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Endocranial preservation of a Carboniferous actinopterygian from Lancashire, UK, and the interrelationships of primitive actinopterygians

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Endocranial preservation of a Carboniferous actinopterygian from Lancashire, UK, and the interrelationships of primitive actinopterygians

Michael I. Coates

Department of Biology, Darwin Building, University College London, Gower Street, London WC1E 6BT, UK (*m.coates@ucl.ac.uk*)

CONTENTS

The gross brain structure of an Upper Carboniferous (*ca.* 310 Myr ago) ray-finned fish (Actinopterygii) is described from exceptionally well-preserved fossil material from the Burnley region of Lancashire, UK. Previously identified as '*Rhadinichthys*' *planti*, the species is reassigned to the genus *Mesopoma*. Morphological characters derived from these data are combined with reviews of cranial skeletal anatomy, enamel composition, oculomoter muscle insertion and paired fin morphology to test and reanalyse hypotheses of primitive actinopterygian interrelationships. Results indicate that ancestral chondrostean (sturgeon and paddlefish) and neopterygian (teleost, amiid and gar) lineages diverged earlier than current theories suggest. Palaeonisciformes, a taxonomic group widely used to include most Palaeozoic actinopterygians, include a significant number of primitive neopterygians, several of which may form a distinct monophyletic clade. Within this revised phylogenetic context, changes in gross brain morphology from primitive conditions, as revealed by fossil data, highlight likely specializations in extant non-teleostean actinopterygians.

Keywords: ray-finned fish; evolution; phylogeny; brain; morphology

1. INTRODUCTION

The Actinopterygii (ray-finned fishes) include at least 23 700 living species (Nelson 1994), and their origin extends back more than 410 Myr ago to the early Devonian (Schultze 1992) or Upper Silurian (Wang & Dong 1989). The major actinopterygian divisions, Cladistia, Chondrostei and Neopterygii (including Teleostei), diverged before the end of the Palaeozoic, but more precise information about their phylogenetic separation and the relationships of early fossil groups to extant lineages is limited. Current hypotheses of their early evolution can be attributed to a handful of influential papers: Patterson on the Holostei (Patterson 1973) and primitive actinopterygians (Patterson 1982); and Gardiner (1984) and Gardiner & Schaeffer (1989) on lower actinopterygian interrelationships. This lack of phylogenetic resolution originates mostly from poor quality fossil data. Palaeozoic actinopterygians are usually preserved as flattened, incomplete dermal

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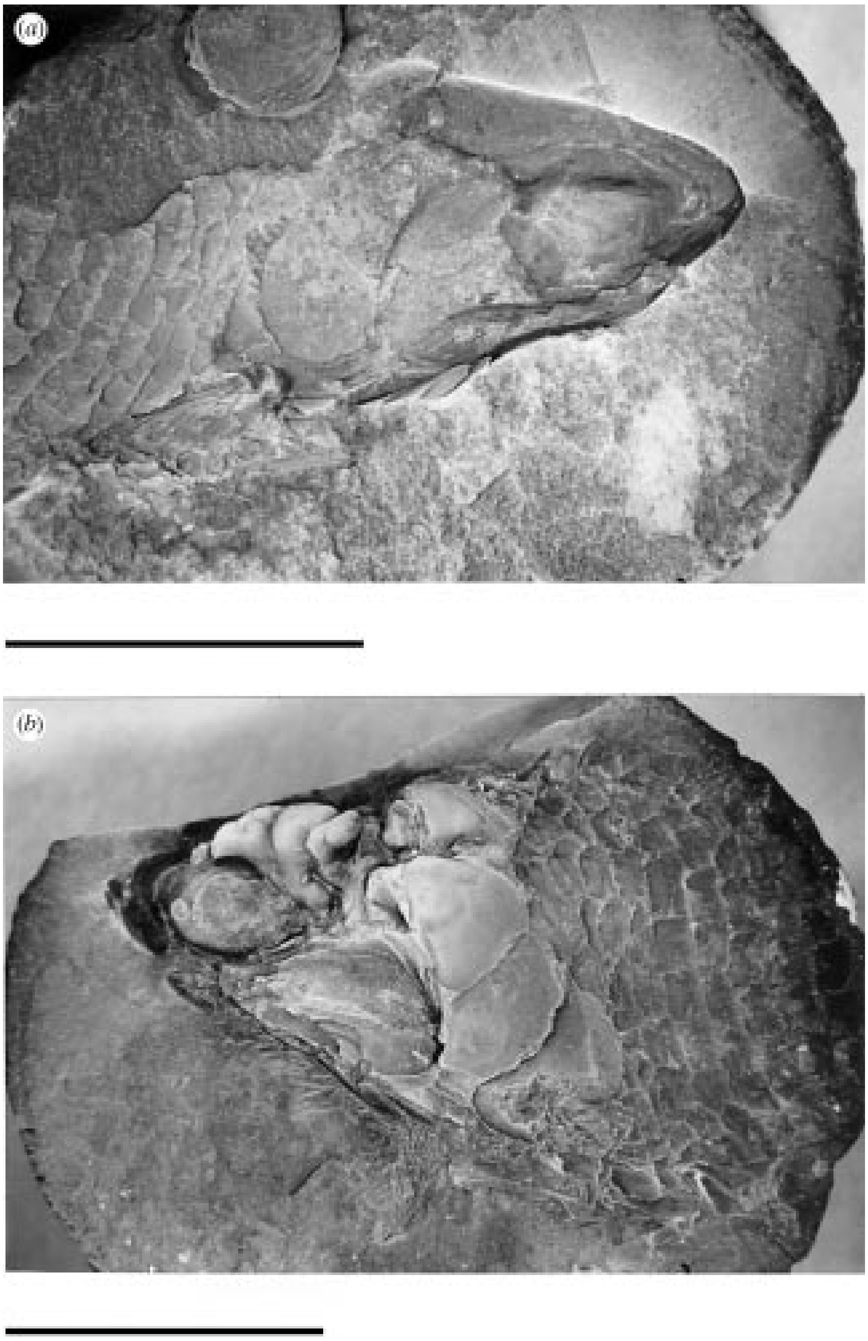

