two-thirds of the length of

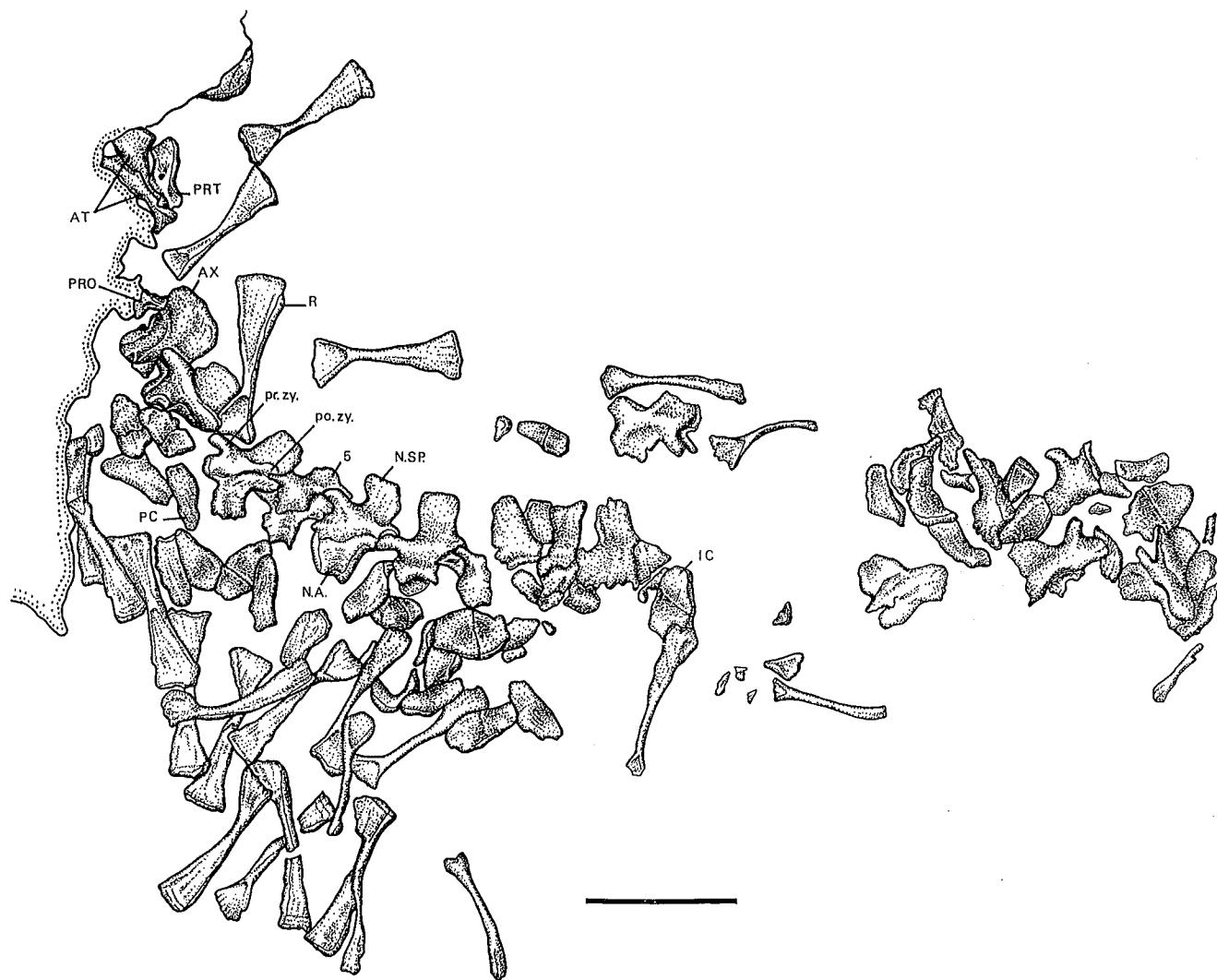


Figure 9 *Balanerpeton woodi* gen. et sp. nov., holotype, GLAHM V2051. Drawing of the cervical region and anterior axial skeleton, scale bar, 10 mm.

the humerus. The ulna is slightly longer than the radius and its expanded proximal end bears a small olecranon process. The distal end is less expanded and the slender shaft has a relatively concave medial edge and a straighter outer edge. The radius has a less expanded proximal end and a more expanded distal end than the ulna. The distal articulation is divided into two distinct faces, one for the radiale and one articulating with centrale 4.

No specimen exhibits a complete carpus in articulation and only a tentative reconstruction can be attempted. In the few later temnospondyls where a carpus is known, 11 carpals are present and this was probably the number present in *Balanerpeton*, although no more than seven can be seen in any one specimen. NMS G 1985.4.1 is the

specimen in which three ossified carpal elements are preserved, together with the impression of a further four carpals in the matrix (Fig. 12D). Surface detail is poor and identification is difficult, but from their position and size it seems that centralium 4, the radiale and an intermedium lie nearest to the epipodials whilst the remaining elements are centralium 2 and distal carpals 1, 2 and 3. The lateral side of the carpus (the ulnare, centralium 3 and distal 4) is missing, but the presence of the fourth digit shows that some carpal elements must have been present. In all probability, the carpus resembled that of later temnospondyls, in possessing radiale, ulnare, intermedium, at least two centralia including C4 and four distal carpals (Fig. 12E).

The distal manus consists of four digits, the phalangeal

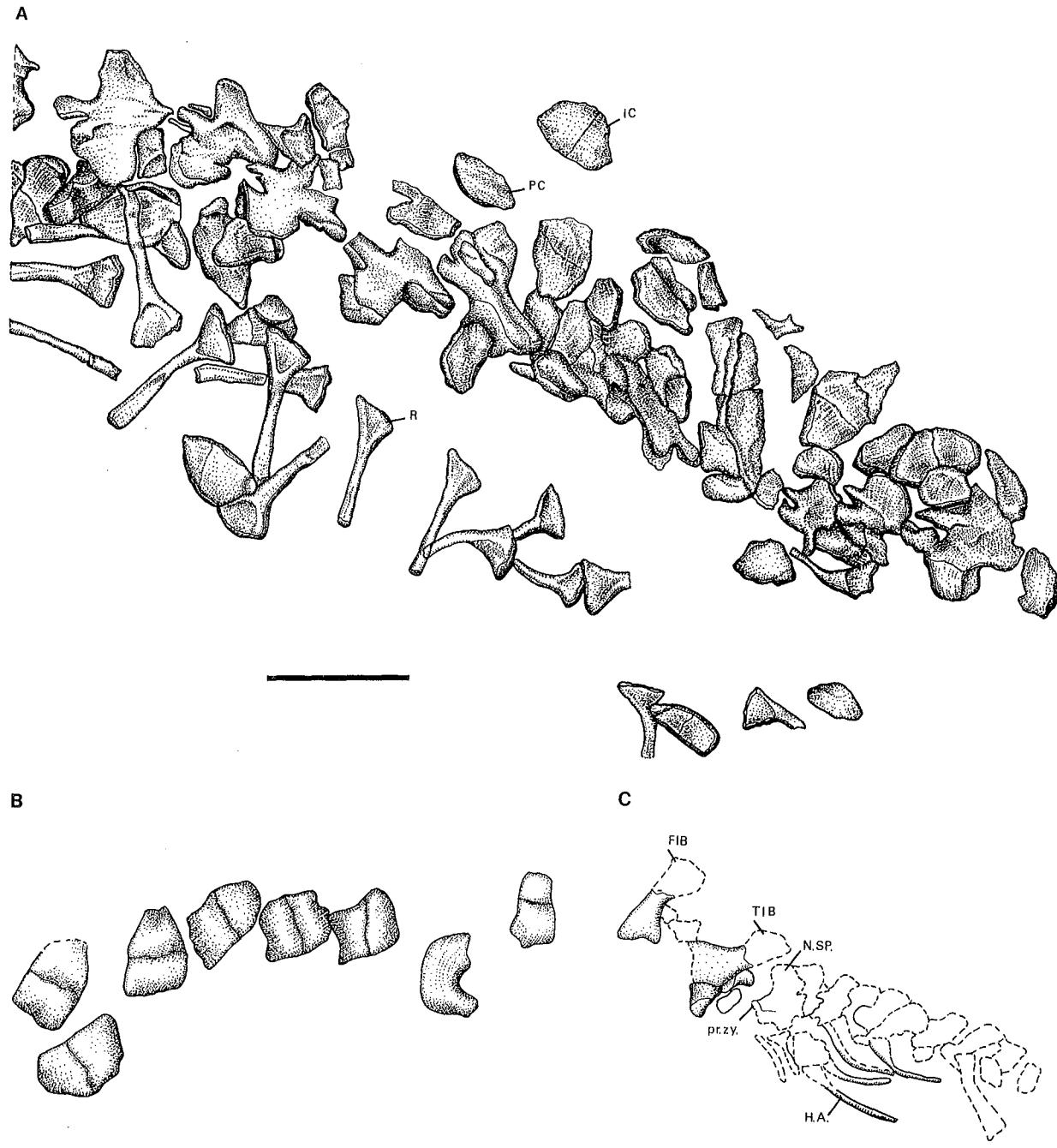


Figure 10 *Balanerpeton woodi* gen. et sp. nov., posterior axial skeleton. (A) GLAHM V2052, posterior trunk region; (B) NMS G 1987.7.32, posterior trunk intercentra; (C) NMS G 1987.7.33, anterior caudal axial skeleton. Scale bars, 10 mm (A, C), 5 mm (B).

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formula of which is not fully determinable from any one specimen. Combining information from both counterparts of NMS G 1985.4.1, it can be seen to have been at least 1 + 2.3.3 and was probably 2.2.3.3 with one of the tiny terminal phalanges having been lost. 2.2.3.3 is one of the commonest formulae for the temnospondyl manus. Metacarpals and phalanges are expanded at both proximal and distal ends, and have slender, waisted shafts. The terminal phalanges are very abbreviated elements.