Figure 1. *Mesopoma planti*. (*a*) NHM P11656, exposed face of nodule showing natural mould of external morphology; anterior to right of figure. (*b*) NMH P7989, exposed face of nodule showing natural cast of cranial interior cavities, operculogular series, pectoral girdle and anterior squamation. Anterior to left of figure. In both photographs surface detail is enhanced using ammonium chloride. Scale bar, 10 mm.

skeletons, and few examples include well-preserved endoskeletal remains. Furthermore, where known, the neurocrania are considered morphologically conservative, while dermal skeletal patterns are uninformative at higher levels of phylogenetic analysis (Gardiner & Schaeffer 1989). Consequently, the earliest actinopterygians (plus a few more recent but nevertheless primitive genera) are usually consigned to the paraphyletic 'palaeonisciforms' (Janvier (1996) includes a concise review of past and present theories of primitive actinopterygian classification and evolution).

New, well-preserved fossil material is therefore significant, and the specimens of '*Rhadinichthys*' *planti* Traquair (1888) reported here and rediagnosed as belonging to the genus *Mesopoma* Traquair (1890), include a well-preserved 'in-the-round' cranial dermal skeleton, which encloses an unusually complete set of endocranial morphologies. These include a cast of the neurocranial cavity which provides exceptional information about the external morphology of the brain, and significant new details of anterior (oblique) oculomotor muscle insertion. The aims of this paper are therefore to present a full description of the material, and to investigate the way in which these data inform questions about early actinopterygian evolution. Inevitably, this is primarily a test of Gardiner & Schaeffer's (1989) phylogeny, because no alternative hypothesis of equivalent depth and taxonomic breadth is available. However, since the publication of their analysis, important new studies of fossil and recent lower actinopterygians have appeared, and several of the characters included in their database are ripe for revision. The phylogenetic analysis presented here includes an amended and expanded character list; it also indicates that the chondrostean–neopterygian phylogenetic split occurred earlier than Gardiner & Schaeffer propose, and it suggests an approximate outline of the early evolution of the gross features of actinopterygian brain morphology.

2. MATERIAL

The main subjects of this study, Natural History Museum, London (NHM) specimens P7989 and P11656 (figure 1), are part and counterpart of a small nodule containing the anterior third of a primitive actinopterygian, catalogued as *Rhadinichthys planti*, but redescribed here as *Mesopoma planti*. Museum labels identify the material as the 'head of *Rhadinichthys* showing all the cranial bones' (NHM P7989) and 'head in counterpart with brain cast' (NHM P11656). These labels also record that the nodule originated from the Ward collection, received in 1894 (therefore postdating the relevant part of Woodward's 1891 catalogue), followed by the R. H. Traquair collection, dated received in 1914, and that it was attributed originally to *Rhadinichthys carinatus* (Agassiz). NHM P7989 is figured as a simple sketch in part V of Traquair's monograph 'The Ganoid fishes of the British Carboniferous formations' (1911, p. 152, text-figure 8), but NHM P11656, including the 'brain cast', has never been described or illustrated. The primary published reference to this specimen, as indicated by a note on the specimen label, occurs later in Traquair's monograph (p. 127) where he comments that 'Eastman . . . described a new species also from the American Upper Devonian, to which he has given the name of *Rhadinichthys Deani* (*sic*). This species is remarkable as having furnished a number of heads in which the form of the brain and details of the labyrinth are preserved, even a few blood vessels being traceable. *I may anticipate a little by stating that in a specimen of* Rh. carinatus (*Ag.*) *in my possession, one of the semicircular canals and also an otolith are distinctly shown*' (italics added). A further brief reference to NHM P11656 is included in Watson's (1925) review of 'The structure of certain Palaeonsicid fishes . . .', where it is described as 'much less perfectly-preserved' (Watson 1925, p. 832) than the nodule-enclosed neurocrania of 'Palaeoniscids A and B' (redescribed in Poplin 1974, 1982, 1984) and, it appears, the 'marvellously-preserved endocranial casts' (Watson 1925, p. 815) of '*Rhadinichthys deani*'.

Subsequent studies of Eastman's (1908) species, summarized in Rayner's (1951) redescription of *Rhadinichthys deani* as *Kentuckia deani*, provide a valuable context for the interpretation of NHM P11656. Chief among these is Moodie's (1915) description of the lectotype, MCZ 5222 (Museum of Comparative Zoology, Harvard), as including a 'fossilised brain', and sections through a further specimen as preserving the 'meningeal space' (Moodie 1920). Rayner, however, recognized the 'brain as a natural endocranial cast, and the 'meningeal space' as a section through cancellar bone of the primary endocranial roof. Other authors who commented on Moodie's misinterpretation include Watson (1925), Stensiö (1925), Nielsen (1942) and Poplin (1974). However, Rayner also acknowledged (after Edinger 1929) that closely fitting braincases can occur in small fishes, and, in the same paper, described the cerebellar lateral lobes in *Kentuckia*, thereby illustrating the unusual information potential of these casts. Furthermore, the presence of only a single meninx in actinopterygians (Bjerring 1991) may allow an exceptionally close correspondence between neurocranial cavity shape and gross brain morphology, although this is no guarantee; endocranial casts of many teleosts would show almost no details of the actual brain surface.