2.4.4. Hindlimb (Figs 13A, 14, 15C–H). An almost complete and entirely ossified right hindlimb, is present in NMS G 1985.4.1; additional data mainly derive from GLAHM V2052. The femur is the longest individual element; it is fully ossified in large specimens. An internal trochanter arises just below the level of the proximal articular head and grades into an extensive adductor crest, which runs down the medial surface of the bone to terminate at the waisted portion of the shaft. The crest outline is fluted, suggesting the possibility that there may be a distally located fourth trochanter. The expanded distal head of the femur articulates broadly with the tibia and fibula. The tibia is slightly shorter and considerably stouter

than the fibula; its proximal end is broadly triangular and is about 30% wider than the distal head. A conspicuous ridge arises on the ventral surface of the proximal tibial head and continues down to end at the rugose distal articular facet of the bone. The fibula is structurally less complex than the tibia. Its proximal articular head is slender and more symmetrical, and the shaft is more uniformly convex and lacks well-defined ridges. The central region of the bone is waisted and expands distally into a broad, shallow blade thus providing a wide surface for contact with the tarsals. The edge of the blade is acutely angled along its articulation with the intermedium.

There appear to have been 13 tarsal elements in the pes of *Balanerpeton*. Twelve are recognisable in the most complete pes, i.e. that of GLAMG G 1985.232.1 (the largest specimen of *Balanerpeton*) and 11, possibly 12, can be seen in NMS G 1985.4.1 (Fig. 14). Several other specimens possess ossified tarsal elements, but they are more disrupted and less easy to interpret. All elements are dorsoventrally flattened. In GLAMG G 1985.232.1, three proximal elements, three central elements and all five distal elements are present and only centrale 1 seems not to be preserved. As

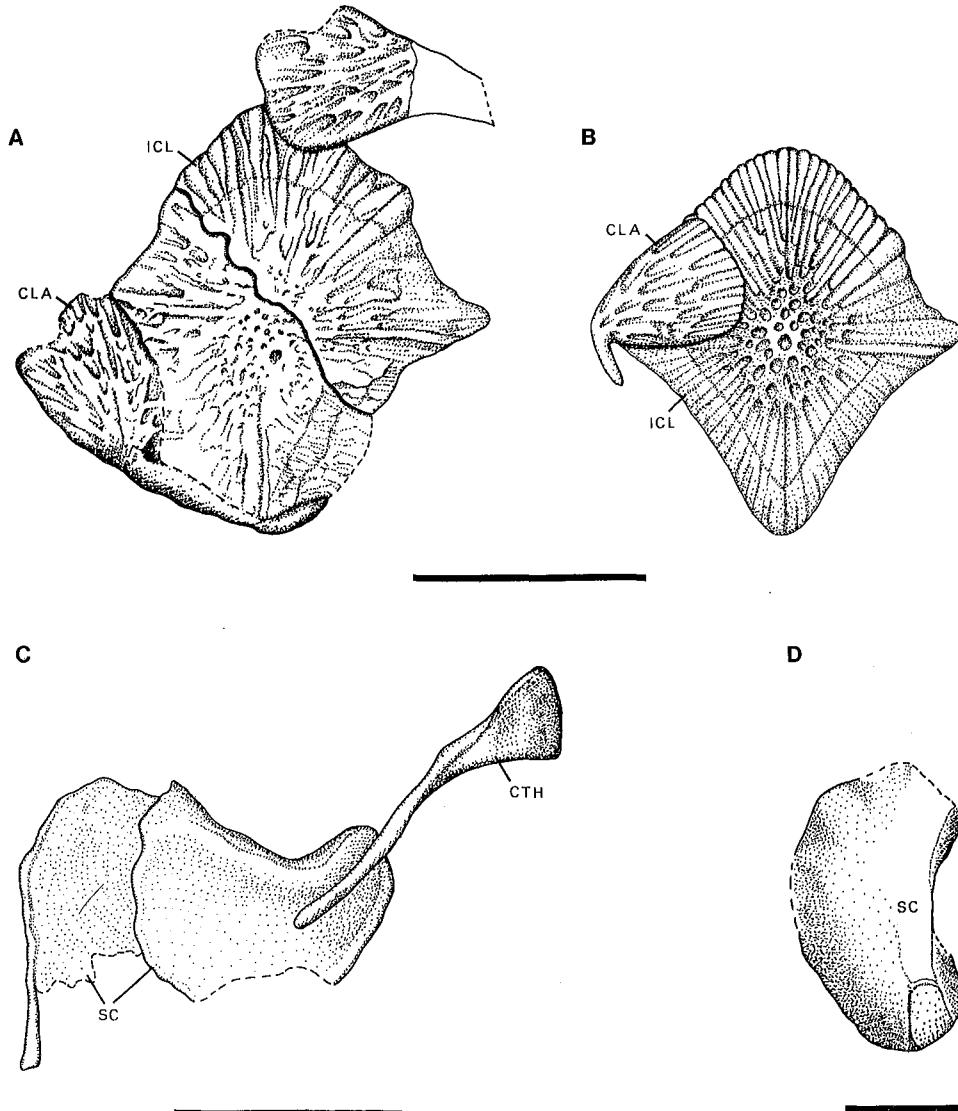


Figure 11 *Balanerpeton woodi* gen. et sp. nov., pectoral girdle. (A) NMS G 1987.7.32, interclavicle and clavicles; (B) reconstruction of interclavicle and clavicle based on NMS G 1987.7.32 and BNMH R12014; (C) scapulocoracoids and cleithra of GLAHM V2051; (D) right scapulocoracoid of NMS G 1985.4.1. Scale bars, 10 mm (A, C), 5 mm (D).

well as these, a small blob of bone next to the distomedial end of the fibula may be the postminimus. In NMS G 1985.4.1, the right ankle is only slightly disarticulated and most elements have not shifted much from their relative positions in life, although the tibiale is partly superimposed on centrale 4, and centrale 1 is preserved only as a faint matrix impression and is difficult to interpret. Distal tarsals remain *in situ* on digits 1 to 4; that of digit 5 being largely obscured by metatarsal 4.

The phalangeal formula of the right pes of NMS G 1985.4.1 is 2.2.3.4.2+ and the fifth pedal digit of UMZC T1261A has three phalanges. The phalangeal formula thus appears to have been 2.2.3.4.3, a common formula for the temnospondyl pes. Metatarsals and phalanges are of similar configuration, with those of digit 3 and 4 being thicker and larger in large specimens (GLAMG G 1985.232.1). All possess a waisted central shaft which expands broadly at both proximal and (with the exception of the terminal phalanges) distal articular surfaces. Terminal phalanges are narrow and pointed at

their distal ends. The structure of the pes is conservative for primitive temnospondyls, there is no evidence of a pretarsal element having been present.

2.5. Scales

2.5.1. Gastralia (Fig. 16). The following description is based on NMS G 1985.4.1, NMS G 1987.7.33, and GLAHM V2052. The ventral integument consists of contralateral rows of gastralia, which overlap along the ventral midline and radiate posterodorsally in a chevron arrangement. The anteriormost rows appear to articulate with the posterolateral margins of the interclavicle. There is a sharp change in the angle of orientation to the midline of rows immediately behind the interclavicle; the initial sequence is parallel to the interclavicle border, but fans outwards to become aligned at right angles to the mid-line at the posteriormost apex of the interclavicle. The remaining following rows slope posterodorsally at an angle of 45° to the ventral midline; each row is overlapped by the posterior margin of the preceding row. The most complete gastralia

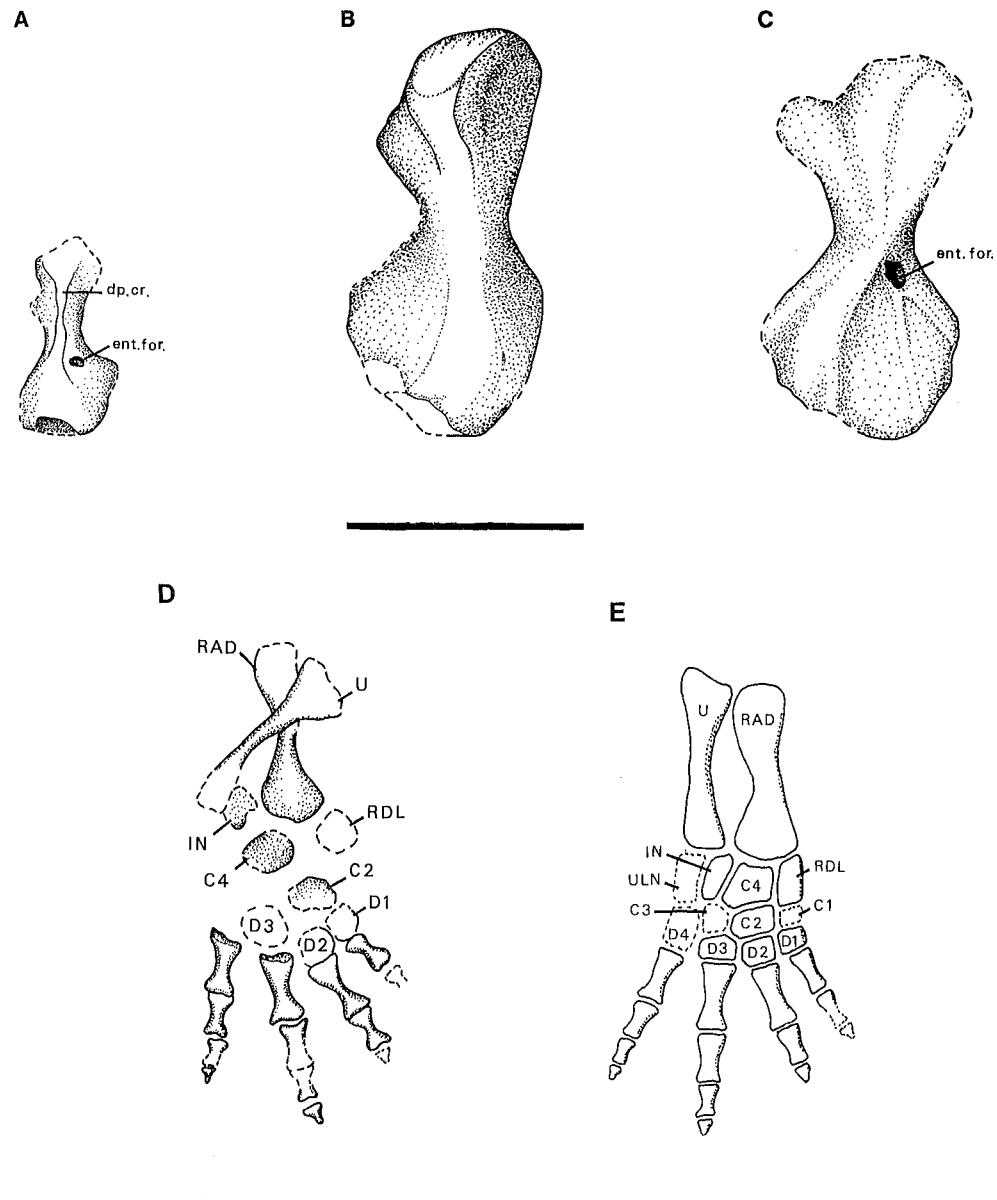


Figure 12 *Balanerpeton woodi* gen. et sp. nov., forelimb. (A) Right humerus of UMZC T1313; (B) right humerus of NMS G 1985.4.1; (C) left humerus of NMS G 1985.4.1; (D) NMS G 1985.4.1, radius, ulna and manus; (E) reconstruction of manus based on NMS G 1985.4.1. Scale bars, 10 mm (A-D).

series preserved in NMS G 1987.7.33 comprises 57 rows, each flank consists of 12–14 elliptical scales of approximate length 2.5–3.0 mm. A pattern of concentric growth rings is present on each scale (Fig. 16B) and the scale perimeter is thickened.

2.5.2. Dorsal osteoderms. There are no clearly identifiable dorsal scales or osteoderms on any specimen although a poorly preserved mineralised region along the back of NMS G 1985.4.1 just posterior to the skull may contain dorsal osteoderms. No individual elements can be seen, but a faint banded pattern is visible. The apparent absence of osteoderms from most specimens suggests that if present at

all, they developed late in ontogeny and were only found in large specimens.

2.6. Ontogeny

Most of the specimens of *Balanerpeton* examined in this study are similar in size with skulls in the 35–48 mm range, but one, UMZCT1313, is significantly smaller with a mid-line skull length of 25 mm (Fig. 17). This individual is considerably less well ossified than the larger specimens and some of the proportions of the skeletal elements are different. The differences are those found in ontogenetic

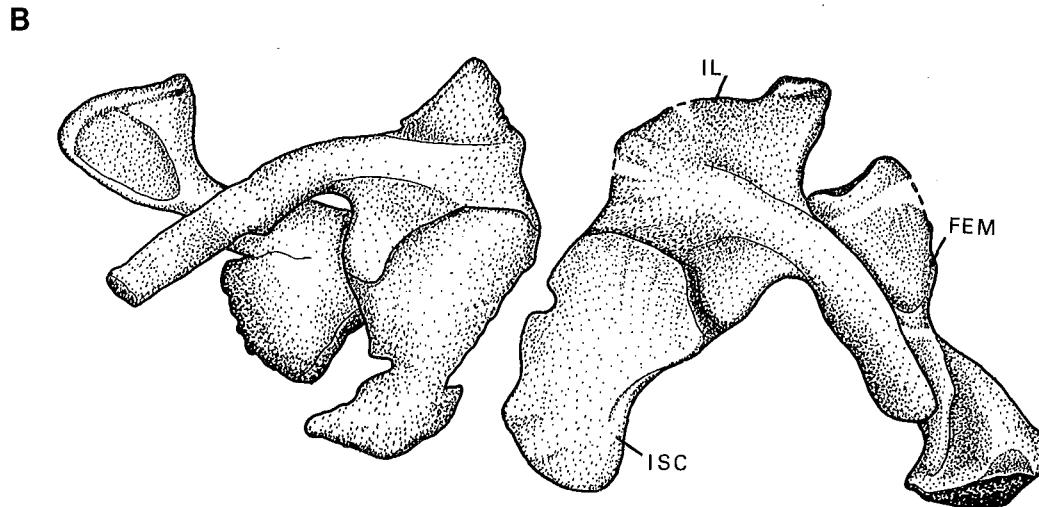


Figure 13 *Balanerpeton woodi* gen. et sp. nov., pelvis and hindlimbs. (A) GLAMG G 1985.232.1, $\times 0.67$; (B) GLAHM V2052, scale bar, 10 mm.

sequences of other temnospondyls and there is no reason to assume that this specimen is not a juvenile of *Balanerpeton*. NMS G 1987.7.33 has a skull length of about 33 mm. It has the same degree of ossification as larger specimens, but some of the proportions bear a greater resemblance to the smaller specimen.

2.6.1. Degree of ossification. The most notable characteristic of juvenility in UMZCT1313 is the reduced degree of ossification of the skeleton, particularly apparent in the vertebral column. No intercentra or pleurocentra are ossified, and relatively few neural arches have developed sufficiently dense bone to permit their postmortem preservation; these are located near the pectoral and pelvic

girdles, but the middle dorsal series is almost invisible. The outline of some middle dorsals may be just discerned in the matrix, showing that the vertebral series was only slightly dispersed by disintegration of the body. The tenuous nature of these impressions suggests that the majority of neural arches were just beginning to ossify at this stage of ontogeny. A few incomplete anterior ribs remain which represent the more robust series associated with the pectoral complex. In the ontogenetic stage chart for juvenile temnospondyl development put forward by Boy (1974), the non-ossification of the centra indicates a specimen at the late larval stage.

In contrast to the axial skeleton, the bones of the skull are

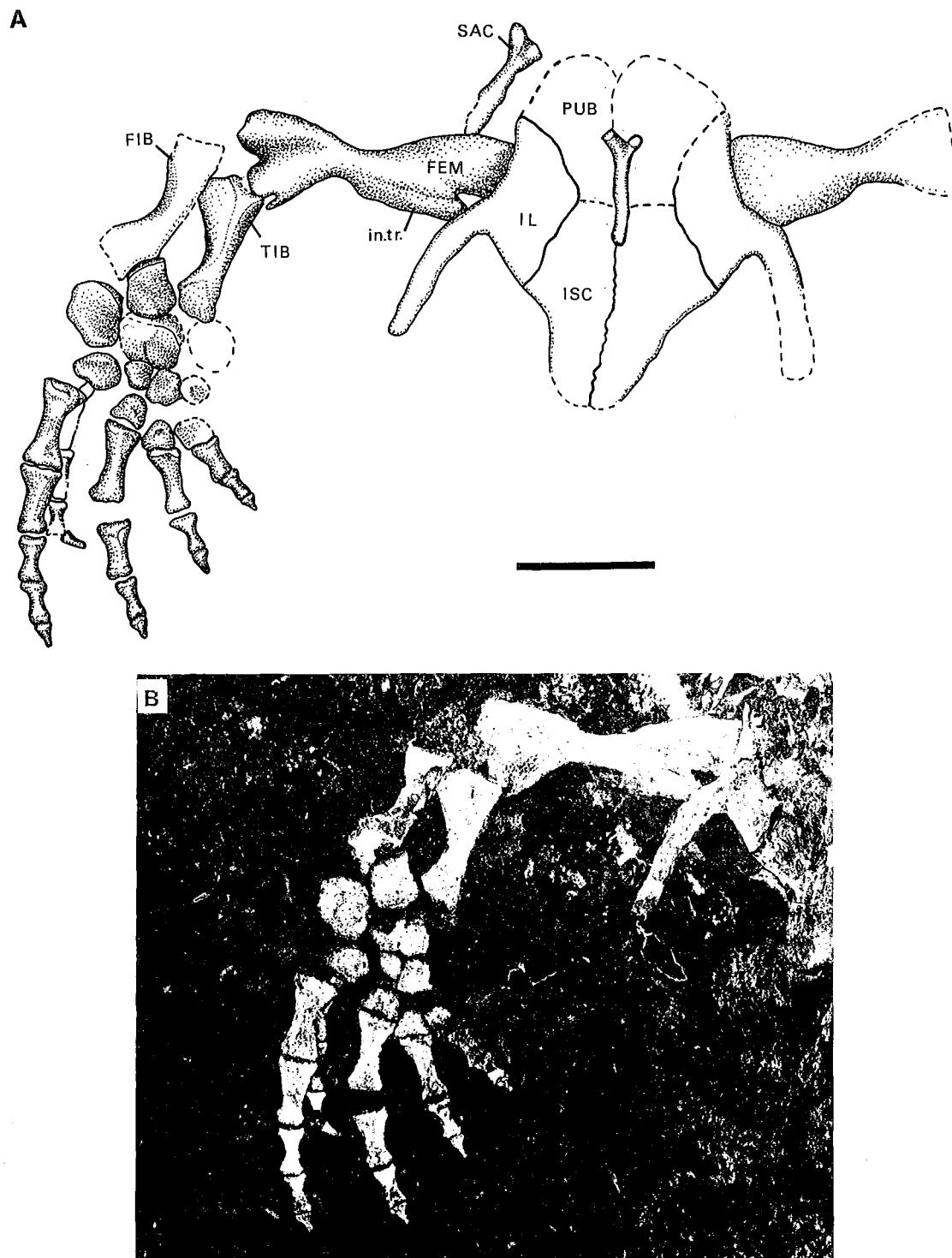


Figure 14 *Balanerpeton woodi* gen. et sp. nov., NMS G 1985.4.1. (A) Drawing of pelvis and hindlimb, scale bar, 10 mm; (B) hindlimb, $\times 2$.