Therefore, while parts of this specimen bear a remarkable resemblance to an actual brain (figures 1 and 4), it is significant that these infilled endocranial cavities (which also include the right orbit and myodomes) are continuous with several spaces occupied by non-neural tissues in life, such as the otic labyrinth and the canal for the internal carotid artery. Furthermore, there is no evidence that NHM P11656 includes any soft tissue preservation resembling that found in fishes of the Cretaceous Santana Formation from Brazil (Maisey 1991; Martill 1993), the Jurassic of Sierra de Varas, Chile (Schultze 1989) or any of the examples researched by Briggs *et al*. (1993) and Allison & Briggs (1991, 1993). Nevertheless, NHM P11656 may be the best preserved example of its kind, and, *contra* Watson (1925), none of the published examples of comparable endocasts (Nielsen 1942, 1949; Poplin 1974, 1984; Thies 1989; Coates 1998) match the detail and completeness of this unique specimen.

The nodule itself consists of a compact laminated mudstone; reaction with 10% hydrochloric acid indicates significant carbonate content, and light weight suggests negligible iron content. The infilling of the endocranial cavities consists of a slightly translucent, hard crystalline material, which includes specks of iron pyrite. There is no resemblance to the 'phosphatic' nodular preservation of Carboniferous actinopterygian neurocrania from Kansas (Poplin 1974, 1982, 1984). The unusual preservation of NHM P7989 and NHM P11656 is complemented by Manchester Museum specimen MM W1146 (figure 5), which was catalogued as unidentified fragments until 1985, when Dr Andrew Milner recognized the material as parts of a palaeonisciform skull. Further inspection identified this as another specimen of *M. planti*, with an incomplete cast of the anterior endocranial cavities, including infilled sclerotic cups, orbits and anterior myodomes. The compaction of this fish within its nodule, including a disrupted neurocranium surrounded by scales and incomplete fins, suggests that it may be regurgita, a gastric pellet or coprolite.

Several specimens of *Rhadinichthys planti* from the Natural History Museum collection were examined during the course of this study, the details of which are listed in later sections. These specimens consist of flattened, incomplete dermal skeletons, and include no endocranial remains.

Institutional abbreviations are as follows: MM, Manchester Museum; NHM, The Natural History Museum, London; NMV, Museum of Victoria, Melbourne.

3. METHODS

NHM P7989 and NHM P11656 have been subjected to very little preparation for this study. Part of the matrix backing NHM P11656 was sliced away using a Well diamond wire saw with a 0.3 mm cutting wire; some matrix removal using a mounted entomological-grade needle exposed details of the branchiostegal plates. Casts of both of these specimens were made using silicone rubber, and Coltene 'President' polysiloxane compound was used to obtain a positive impression of NHM P7989. This produced a higher-definition cast than the silicone rubber.

All drawings were made using a Zeiss Stemi SV6 microscope with drawing tube. Photographs were taken using Nikon and Zeiss photomicroscopes, with the specimen immersed in isopropyl alcohol for contrast enhancement.

4. SYSTEMATIC PALAEONTOLOGY

Actinopterygii Woodward, 1891
Actinopteri Cope, 1871

Neopterygii Regan, 1923
Genus *Mesopoma* Traquair, 1890

Generic diagnosis (emended after Coates 1993). Scales in 30–40 vertically orientated sigmoid rows; leading edges of all fins bear fringing fulcra except dorsal edge of caudal fin; dorsal opposite anal fin; pelvic fin insertion narrow; pectoral fin rays proximally unjointed; antero-posteriorly narrow post-temporal; branchiostegal series with eight or fewer members; lateral gulars subtriangular; suboperculum with posterodorsally inclined dorsal rim; surangular present; length of postorbital region of maxilla equal to or less than that of suborbital region; jaw articulation sited level with extrascapular series; marginal dentition consisting of uniformly sized conical teeth; preoperculum with short anterodorsal limb; posterior infraorbital narrow; parietals less than half the length of frontals; anterior extent of dermopterotic borders less than one-third of frontal lateral edge; dermosphenotic contacts nasal; hyomandibula with opercular process; dermohyal separate from hyomandibula; anterior ceratohyal with sigmoid groove.

Species *Mesopoma planti* (Traquair 1888)
Synonymy: *Rhadinichthys planti* Traquair (1886, p. 441)
Rhadinichthys planti (Traquair); Ward (1890, p. 177, plate 4, figure 6)
Rhadinichthys planti (Traquair); Woodward (1891, p. 469)
Rhadinichthys planti (Traquair); Wellburn (1901, pp. 168 & 174)
Rhadinichthys planti (Traquair); Traquair (1911, pp. 151 & 152, text-figure 8, plate 33, figures 9 & 10)

Lectotype: NHM P8497 (figured in Traquair (1911), plate 33, figures 9 & 10), part and counterpart. No holotype is designated in Traquair (1888; or Woodward 1891; or Traquair 1911), but the specimen label records this as the type of the original description, and Traquair (1911, p. 151) describes this as 'The most perfect specimen I have seen'.

Specific diagnosis, emended after Traquair (1888) and (1911): a primitive stem-group neopterygian, usually around 60 mm in total length. Bulbous rostral enclosing prominent snout; single ovoid suborbital; slender dermohyal extending for almost complete length of preopercular anterodorsal limb; dermopterotic with anterior extension forming nonlinear suture with posterior third of frontal lateral edge; opercular–subopercular suture steeply inclined posterodorsally; seven or eight branchiostegal plates; between 35 and 40 scale rows from pectoral girdle to origin of tail; dorsal fin includes about 25 rays, anal about 22 rays, and caudal fin about 60 rays. Scale ornament faint, and consists of around five grooves parallel to anterior edge, sometimes extending to parallel ventral edge; four-plus posteriorly directed narrow chevrons on otherwise smooth remaining surface; posterior edge serrated.