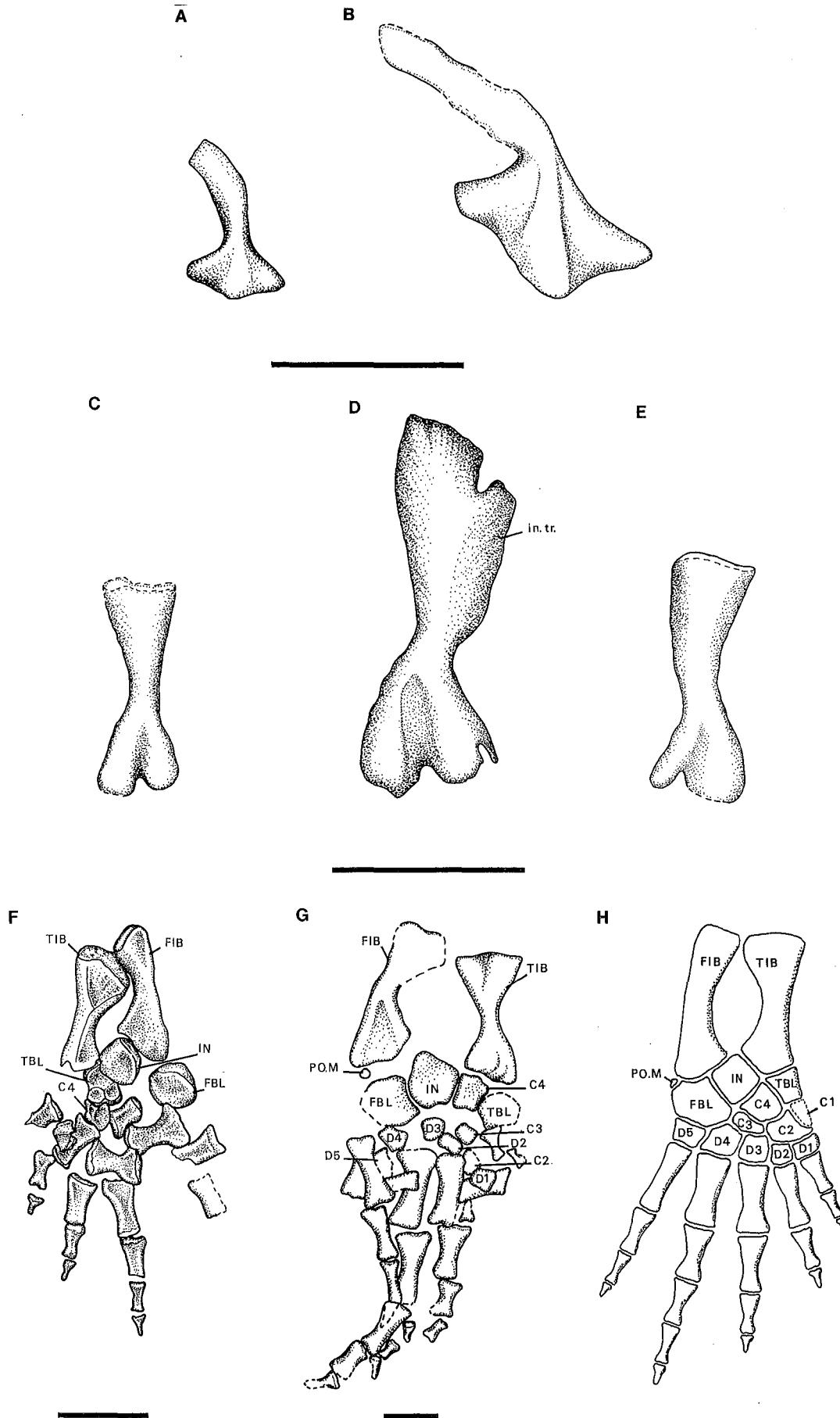


Figure 15 *Balanerpeton woodi* gen. et sp. nov., pelvis and hindlimb. (A) Left ilium of juvenile UMZCT1313 in medial aspect; (B) left ilium of NMS G 1985.4.1 in medial aspect; (C) right femur of juvenile UMZCT1313; (D) right femur of NMS G 1985.4.1; (E) right femur of BMNH R10955; (F) pes of GLAHM V2052; (G) pes of GLAMG G 1985.232.1; (H) composite reconstruction of pes based on NMS G 1985.4.1, GLAHM V2052 and GLAMG G 1985.232.1. Scale bars, 10 mm (A-G).

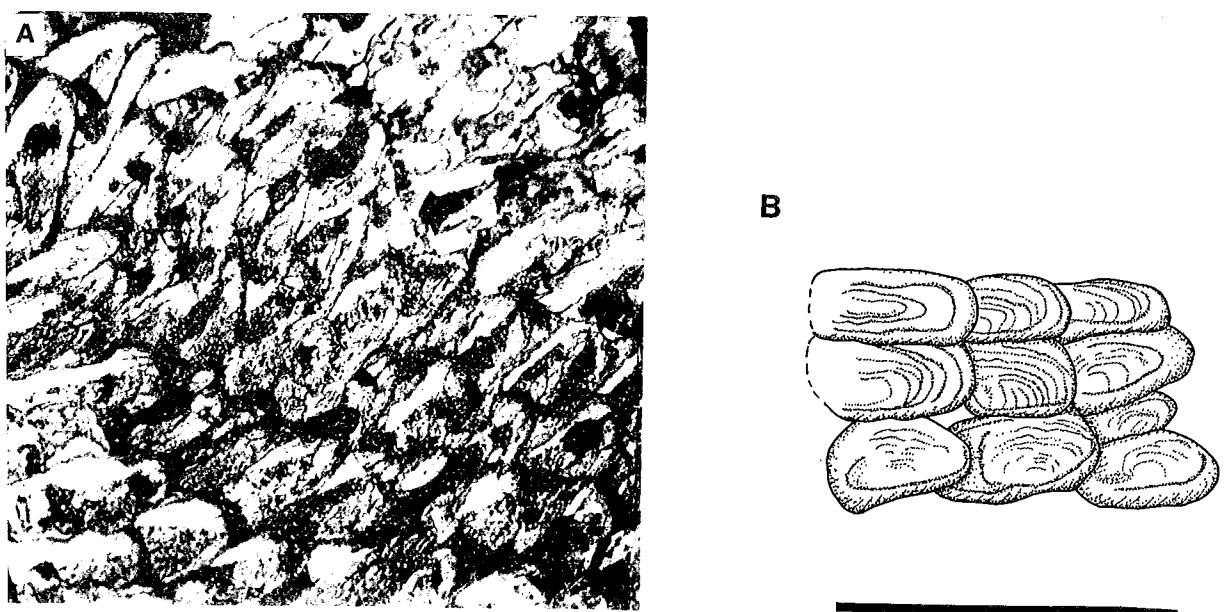


Figure 16 *Balanerpeton woodi* gen. et sp. nov., gastral area. (A) GLAHM V2052, gastral area from posterior trunk, $\times 10$; (B) NMS G 1987.7.33, drawing of gastral area. Scale bar, 5 mm.

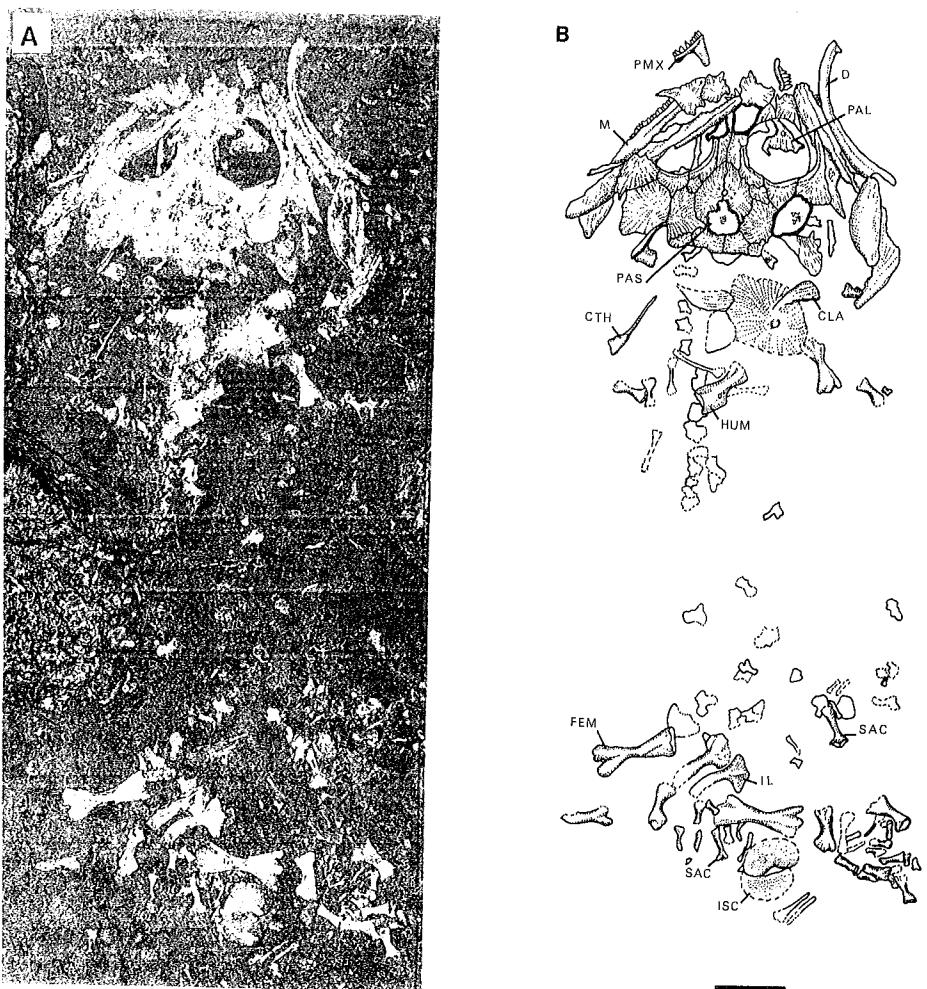


Figure 17 *Balanerpeton woodi* gen. et sp. nov., juvenile specimen UMZC T1313. (A) Specimen, $\times 1$; (B) interpretive drawing of A, Scale bar, 10 mm.

already more fully ossified. Most cranial bones are firmly articulated and there is little disruption of sutures, except around the anterior end of the snout and the posterior cheek region where the elements are disarticulated. These areas may have been incompletely ossified and, as such, may represent regions of rapid growth during postmetamorphic differentiation. Disruption of the anterior snout is common even in more mature specimens of *Balanerpeton*. Patterns of juvenile dermal ornament are similar to those of larger individuals and consist of a pitted region marking the centre of ossification, from which elongate grooves radiate towards the bone margins. However, there is a more dense concentration of grooves in the juvenile since large areas of skull are undergoing active growth. The pineal remains open in all specimens.

Both palatal and marginal dentition are well developed in UMZC T1313 and are as comprehensive as those in more mature individuals. Tooth series in exposed regions of marginal dentition are almost complete and there is a marked absence of replacement pits; several tiny teeth remain *in situ* whilst the impressions of the remainder may be discerned in the matrix. Marginal teeth at the lateral ends of the premaxillaries appear to be considerably larger than other marginal teeth; this feature has not been seen in the holotype or other specimens and may either be characteristic of juveniles, or may represent a transient stage in dentition replacement between one tooth size and the next. The left palatine, exposed in the left orbital space, bears a palatine fang. Patches of palatal denticles are also preserved and an isolated patch is present on the basal plate of the parasphenoid. Dentary teeth are barely represented in UMZC T1313 and their size relative to the upper marginals cannot be assessed.