Locality and horizon: NHM P7989 and NHM P11656 are recorded as originating from 'Coal Measures, Burnley, Lancs' and 'Burnley Coal-field, L. Coal Meas.' Further details were researched, in case of finding other specimens from the same locality with a similar exceptional quality of preservation. According to Traquair (1911) '*Rhadinichthys*' *planti* was first collected from Collyhurst, Bradford, by John Plant of the Royal Museum Salford; from the Deep Mine Ironstone Shale, Longton, Staffordshire, by John Ward; and from Burnley, Lancashire, by George Wild. Wellburn (1901) notes a further record of '*R.*' *planti* from the Cannel Coal above the Black Bed, near Low Moor in the Yorkshire Coal Measures. However, Wild's collection catalogue (1897, now at Manchester Museum) contains no entries for '*R.*' *planti* or *carinatus*, Traquair's (1888) original description of '*Rhadinichthys*' *planti* is based exclusively on material from Collyhurst and Longton, and Ward (1890) simply records the presence of '*R.*' *planti* in the North Staffordshire coalfield. More precise details about the original site of the nodule have therefore been inferred from comparison with similarly preserved specimens from the Burnley region.

Apart from NHM P7989 and NHM P11656, all Natural History Museum '*R.*' *planti* specimens originate from Collyhurst and Longton, and a review of locality records for the entire fossil fish collections produced no positive (Burnley) matches. The Manchester Museum fossil collection, however, includes several nodule-enclosed actinopterygians from near Burnley: MM (Manchester Museum) L1296, *Elonichthys aitkeni*, from the Soapstone Bed, 1.2 m over Bullion Coal, Burnley; MM W1139, unidentified fragments, also from the Soapstone Bed; MM L2451, *Coccocephalus wildi*, from the roof of the Mountain 1.2 m coal, Carre Heys, Trawden, Lancs (neurocranium described by Watson (1925); redescriptions by Poplin 1974; Poplin & Véran 1996); and, most significantly, MM W1146: described here as *M. planti*, again from the Soapstone Bed, roof of the Mountain 1.2 m coal, Carre Heys (?), Colne, Lancs.

It is therefore likely that the nodule (NHM P7989 and NHM P11656) originated from the Soapstone Bed in the Colne and Trawden region of the Burnley coalfield. Wild's (1862) log of the Fulledge section of the Burnley coal field, and Bolton's (1905) notes on the geology and palaeontology of the Soapstone Bed provide the following details. The Bullion coal (worked at Spa Clough, Burnt Hills, Dodbottom, Townhouse and Carre Heys collieries) and Mountain 1.2 m coals are mutually continuous and lie 1.2–2.1 m beneath the Soapstone Bed. The Bullion coal lies between 135 m and 206.4 m beneath the Arley seam, which correlates with the Westphalian A (Langsettian) chronozone (Ramsbottom *et al.* 1978), suggesting a date of around 311 Myr ago (Harland *et al.* 1989) for NHM P7989 and 11656, and MM W1146. The Soapstone Bed is a thin band of light-grey shale, including numerous small nodules consisting of 'earthy carbonate of iron' (Bolton 1905). This is at least consistent with the size and apparent carbonate content of NHM P7989 and P11656 (see § 2). Vertebrates recorded from the Soapstone Bed include *Acanthodes wardi*, *Elonichthys aitkeni*, *Hylonomus wildi*, and 'unidentified microsaurian remains'. However, the prospect of further collections from the Soapstone Bed are limited: Bolton (1905) reported direct examination of the Soapstone Bed in the Carre Heys region as (already) impossible because of mine closure, although occasional nodules could be found in overgrown spoil heaps.

Referred material: NHM P7989 and NHM P11656, counterparts of single nodule, NHM P7985, NHM

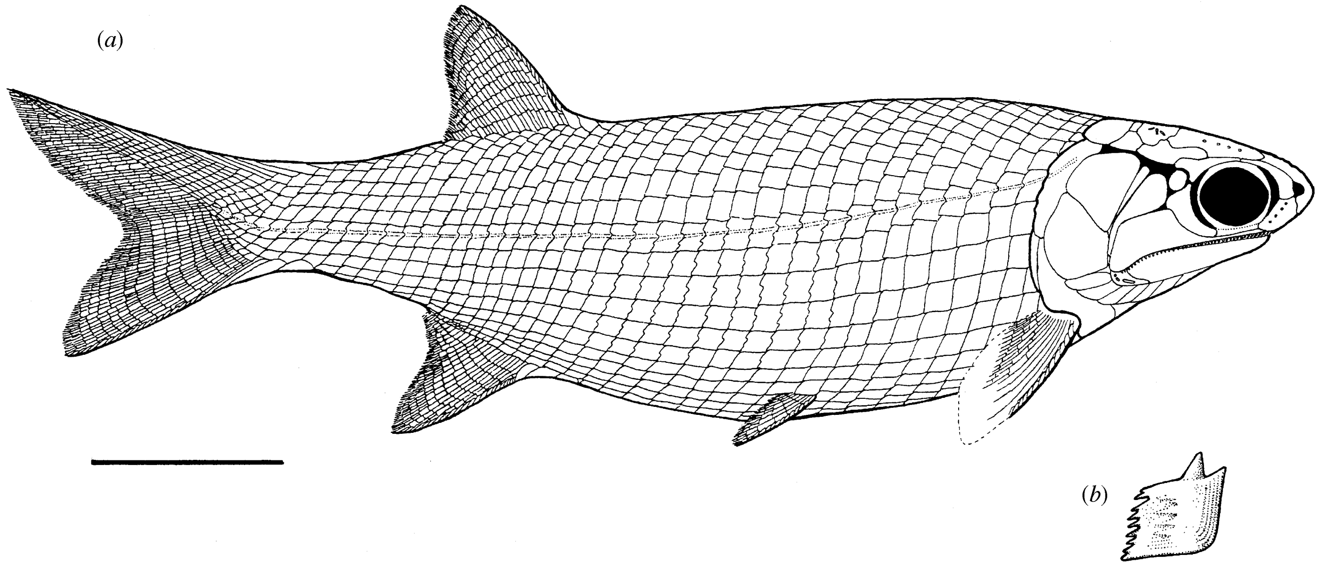

Figure 2. *Mesopoma planti*. (*a*) Reconstruction, with postcranium (excluding pectoral girdle and fin) after *M. carricki* (Coates 1993); dermal skull mostly after NHM P7989, except for dermohyal, suborbital, dermosphenotic and posterior infraorbital after NHM P8500, pores on premaxilla after NHM P8501E. Scale bar, 10 mm. (*b*) Flank scale.

P8500, NHM P8501B and E, NHM P8502, and MM W1146, fragmented, incomplete nodule.

5. TAXONOMIC NOTE

Traquair's (1888) original description of this species states that it was placed only provisionally under *Rhadinichthys*, and that a new genus would ultimately have to be established for it, characterized by the prominent snout and similar levels of dorsal and anal fins. Traquair recognized that both of these characters were significantly unlike their equivalents in other *Rhadinichthys* species. It now appears that '*R.*' *planti* displays strongest affinities with members of the genus *Mesopoma*. The two characters which Traquair discusses are unambiguously displayed by *M. carricki*, and the distinctive rostral and nasal patterns also occur in *M. pancheni* (Coates 1993). The skull table, however, combines features known from *Mesopoma* and *Rhadinichthys*, although it may be significant that these similarities, in addition to details of the snout, are shared most closely with *R. canobiensis* of this ill-defined and probably non-monophyletic genus (after descriptions in Moy-Thomas & Bradley Dyne 1938; Gardiner & Schaeffer 1989; and personal observation). Further *Mesopoma*-like characteristics which are absent in *Rhadinichthys* include the proportions of the maxilla (especially the long anterior ramus), the anteroposteriorly broad operculum and suboperculum with a posterodorsally inclined intervening suture, the branchiostegal series including fewer plates, and details of the squamation.

Mesopoma planti is the most recent stratigraphic record of this genus: all other species are from either Namurian or Viséan localities (reviewed in Coates 1993).

6. DESCRIPTION

(a) *External morphology*

The external features of NHM P7989 (figures 2 and 3) bear a striking resemblance to *M. carricki* and, to a less certain extent, *M. pancheni*, both of which are known from the Basal Namurian of Bearsden, Glasgow (Coates 1993). The preserved portion of NHM P7989 measures 25 mm from the rostral apex to the nodule edge, of which the total head length, from rostral apex to posteriormost edge of the suboperculum, is 16 mm, and the total body length is likely to have been around 70 mm.

The skull table (figure 3*a*) consists of paired frontals, parietals and post-temporals, flanked by a dermopterotic, dermosphenotic and two extrascapulars on either side of the dorsal midline. The distinctive dermal ornament of flattened tubercles and ridges (as described in Traquair 1888) resembles that of *M. carricki*. MM W1146 includes natural moulds of the frontals, which show clearly that this is the same taxon as NHM P7989. The posterolateral frontal edge has a complex, notched profile where it sutures with the anterior limb of the dermopterotic. This anterior limb extends for about one-third of the frontal lateral edge, and naso-dermopterotic contact is occluded by fronto-dermosphenotic contact. In NHM P7989, the posterior of the narrow triangular dermosphenotic lacks the T-shaped morphology present in most species of *Mesopoma*, but this is present in other specimens, including NHM P7985, NHM P8497 and NHM P8500.

The ethmoid complex (figure 3*b*,*c*) includes a rostral flanked by nasals and bordered ventrally by premaxillae. Traquair (1888) comments on the 'peculiarly large development of the snout', of which the most prominent part is the bulbous rostral. This has a bilaterally symmetrical ornament of broad tubercles which are extremely similar to those of *M. carricki*, *M. pancheni* and, to a lesser extent, *Rhadinichthys canobiensis* (Moy-Thomas & Bradley Dyne 1938; similarities noted previously in Coates (1993)). Patches of this rostral ornament are also preserved on MM W1146. As in *M. carricki*, the premaxilla is broad, tall, subrectangular and contributes to the anteroventral orbital rim. A Collyhurst specimen, NHM P8501E, has a premaxilla with pores marking the path of the sensory canals, and these match the pattern in other *Mesopoma*