The dermal pectoral girdle (interclavicle, clavicles and cleithra) is already well ossified although the margins of the interclavicle and the dorsal blades of the clavicles are still poorly defined. The endochondral scapulocoracoids are poorly ossified, such relatively late ossification being typical in developing temnospondyls (Boy 1974) and corresponding to the earliest postmetamorphic phase. The humeri are robust and epipodials are present, but distal forelimb elements are represented by only one indeterminate element—a metacarpal or phalanx. This absence contrasts with the range of hindlimb elements present in this individual. This could be due to incomplete forelimb ossification at this stage or to selective local disintegration and dispersal although the latter seems less likely. Forelimbs are more completely ossified in the larger, postmetamorphic individuals, such as NMS G 1985.4.1, although the carpal appear to be incompletely ossified in that specimen.

The pubis is the only component of the pelvic girdle which is not certainly represented in the juvenile, but this is to be expected since this endochondral element characteristically ossifies at a very late stage of ontogeny in many Palaeozoic amphibians, well after metamorphosis, if at all (Boy 1974). A weakly ossified element adjacent to the right femur may be a displaced pubis. Both ilia are preserved and exposed in medial view on the part and counterpart; their bases are completely ossified and the prominent central ridge, which is continuous with the dorsal iliac blade, has already developed. A pair of flattened, kidney-shaped bones are interpreted as the ischial plates; they are substantially ossified structures which have remained associated along their central suture. Both sacral ribs are present; one is almost complete and is stout with a well-developed bicipital head. The femora are the largest posterior appendicular elements; they are heavily ossified except at the proximal ar-

ticular head, which is less well defined and may have been capped with cartilage. Although the proximal portion of the shaft is broad, a well-defined trochanter is not yet visible. Epipodials, metatarsals and phalanges are present, but tarsals are not certainly identifiable and are probably unossified.

No trace of integument persists implying that dermal scales and osteoderms were not ossified at this stage, and this corresponds to the latest larval stage in the stage charts of Boy (1974).

In conclusion, the presence of most ossified elements shows that this specimen is no younger than the latest larval stage, but the absence of ossified centra and gastralia suggests a late larva, while the partly ossified coracoid suggests an early postmetamorphic individual. It is possible that this specimen, found in an ostracode-rich black shale, was a still-aquatic late larva of *Balanerpeton* living in the lake at the time the black shale was laid down.

2.6.2. Allometric growth. Slight negative allometry of the orbits relative to total skull lengths is the only significant, ontogenetically dependent proportional change in the skull of *Balanerpeton*. The ratio of orbit diameter to total skull length in small specimens (<33 mm long skulls; UMZC T1313, NMS G 1987.7.33) is approximately 1:2.6, but this ratio consistently increases to more than 1:3.0 in larger specimens with total skull lengths in excess of 39.0 mm (GLAHM V2051, BMNH R12014, BMNH R12016, NMS G 1985.4.2, UMZC T1312). Proportional changes in skull-table width compared to total skull length show a similar, but less pronounced pattern in which there is a small decrease in the relative skull-table width; there is no trend towards posterolateral elongation of the tabulars into 'horns' during ontogeny in *Balanerpeton*. The position of the suspensorium relative to the posterior margin of the skull table does not differ greatly between UMZC T1313 and larger individuals, but it does seem to be slightly more posteriorly extensive in UMZC T1313. The basal plate of the parasphenoid of UMZC T1313 is almost square in outline and is of very similar form to those found in the postmetamorphic individuals NMS G 1990.79.3 and NMS G 1991.47.2; here there is some ontogenetic tendency towards slight anteroposterior elongation of the braincase with increasing skull length.

Pectoral girdle elements are seldom well ossified. The interclavicle of the juvenile UMZC T1313 has a width to length ratio of about 1:1.5, whereas larger specimens have a ratio of 1:1.1, suggesting a relative increase in width with size increase. Forelimb differentiation is well established in UMZC T1313; there is positive allometric elongation of the humerus with respect to the interclavicular length during ontogeny, but this probably represents progressive ossification of the element both distalwards and proximalwards from the central shaft. Allometric change in the pelvic girdle affects both the ilia and the ischia. There is an acceleration in the developmental rate of baseplate elongation in the ilium with respect to dorsal blade elongation; juvenile baseplate length to blade height ratios (measured from top blade to top of baseplate) are 1:1.13 whilst those of NMS G 1985.4.1 are 1:1.09. The ischial plates undergo similar allometric elongation, resulting in a length:width ratio increase from 2:1 for the juvenile UMZC T1313 to 4:1 for NMS G 1985.4.1. Hindlimb proportions in the juvenile are very similar to those of NMS G 1985.4.1, postmetamorphic changes in these elements are essentially isometric.

2.7. Reconstruction (Figs 5, 12E, 15H, 18)

The cranial reconstructions in Fig. 5 are composite and are based on specimens BMNH R12014 (skull roof),

UMZC T1312 (skull roof), GLAHM V2051 (palate, brain-case and occiput) and NMS G 1985.4.2 (palate). The three-dimensional shape was restored by analogy with three-dimensional dissorophid skulls from the Lower Permian of Texas and by trial-and-error fit of the palate to the cheeks. The resulting skull looks and is less wide than those of the figured specimens, because the latter are almost invariably flattened dorsoventrally with one or both cheeks splayed out sideways. The marginal dentition is stylised and does not represent an actual replacement sequence. The mandibular reconstruction in Figure 5C-D is based on GLAHM V2051 (medial aspect and ventrolateral aspect) and BMNH R12015 (some lateral sutures). The manual (Fig. 12E) and pedal (Fig. 15H) reconstructions are based largely on NMS G 1985.4.1 with some information from the pedes of GLAHM V2052 and GLAMG G 1985.232.1.

The whole skeleton reconstruction in Figure 18A is based on NMS G 1985.4.1, (general shape, forelimb, pelvis and hindlimb), GLAHM V2051 (anterior vertebrae) and GLAHM V2052 (posterior vertebrae, base of tail and hindlimb). The tail is not known beyond the first few caudal vertebrae. The restoration in Figure 18B is based on 'fleshing' out the skeletal reconstruction in Figure 18A. The resulting animal is very reminiscent of the living salamander *Dicamptodon*, but with larger laterally directed eyes and obvious ear-drums.

2.8. Lifestyle

Balanerpeton has the following morphological features suggestive of a terrestrial habit for the adult:

- (i) absence of lateral-line sulci,
- (ii) absence of any trace of an ossified branchial system,
- (iii) possible presence of eyelids,
- (iv) presence of a large tympanic ear and a relatively rod-like stapes suggesting the ability to perceive high-frequency airborne sound,
- (v) ossified carpals and tarsals,

These morphological features are consistent with the view, based on taphonomic and general faunal evidence, that most of the tetrapods in the East Kirkton Limestone were terrestrial animals.

Specimen UMZC T1313, representing either a late larva or an immediate post-larva is preserved in a black shale, probably from Unit 82. The Unit 82 shales have produced most of the ostracode-rich horizons, the filter-feeding eurypterid specimens and one of the few other apparently aquatic tetrapod specimens, namely the holotype of the anthracosaur *Silvanerpeton miripedes* (Clack, this volume). It appears that during the Unit 82 interval, the East Kirkton water body may have sustained an extended food chain including the larvae of *Balanerpeton*.

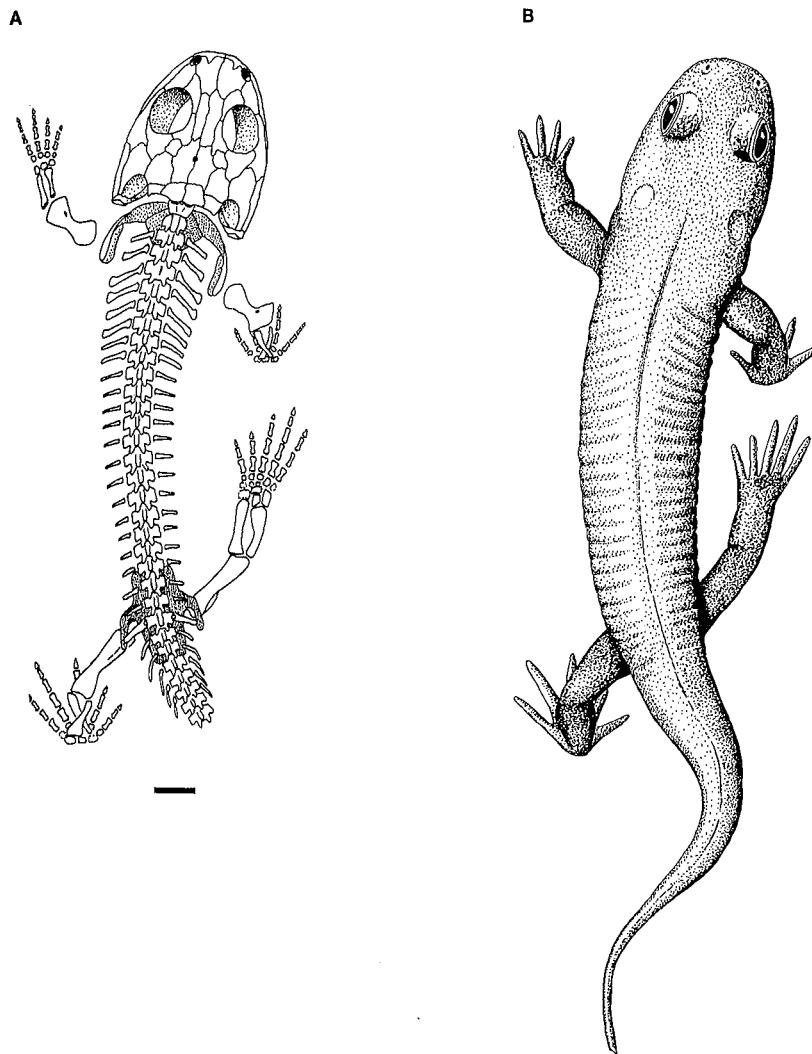


Figure 18 *Balanerpeton woodi* gen. et sp. nov. (A) Reconstruction of skeleton in dorsal aspect; (B) restoration in dorsal aspect. Scale bar, 10 mm.

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3. A second temnospondyl from East Kirkton?

Although all the good to reasonably well-preserved specimens of temnospondyls from the limestone and shale appear to belong to a single taxon, there is fragmentary evidence for a second larger temnospondyl in the East Kirkton fauna in the form of three isolated ribs. There are many other fragments of large tetrapods in the East Kirkton Limestone, particularly in the tuff layers, but we have seen no others that were diagnostically temnospondyl.

3.1. Material

NMS G 1987.7.41, an anterior thoracic rib, about 40 mm in length in nodular limestone (Fig. 19A).