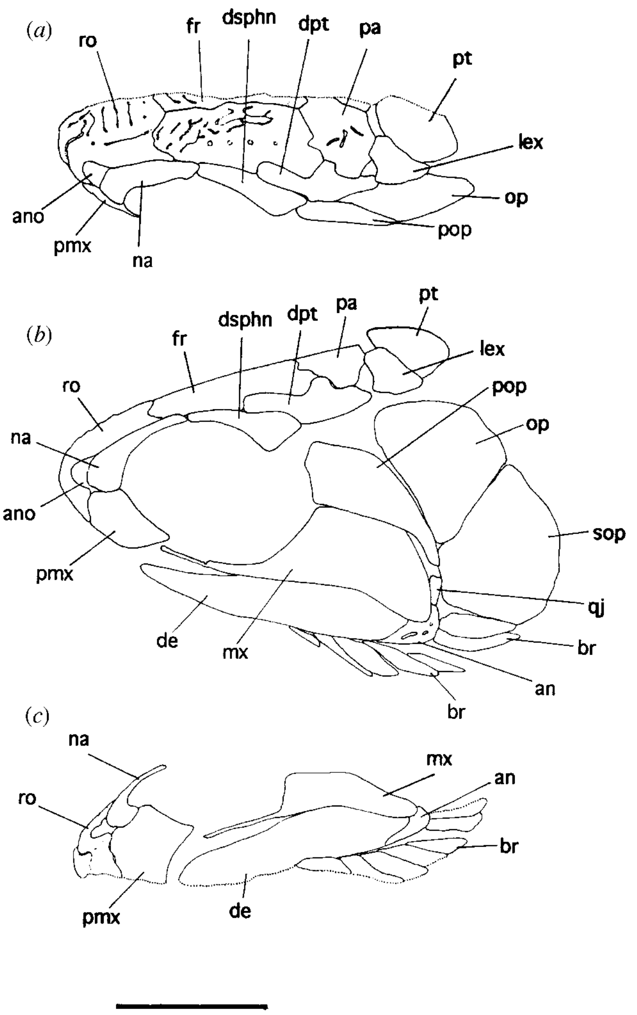

Figure 3. *Mesopoma planti* NHM P7989. (*a*) Dorsal view of skull roof; (*b*) lateral view, showing cheek region; (*c*) ventral view, showing lower jaw, branchiostegal series, and relation of premaxilla to rostronasal bones. All drawings from cast of natural mould; dotted line indicates margin of bone-mould with surrounding matrix. Scale bar, 5 mm. For a list of abbreviations, see Appendix A.

species (Coates 1993). The narrow nasal is mostly smooth, and bears shallow notches anteriorly and posteriorly at the level of anterior and posterior nostrils.

In NHM P7989 the cheek region (figure 3*b*) includes a preoperculum with a distinct, anteriorly expanded, anterodorsal limb, above which lies a space for a dermohyal. Beneath the rear of the preoperculum there appears to be a short quadratojugal, although evidence for this on the cast (NHM P P7989) is equivocal. NHM P8497 and NHM P8500 each include a long, slender dermohyal, which mostly occluded preopercular–opercular contact. From these specimens, and the condition of the incomplete hyomandibula in NHM P11656 (figure 4), it appears that the dermohyal is not fused to the hyomandibula. The anterior infraorbital is assumed to have resembled those of other *Mesopoma* species. NHM P8500 includes the best preserved posterior infraorbital and single suborbital, and these resemble closely the pattern of *M. carricki*. The narrow, anterior, suborbital process of the maxilla is of about the same length as the near-rectangular, posterior, expanded region (in contrast to *Rhadinichthys*).

The lower jaw is unremarkable except for the presence of a distinct angular pierced by at least two large sensory canal pores. The larger, anteriormost of these may represent an angular pit line. The marginal dentition consists of uniformly small, conical teeth. From external inspection, it is unclear if these bear acrodin caps.

The operculum and suboperculum are anteroposteriorly broad. The operculum is equal to or smaller than the suboperculum, and divided from it by a steep, posterodorsally inclined suture. As noted by Traquair (1888), these bones are smooth except for a few, faint concentric striae. The branchiostegal series includes about seven or eight plates (figure 3*c*), the posteriormost of which may be overlapped slightly by the ventral edge of the suboperculum. The condition of the gular plates in this species is unknown, although in other species of *Mesopoma* it is clear that the lateral gulars are subtriangular and little more than twice the anteroposterior length of the branchiostegal plates (Coates 1993).

No specimens include a well-preserved postcranium (speculative reconstruction in figure 2*a* based on *M. carricki*, Coates (1993)). However, data from NHM P7989, NHM P8497 and NHM P8501B provide the following details. The pectoral girdle resembles that of *M. carricki*, with a short cleithrum, dorsoventrally deep supracleithrum, and postcleithrum. The leading edges of all fins appear to have fringing fulcra, except the dorsal edge of the caudal fin. The pectoral fin includes numerous, proximally unjointed lepidotrichia. The dorsal and anal fins are situated opposite each other in the rear half of the body. The dorsal fin includes at least 25 rays, the anal fin at least 22 rays and the caudal fin at least 60 rays. All median fins are preceded by an uncertain number of unpaired basal fulcra. The scales are arranged in between 35 and 40 rows, counting from the rear of the pectoral girdle to the origin of the tail. The prominence of the scale ornament (figure 2*b*) varies considerably between individuals. In NHM P7989 the scales are almost entirely smooth, whereas in NHM P8502 the ornament consists of around five grooves parallel to the anterior and ventral edges, with four-plus posteriorly directed narrow chevrons on otherwise smooth central surface. Many scales have a serrated posterior edge, but, because of poor preservation, it is not clear if this feature is confined to certain regions of the squamation (cf. *M. carricki*, Coates 1993).

(b) *Internal morphology: general features*

NHM P11656 includes details of several internal cranial structures in addition to the 'brain cast' (figure 4). The oral surfaces of the palate and mandible bear a shagreen of denticles, but sutures between the contributing dermal bones are not identifiable. Preserved parts of the hyoid arch include the ceratohyal and expanded head of the hyomandibula. The ceratohyal (figure 4, chy) resembles the anterior ceratohyal ossification of *Pteronisculus* (Nielsen 1942), and the specimen associated with *Kansasiella* (Poplin 1974). However, the hyomandibula, except for an apparent lack of any fused part of the dermohyal, is too poorly preserved for an informative comparison. The ceratohyal shaft is constricted in the mid-region, subcylindrical in cross-section, and the lateral surface bears a well-defined, slightly sigmoid groove for the afferent hyoidean artery.

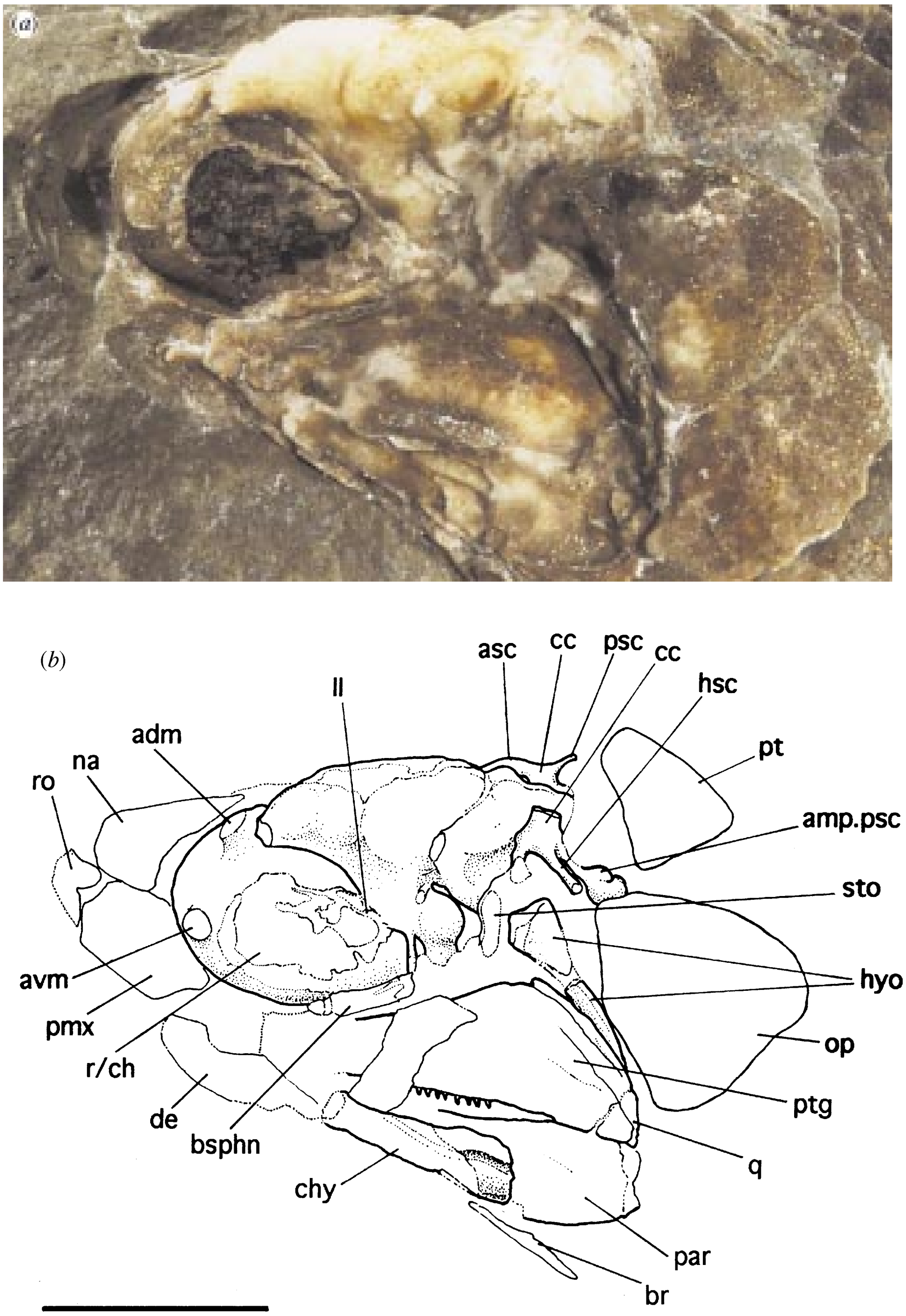

Figure 4. *Mesopoma planti* NHM P11656. (a) Specimen immersed in isopropyl alcohol, showing enhanced contrast between skeletal structures and endocranial infilling. (*b*) Line drawing interpretation of area covered in photograph, incorporating additional information from silastic cast of specimen. Orientation of specimen in this drawing shows slightly more of the dorsal surface, relative to the photograph, thereby including more detail of the inner ear structure. Scale bar, 5 mm. For a list of abbreviations, see Appendix A.

The right orbit of NHM P11656 is infilled and projects from beneath the fore- and midbrain regions. The anterior orbital surface bears incomplete natural casts of the anterodorsal and anteroventral myodome cavities for the oblique muscles (figure 4*b*, adm, avm). There is no trace of phosphatized muscle within these structures. The medial surface of the orbit bears at least two further layers of material (figure 4), the significance of which is uncertain. Of these, the superficial layer, a black film (figure 4*b*, r/ch) covers most of this area, sandwiching a subjacent layer of pale, crystalline material against the rear of the orbit. The layer of black material extends from the rear of the orbit towards the likely point of entry for the optic nerve (figure 4*b*, II). These layers may represent preservation of the scleral cup and the retinal pigment and/or choroid coat.

These details of NHM P11656 are complemented by the similarly unusual preservation of MM W1146. A central fragment of this nodule consists of the infilled orbit and scleral cup from both sides of the head, united by part of the interorbital septum and infilled cavities of the anterior neurocranium (figure 5). The scleral cup extends from the medial to external surfaces of the eye, and there is no evidence of a separate ring of scleral plates as in many other early actinopterygians (e.g. *Cheirolepis*, Pearson & Westoll 1979). The externally visible surface of this extremely thin scleral layer provides no evidence of dermal ornament or any division into dorsal and ventral halves (as in *Mimia*, Gardiner 1984), although anterior and posterior visible surfaces are much narrower (figures 2 and 5*a*,*d*). The portions of ossified orbital wall in MM W1146 include unusual details of the anterior