NMS G 1987.7.42, an anterior thoracic rib, about 90 mm in length in limestone (Fig. 19B).

NMS G 1993.33.1, a thoracic rib prepared out by Dr R. L. Paton in 1993.

3.2. Description

NMS G 1987.7.41 and NMS G 1987.7.42 share three characteristics, namely that they are relatively large, they are straight, and they bear uncinate processes. The smaller rib, NMS G 1987.7.41, has a sharply expanded head, a flattened shaft showing slight curvature, and an expanded distal end with a small uncinate process close to the distal end. The larger rib, NMS G 1987.7.42, has a slightly expanded head, a straight, flattened shaft only slightly expanded distally, and a large uncinate process, as big as the rib head, halfway down the shaft. The rib head of this specimen appears to be bilobed and probably represents a crushed double-headed rib.

3.3. Systematic position

The size of these ribs suggests that they belonged to tetrapods between one and two metres in length. They are thus unlikely to have belonged to microsaurs, nectrideans, aistopods or adelognathids, none of which grew to an

appropriate size. Such relatively short straight ribs do not occur in anthracosaurs, amniotes or nectrideans, all of which had slender recurved ribs, as associated with costal breathing in the case of the anthracosaurs and amniotes. Of the major early tetrapod groups, only the temnospondyls and colosteids included forms which were suitably large and had straight trunk ribs with uncinate processes. As the colosteids were specialised aquatic forms and there is no other evidence for such forms in the East Kirkton assemblage, the ribs are most likely to have belonged to a large temnospondyl. The genus *Edops* from the basal Permian of Texas is one of the most primitive temnospondyls despite its stratigraphical age, and, from the size of its skull, must have grown to 2 m total length. Such a form could have been the source of these ribs. *Balanerpeton* has relatively small ribs for its size and is much too small to be a plausible source of these elements. The ribs are argued, therefore, to be evidence for a second, possibly *Edops*-like, temnospondyl in the East Kirkton assemblage.

4. The systematic position of *Balanerpeton*

4.1. The relatives of temnospondyls and the base of the Temnospondyli

Before considering the position of *Balanerpeton* among the primitive temnospondyls, it is first useful to establish a basal node at which the temnospondyl grade can be well defined. As noted in the introduction, ichthyostegarians and loxommatids are no longer considered to be temnospondyls. Godfrey *et al.* (1987) and Godfrey (1989) have argued that colosteids are the plesiomorphic offshoot within the temnospondyls, sequentially followed by *Caerorhachis*, *Dendrerpeton*, a trimerorhachoid-edopoid plesion and then an eryopoid-dissorophoid (+lissamphibian) group. Godfrey's post-*Caerorhachis* clade, considered here to be the Temnospondyli, can be readily defined by characters found in most later temnospondyls namely:

- (1) Rounded interpterygoid vacuities at least half the



Figure 19 Unidentified temnospondyl ribs, East Kirkton, Bathgate; East Kirkton Limestone. (A) NMS G 1987.7.41, $\times 2$; (B) NMS G 1987.7.42, $\times 0.8$.

width of the skull, primitively bordered only by the pterygoids (*Edops*), but in most temnospondyls bordered by the vomers and sometimes the palatines and ectopterygoids. The cultriform process of the parasphenoid extends between the vomers.

(2) Broad vomers widely separating the choanae.

(3) Dorsolaterally orientated rod-like stapes associated with a large tympanic notch.

(4) Short straight ribs.

The situation for colosteids and *Caerorhachis* is much less obvious and their systematic position is discussed below.

4.1.1. The Colosteidae. This family comprises the genera *Colosteus*, *Greererpeton* and *Pholidogaster*. For the last few decades, the superficial similarity of the Colosteidae to trimerorhachoid temnospondyls led to them being first confused and later associated. For many years the Colosteidae was restricted to the type genus *Colosteus* and a referred genus *Erpetosaurus*, both from Linton, Ohio. On the basis of this content, the Colosteidae was associated with the temnospondyl family Trimerorhachidae and related forms by Tatarinov (1964) who placed them, together with the metoposaurs, in the Colosteoidea. Carroll and Winer (1977) grouped the colosteids and trimerorhachids together in the Trimerorhachoidea. Both groups were within the Temnospondyli. Later, Smithson (1982) and Hook (1983) both argued that *Erpetosaurus* is a trimerorhachoid, with only minor similarities to *Colosteus*, and this, together with the redescriptions of *Pholidogaster* (Panchen 1975), *Colosteus* (Hook 1983) and *Greererpeton* (Smithson 1982; Godfrey 1989) has led to the conclusion that they are, at the very least, the most basal members of the temnospondyl grade (Godfrey *et al.* 1987, 1989). Milner *et al.* (1986), informally in a diagram, Panchen and Smithson (1988, quoting Milner) and Milner (1990) have suggested that the Colosteidae may be a more plesiomorphic group than previously perceived, with the microsaurs being closer to the base of the temnospondyl grade. If the microsaurs are closer to the temnospondyls, then colosteids cannot be called temnospondyls unless microsaurs are as well. It would be too confusing to place the Microsauria within the temnospondyl grade and less destabilising to remove the Colosteidae and treat them as a separate taxon.

The cladistic arguments for colosteids being temnospondyls are summarised by Godfrey *et al.* (1987, p. 804) who united the colosteids with the temnospondyl grade using four characters, namely:

(1) Postparietal-exoccipital contact. This, however, occurs in microsaurs and at least some nectrideans and appears to define a wider group (Panchen & Smithson 1988).

(2) Interpterygoid vacuities. These are not wide structures in colosteids and similar modest vacuities occur in primitive microsaurs and some nectrideans.

(3) Small uncinate processes on the ribs. These occur only sporadically in large temnospondyls and can be argued to be a size-linked feature not to be expected in nectrideans or microsaurs by virtue of their small size.

(4) A single undivided iliac blade. This is the most plausible synapomorphy for temnospondyls and colosteids. It should be noted however, that all nectrideans and many microsaurs also have this type of ilium although the most primitive microsaurs, the tuditanids and hapsidopareiontids, retain a double-headed ilium. Some of the ilia attributed to the primitive temnospondyl *Dendrerpeton* (Carroll 1967, p. 127) tend to being double-headed, but they are not firmly associated and may not be temnospondyl ilia at all. This may be a valid character uniting colosteids with the

temnospondyls, but even if so, it has occurred convergently within the microsaurs and in the origin of the Nectridea and would thus appear to be a rather labile feature.

One character positively supports a temnospondyl-microsaur relationship excluding the colosteids, namely the construction of the humerus. Colosteids retain a primitive tetrapod humerus, which is compact and L-shaped because of the large entepicondylar blade. Such primitive humeri occur not only in ichthyostegids and anthracosaurs, but also in colosteids and some nectrideans. In contrast, primitive microsaurs such as tuditanids, and primitive temnospondyls such as *Edops*, *Dendrerpeton* and *Balanerpeton*, have a humerus with a straight axis, a pronounced waist and simple 'torsion' to give the characteristic 'propellor-blade' appearance. This does not appear to occur convergently elsewhere.

At most, the case for colosteids being temnospondyls is ambiguous, and a microsaur-temnospondyl clade can be defined by a slightly more robust character.

4.1.2. Caerorhachis. *Caerorhachis bairdi* was collected in the nineteenth century, but was only described in 1977 by Holmes and Carroll. It comprises a single incomplete skeleton preserved as an acid-etched mould in coal and is believed to have come from the Namurian of the Scottish Midland Valley, although the exact provenance is not well documented. It was described as a dendrerpetontid by Holmes and Carroll. Milner (1980) argued that it could not be placed in a cladistically defined Dendrerpetontidae and was subject to several interpretations. Godfrey *et al.* (1987) treated it as the sister-taxon to all temnospondyls (bar the colosteids). In this they were followed by Milner (1990) who treated it as the most plesiomorphic temnospondyl.

In 1991, we were able to examine casts and the original specimen of *Caerorhachis* and can make the following observations. Several of the temnospondyl-like features of *Caerorhachis*, such as the dermal-ornament pattern and the supratemporal-postparietal contact, are primitive tetrapod characters. Some other temnospondyl-like characters are of ambiguous polarity and subject to convergence, examples being the cheek solidly fused to the skull table and the absence of an anterior process on the ilium. The otic region is unknown, as are the anterior end of the cultriform process, the humerus and the manual digit count, so potential resemblances to temnospondyls in these structures cannot be assessed.

The vertebrae have enlarged pleurocentra and appear to be gastrocentrous. In the context of Carboniferous tetrapods, this is a derived character usually associated with the stem-amniotes such as the anthracosaurs and seymouriamorphs.

The only temnospondyl-like feature of *Caerorhachis* is the interpterygoid vacuities as reconstructed by Holmes and Carroll (1977, fig. 4), but the crushed palate of the original does not unambiguously clarify this reconstruction. A closed loxommatid-type palate with a short cultriform process could be crushed to a similar configuration. The anterior palate as preserved (Holmes & Carroll 1977, fig. 5) bears a distinct resemblance to that of *Baphetes* (Beaumont 1977) in the shape of the choana and its proximity to the jaw margin, and in the configuration of the vomer and the palatine. This is not to say that the specimen is a loxommatid; the antorbital region is not preserved, but it appears to us to be just as likely to be a small loxommatid, or a tetrapod of comparable grade of organisation, as a primitive temnospondyl. Panchen and Smithson (1988) have suggested that loxommatids are related to basal amniotes such as the

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anthracosaurs, whereas Milner *et al.* (1986) have suggested that loxommatids are stem-tetrapods. Either way, *Caerorhachis* can be considered as a potential member of such a grade of organisation. For the time being, *Caerorhachis* should be considered as a primitive tetrapod of uncertain affinities rather than a basal temnospondyl.

4.2. Primitive temnospondyls and the position of *Balanerpeton*

A cladogram depicting the interrelationships of early temnospondyls was produced by Godfrey *et al.* 1987. In that paper, *Dendrerpeton* represented the first post-*Caerorhachis* offshoot and would be the most primitive temnospondyl in the context of the present work. This was followed by a dichotomy into a trimerorhachoid-edopoid clade and an eryopoid-dissorophoid clade.

The redescription of *Capetus* from Nýřany (Sequeira & Milner 1993) and this description of *Balanerpeton*, have led to some reconsideration of these relationships. The following discussion considers the early temnospondyl genera *Balanerpeton*, *Chenoprosopus*, *Cochleosaurus*, *Dendrerpeton*, *Edops*, *Eryops*, *Sclerocephalus* and *Trimerorhachis* (sources: Langston (1953) for *Chenoprosopus*; Boy (1988) and Watson (1962) for *Sclerocephalus* (=Actinodon); personal observation for all other forms). Outgroups used in this discussion are the loxommatids, *Loxomma* and *Baphetes* (not the more specialised *Megaloceraspis*) (source; Beaumont 1977) and the colosteids, *Pholidogaster* and *Greererpeton* (sources: Panchen 1975; Smithson 1982; Godfrey 1989). Characters 3A–7A are summarised only briefly as they simply serve to define the Cochleosauridae against other primitive temnospondyls and are more fully discussed by Godfrey and Holmes (in press) and Sequeira and Milner (1993). The analysis presented here is deliberately restricted to the basal temnospondyl genera (the ‘edopoid grade’) and a few well-described eryopoids and a trimerorhachoid. It is intended to demonstrate that *Balanerpeton* is more derived than several later temnospondyls and is not intended to be an exhaustive comparison of Palaeozoic temnospondyls, which is beyond the scope of this work. The authors are currently compiling a more extensive database which is planned to form the basis of a wider analysis of the relationships of Palaeozoic temnospondyls.

1. Premaxillary shape. In the outgroups, the premaxillaries are relatively simple structures. In loxommatids, they are relatively massive structures with some anteroposterior length, but without showing significant elongation. Each has a simple posterior dorsal edge with no alary process extending over the nasal. This type of premaxillary is associated with a small laterally placed external naris. In colosteids they are similar, but do show some marginal, posterior elongation relative to the midline. One large dendrerpetontid (Carroll 1967, fig. 6A) shows the premaxillary clearly and such areas as are visible suggest that the plesiomorphic condition, as found in loxommatids, is present. This does not preclude immediate relationship to either of the following groups, but does preclude *Dendrerpeton* falling within either group. Two different derived states occur in other early temnospondyls. Neither appears to be derived from the other.

1A. In *Edops*, *Cochleosaurus* and *Chenoprosopus*, the premaxillary is anteroposteriorly elongate marginally, but not medially—the primitive condition as seen on *Greererpeton*—but has a substantial flat and expanded

antero-medial dorsal surface—a unique feature. It is one of the major elements involved in snout elongation. It is associated with a small dorsally placed external naris.

1B. In *Balanerpeton*, *Capetus*, *Eryops*, *Sclerocephalus* and *Trimerorhachis* (cf. Case 1935), the premaxillary is a smaller, generally anteroposteriorly narrow structure, with a prominent alary process extending over the adjoining nasal. This is associated with a relatively larger dorsolaterally situated external naris and is the condition found in most Palaeozoic temnospondyls and also in many lissamphibians.

2. Lacrimal configuration. In primitive tetrapods, the lacrimal generally enters the orbit margin and this is taken to be the primitive situation. It occurs in *Dendrerpeton*, *Balanerpeton*, *Trimerorhachis* and *Capetus*.

2A. An extensive anterior jugal sutures with the prefrontal, excluding the lacrimal from the orbit margin in *Edops*, *Cochleosaurus*, *Chenoprosopus*, *Sclerocephalus* and *Eryops*. The absence of this character in *Capetus* shows that it is not simply correlated with the presence of a long or broad muzzle.

3. Vomer shape. In the outgroups the vomers are relatively small, flat plates, usually about as long as wide. Such vomers, with no elongation, occur in *Edops*, *Balanerpeton*, *Capetus*, *Eryops*, *Sclerocephalus* and *Trimerorhachis*. The vomers associated with *Dendrerpeton* specimens are also relatively abbreviated despite the appearance in some reconstructions (Milner, in press).

3A. In *Cochleosaurus* and *Chenoprosopus*, the vomers are highly elongate, both in the prechoanal region and the interchoanal region.

4. Pineal foramen. In the outgroups and in most Palaeozoic tetrapods, there is a distinct pineal foramen situated between the parietals. Such a foramen is present in most of the temnospondyls reviewed here.

4A. In large specimens of *Cochleosaurus* and *Chenoprosopus*, the pineal foramen is obliterated by bone.

5. Areas of depressed sculpture. In the outgroups and most temnospondyls, there is relatively uniform dermal ornament across the middle region of the skull roof.

5A. In *Cochleosaurus* and *Chenoprosopus*, there are pronounced anteroposterior ridges of deeply indented sculpture along either side of the skull table and the sculpture is very weakly developed along the midline (Godfrey & Holmes, in press).

6. Pterygoid-jugal suture. In the outgroups and most temnospondyls, the ectopterygoid forms the anterior margin of the subtemporal fossa.

6A. In *Cochleosaurus* and *Chenoprosopus*, a lateral extension of the pterygoid meets a medial extension of the jugal which thus not only separates the maxillary from the quadratojugal but also the ectopterygoid from the subtemporal fossa (Godfrey & Holmes, in press).

7. Choanal shape. In the outgroups and most temnospondyls, the choana is ovoid or slightly elongate.

7A. In *Cochleosaurus* and *Chenoprosopus*, the choana is wider anteriorly than posteriorly (Godfrey & Holmes, in press).

8. Entepicondylar foramen in humerus. In the outgroups, an entepicondylar foramen is present in the humerus. Such a foramen is present in *Dendrerpeton* and *Balanerpeton*. The condition in *Chenoprosopus*, *Cochleosaurus* and *Capetus* is unknown.

8A. There is no foramen in the humerus of *Edops* (one element only), *Eryops*, *Sclerocephalus* and *Trimerorhachis*.

9. Interpterygoid vacuity shape. In the outgroups, the interpterygoid vacuities are either absent or very slender. In primitive temnospondyls the vacuities are relatively small,

narrowing to a point anteriorly. This is the condition in *Edops*, *Cochleosaurus* and *Chenoprosopus*.

9A. The interpterygoid vacuities are rounded anteriorly in *Dendrerpeton*, *Balanerpeton*, *Trimerorhachis*, *Capetus*, *Sclerocephalus* and *Eryops*.

10. Extent of palatine rami of pterygoids. In the outgroups the pterygoids bear large anterior or palatine rami which meet broadly anteriorly. Interpterygoid vacuities are absent (loxommatids) or very slender (colosteids). In temnospondyls, the most primitive state is for the palatine rami of the pterygoids to meet ahead of the interpterygoid vacuities, thus excluding the vomers from the interpterygoid margin. This occurs in *Edops*, *Cochleosaurus* and *Chenoprosopus*. In *Capetus*, the only palate is obscured in this region, but the pterygoid appears to exclude the vomer from most, if not all, of the vacuity margin.

10A. In *Dendrerpeton*, *Balanerpeton*, *Eryops*, *Sclerocephalus* and *Trimerorhachis*, the palatine ramus of the pterygoid is reduced and the vomer forms most of the anterior margin of the interpterygoid vacuity.

11. Anterior extent of the jugal. In the outgroups, the jugal extends broadly to, or almost to, the level of the leading edge of the orbit where it fuses broadly with the lacrimal. The only temnospondyl which appears to correspond to this condition is *Dendrerpeton* (*Erpetocephalus*) *rugosum*. This is not incorporated in the cladogram, but will be discussed in a future paper by the senior author. The two derived states may be derivable from each other.

11A. In *Edops*, *Cochleosaurus*, *Chenoprosopus*, *Capetus*, *Sclerocephalus* and *Eryops*, the jugal-lacrimal connection remains broad, but the jugal extends ahead of the orbit as part of a long, broad muzzle.

11B. In *Dendrerpeton*, *Balanerpeton*, trimerorhachids and dissorophoids, the jugal is reduced anteriorly. In *Trimerorhachis*, it narrows slightly and makes a reduced contact with the lacrimal. In *Dendrerpeton* and *Balanerpeton* it just reaches the lacrimal and makes a point contact with

it. In the dissorophoids, it does not reach the lacrimal and either the maxillary or a dorsal exposure of the palatine intervenes.

12. Occipital condyle. The primitive occipital condyle in post-Devonian tetrapods is a simple single articulating surface made up of a large basioccipital and paired exoccipitals. This appears to be the situation in *Edops*, *Chenoprosopus*, *Dendrerpeton*, *Balanerpeton*, and *Trimerorhachis*. The occiputs of *Cochleosaurus* and *Capetus* have not been described.

12A. In *Eryops*, the occipital condyle is bilobed with prominent lateral exoccipitals and a reduced median basioccipital. The condyle has not been described in *Sclerocephalus haueseri*, but Watson (1962) described an *Eryops*-like condyle in *Actinodon frossardi* from Autun, France. *Actinodon* is almost certainly congeneric with *Sclerocephalus* and it is suggested that the condyle of *Sclerocephalus* was *Eryops*-like.

13. Intertemporal. The polarity of intertemporal presence has been the subject of some discussion in view of its absence in *Ichthyostega*, *Acanthostega* and *Megalocephalus*. Intertemporals are, however, present in *Crassigyrinus*, in the primitive loxommatid *Loxomma*, in *Greererpeton* as rudiments, and in anthracosaurs and seymouriamorphs. The simplest hypotheses would appear to be that they are acquired at a post-*Acanthostega* level and lost several times, or that they are a basal tetrapod character lost even more times. Either way, they appear to be a basal tetrapod feature with their loss being the derived condition. They are present in *Edops*, *Cochleosaurus*, *Chenoprosopus*, *Dendrerpeton*, *Balanerpeton*, *Trimerorhachis* and *Capetus*.

13A. Intertemporals are absent in *Sclerocephalus* and *Eryops*.

The cladogram in Figure 20 depicts the set of relationships suggested by the distribution of the above character-states and is a development of that put forward by Sequeira and Milner (1993). The most primitive temnospondyls appear to be not *Dendrerpeton* but the long-snouted members of the

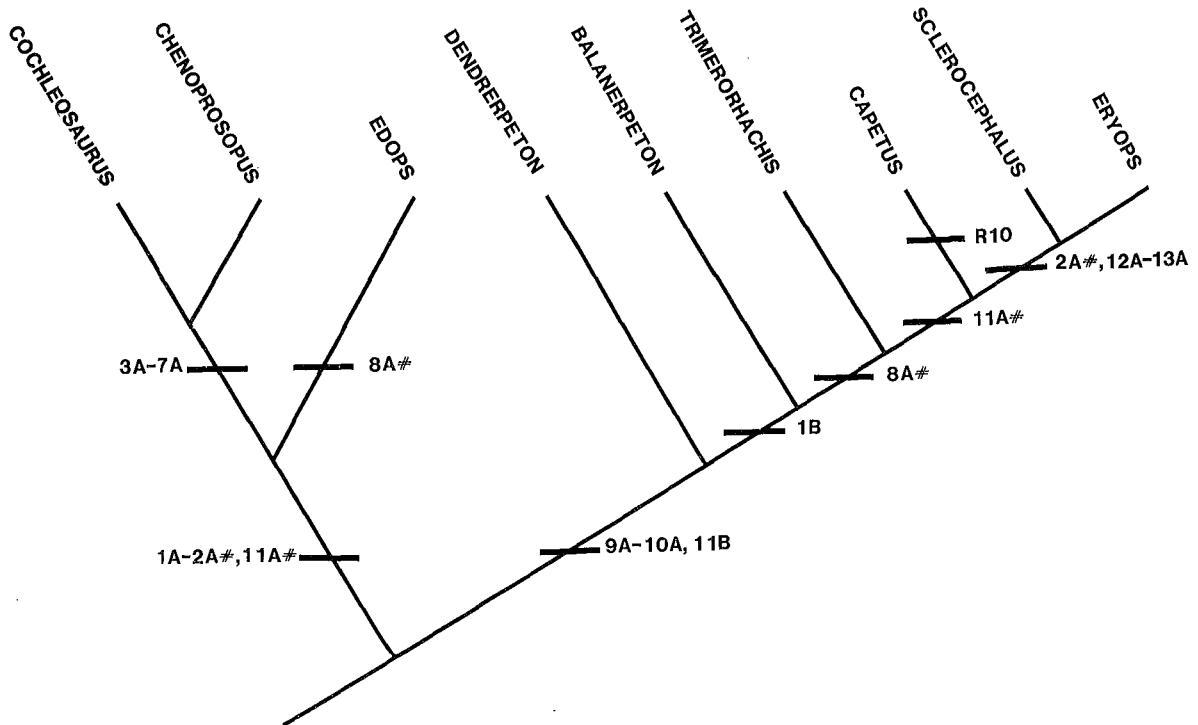


Figure 20 Cladogram depicting relationships of several basal temnospondyls. Characters 1–13 with derived states 1A–13A are described and discussed in Section 4. R10 indicates a reversal of character 10A to the primitive condition. The symbol # indicates a convergent character acquisition.

clade Edopoidea forming a small early adaptive radiation of crocodile-like forms. *Dendrerpeton* and *Balanerpeton* are successive offshoots on the main temnospondyl stem, followed by *Trimerorhachis* representing at least the Trimerorhachidae and possibly the rest of the Trimerorhachioidea although this remains to be demonstrated. *Capetus*, *Sclerocephalus* and *Eryops* are post-trimerorhachoid forms.

4.3. Defining *Balanerpeton*

As can be seen from the diagnosis and the above cladistic analysis, most of the characters of *Balanerpeton* are either shared with most other more-derived temnospondyls, or are shared with more primitive tetrapods. It can be placed at a grade of organisation higher than the edopoids and *Dendrerpeton*, but lower than the trimerorhachoids and 'higher' temnospondyls. Following the taxonomic practice of Patterson and Rosen (1977), it represents a plesiomorph ranked between *Dendrerpeton* and the Trimerorhachioidea. Three characters can be provisionally suggested as autapomorphies defining *Balanerpeton* as a valid taxon rather than a grade of organisation. Two are not unique and the third is of uncertain distribution, but all serve to define *Balanerpeton* in the phylogenetic context proposed here.

Dentition. The dimorphic dentition with space for 40–42 teeth on each upper jaw ramus and 25–30 larger teeth on each mandible is, to our knowledge, unique among temnospondyls, but does occur in some colosteids (*Greererpeton*, Smithson 1982).

Orbit size. The proportionately large orbits and narrow interorbital region occur in later temnospondyls, including the Westphalian-Autunian Micromelerpetontidae and Brachiosauridae and the Triassic Plagiosauridae. All three families fall unambiguously within the higher Temnospondyli (Milner 1990). Such relatively large orbits do not occur in edopoids, *Dendrerpeton*, or trimerorhachids and serve to define *Balanerpeton* in the context of these groups.

Reduced neural spine. The reduced neural spine of the fifth trunk vertebra is at present unique to *Balanerpeton*. The distribution of this character is poorly reported. The neural spine of the fourth trunk vertebra is reduced in 'higher' temnospondyls such as *Eryops* (Moulton 1974), *Sclerocephalus* (Boy 1988), *Platyrhinops* (personal observation) and *Trimerorhachis* (Berman & Reisz 1980), and in lower tetrapods such as *Acanthostega* (Clack personal communication). Until the distribution and variability of this character is better known, it is of uncertain significance.

All three of the above character-states occur in the holotype specimen, but only the relatively large orbits are readily seen in most of the referred specimens.

4.4. Chronological and evolutionary implications

It was clear from its initial discovery that the East Kirkton material demonstrated the presence of unequivocal temnospondyl amphibians in the late Viséan (Wood *et al.* 1985). Study and description of the material suggests the presence of a second larger probable temnospondyl, indicating the presence of at least two types of temnospondyl at this time. The presence of large terrestrial temnospondyls has been indicated previously by the presence of large four-toed footprints (*Megapezia*) in the Mississippian of Nova Scotia (Sarjeant & Mossman 1978) and by two large rhachitomous vertebrae from the Upper Mississippian Bickett Shale at Greer, West Virginia (Godfrey 1988).

Consideration of the phylogenetic relationships of the temnospondyls reinforces the view that their diversification was under way in the Viséan. As can be seen from the

cladogram in Figure 20, the edopoids are a more primitive offshoot of the temnospondyls than *Balanerpeton* and early members of this group must have been present in the Viséan, contemporaneous with *Balanerpeton*. They may or may not have differentiated into the Edopidae and the Coelosauridae, but had certainly done so by the early Westphalian, as a coelosaurid is present in the Westphalian A assemblage in the Jarrow Coal from Kilkenny in Ireland (Sequeira *in press*). Outgroup comparison indicates that *Edops* is the most plesiomorphic temnospondyl, despite its basal Permian age, and it appears to be a late relict of the earliest phase of temnospondyl diversification. *Edops* is one of the largest Palaeozoic temnospondyls, and it may be that the large isolated elements and footprints from the Viséan belong to early members of the Edopidae related immediately to *Edops*.

The Dendrerpetontidae also appear to be a more primitive offshoot of the temnospondyls than is *Balanerpeton*. These forms are all known from the Westphalian A–B, but the more derived condition of *Balanerpeton* indicates that one or more lineages of dendrerpetontid must also have been present in the Viséan.

In conclusion, the presence of *Balanerpeton* in the late Viséan of Scotland implies that the temnospondyl amphibians had diversified into at least three lineages (edopoid, dendrerpetontid and *Balanerpeton* itself). The same phylogenetic analysis implies that *Edops* is a late relict. The prediction, based on these phylogenetic observations, is that edopoid and dendrerpetontid temnospondyls were also present in the Viséan and will ultimately be discovered in strata of this age.

Previously described Viséan and Namurian assemblages have not produced any temnospondyls resembling *Balanerpeton* presumably because the specialised assemblages represented include mainly aquatic forms with few or no exotic terrestrial elements. Taxa such as *Crassigyrinus*, *Loxomma*, *Spathicephalus*, the Colosteidae, the Adelognathidae, and *Acheroniscus* all appear to be specialised aquatic forms with few or no later relatives. The absence of temnospondyls from such assemblages and their presence at East Kirkton, combined with the structural features associated with terrestriality, suggests that the temnospondyls may have arisen initially as a group with terrestrial adults. One of their most characteristic features is the large tympanic ear and relatively rod-like stapes, associated with the perception of air-borne sound. Clack (1992) has suggested that the tetrapod stapes originally retained an accessory role in respiratory movements of the palate, and that temnospondyls were one of the first groups in which the stapes became decoupled from respiration. The interpterygoid vacuities formed the basis of a buccal pumping system, permitting the skull to become akinetic and to support rigidly held tympana, and the stapes to become a specialised auditory structure. The presence of *Balanerpeton* in the Viséan gives support to this hypothesis.

5. Explanation of figure lettering

A	Angular
a.m.f.	anterior meckelian fossa
ART	Articular
AT	Atlas
AX	Axis
BO	Basioccipital
C1–C4	Centralia 1–4
c.for.	carotid foramen

CLA	Clavicle
COR1-2	Coronoids 1-2
CTH	Cleithrum
D	Dentary
D1-D5	Distal elements (carpals/tarsals) 1-5
dp.cr.	deltpectoral crest
?e	?eyelid, possible palpebral ossification
ECT	Ectopterygoid
ent.for.	entepicondylar foramen
EO	Exoccipital
EPT	Epipterygoid
F	Frontal
FBL	Fibulare
FEM	Femur
FIB	Fibula
H.A.	Haemal Arch
HUM	Humerus
IC	Intercentrum
ICL	Interclavicle
IL	Ilium
IN	Intermedium
in. tr.	internal trochanter
ISC	Ischium
IT	Intertemporal
J	Jugal
L	Lacrimal
M	Maxillary
m. for.	meckelian foramen
N	Nasal
N.A.	Neural Arch
N.SP.	Neural Spine
P	Parietal
PAL	Palatine
PAS	Parasphenoid
PC	Pleurocentrum
PF	Postfrontal
p.m.f.	posterior meckelian fossa
PMX	Premaxillary
PO	Postorbital
PO.M	Postminimus
po.zy.	postzygapophysis
PP	Postparietal
PRA	Prearticular
PRF	Prefrontal
PRO	Proatlas
PRT	Prootic
pr.zy.	prezygapophysis
PT	Pterygoid
PUB	Pubis
Q	Quadrata
QJ	Quadratojugal
R	Rib
RAD	Radius
RDL	Radiale
SA	Surangular
SAC	Sacral Rib
SC	Scapulocoracoid
SCL	Sclerotic plates
SPH	Sphenethmoid
SPL	Splenial
SPP	Postsplenial
SQ	Squamosal
ST	Supratemporal
STA	Stapes
st.for.	stapedial foramen
SYM.F.	Symphyseal fang
T	Tabular

TIB	Tibia
TBL	Tibiale
U	Ulna
ULN	Ulnare
V	Vomer
5	Reduced fifth neural spine

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