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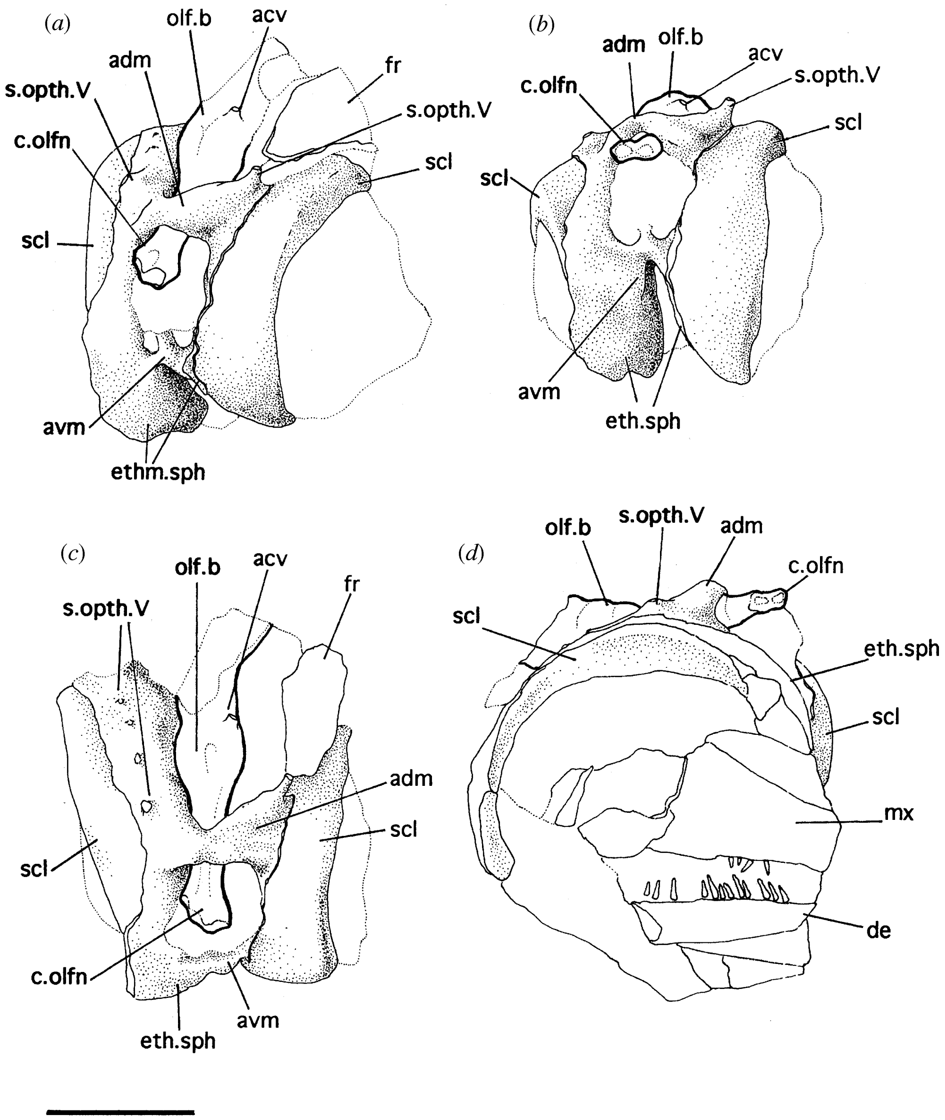

Figure 5. *Mesopoma planti* MM W1146. Infilled sclerotic cups, orbits, anterior myodomes and endocranial cavity enclosing the forebrain, showing previously undescribed spatial relations between these structures: (*a*) anterolateral view; (*b*) anterodorsal view; (*c*) dorsal view; (*d*) lateral view, including dermal jaw and tooth fragments. Scale bar, 2 mm. For a list of abbreviations, see Appendix A.

myodome configuration which are missing from NHM P.11656. The anteroventral myodome from each orbit projects towards the midline where they meet, forming an extremely narrow bridge with a short, dorsal projection (figure 5*a*,*b*, avm). It is unclear if these cavities, housing the inferior oblique muscles, were confluent. The anterodorsal myodomes are more extensively developed and have much more substantial contact across the mid-line, dorsal to the canal for the olfactory nerve (figure 5*b*,*c*, adm). Effectively, this constitutes a single, anterodorsal myodome for the superior oblique muscles, saddling the anterior forebrain cavity. This unusual morphology is not unique: Poplin (1974, fig. 20) illustrates a single anterodorsal myodome in *Kansasiella*, plus a variation on the condition of the anteroventral myodome, in which those of left and right sides are united as a single, median recess in the posterior ethmoidal wall. In *M. planti* narrow canals project dorsally from the roof of the anterodorsal myodome (figure 5*b*,*c*, s.opth.V) and orbital roof. These probably carried ascending twigs of the superficial ophthalmic nerve V.

(c) *The 'brain cast' and otic capsule*

The endocranial cast of NMH P11656 (figures 4 and 6) is interpreted as if the dorsal and lateral surfaces reflect fairly closely the enclosed brain morphology (cf. Rayner (1951) on *Kentuckia*). The most immediate features of the total shape are its compactness, and that the olfactory bulb and olfactory nerves are directed anteriorly (figure 6, olf.b). In these respects *M. planti* resembles *Lepisosteus* (figure 7*e*,*f*; Balfour & Parker 1882; Herrick 1891; Northcutt & Butler 1976) and teleosts (e.g. *Salmo*, figure 7*i*,*j*; Nieuwenhuys 1982), but is quite unlike living chondrosteans, such as *Acipenser* (Marinelli & Strenger 1973; Nieuwenhuys & Pouwels 1983), in which the brain is elongate and the olfactory bulbs and connections to the nasal sacs are directed anterolaterally (figure 7*c*,*d*). Linear brain morphology resembling that of acipenserids is also found in polypterids (figure 7*a*,*b*; Senn 1976; Nieuwenhuys 1982; Bjerring 1991), *Amia* (figure 7*g*,*h*; McCormick 1983), and outgroups such as sarcopterygians (*Lepidosiren*, Thors & Nieuwenhuys 1979; *Latimeria*, Nieuwenhuys 1969) and neoselachians (e.g. *Squalus*, Stensiö 1963). Both NHM P11656 and MM W1146 show that the olfactory bulb is small and of similar size to the telencephalon, which is much shorter than the proportionately longer telencephalon in polypterids, *Acipenser* and sarcopterygians. In *M. planti* the orbit extends well beyond the anterior margin of the olfactory bulb (figures 4 and 5*c*), which is almost certainly derived relative to the

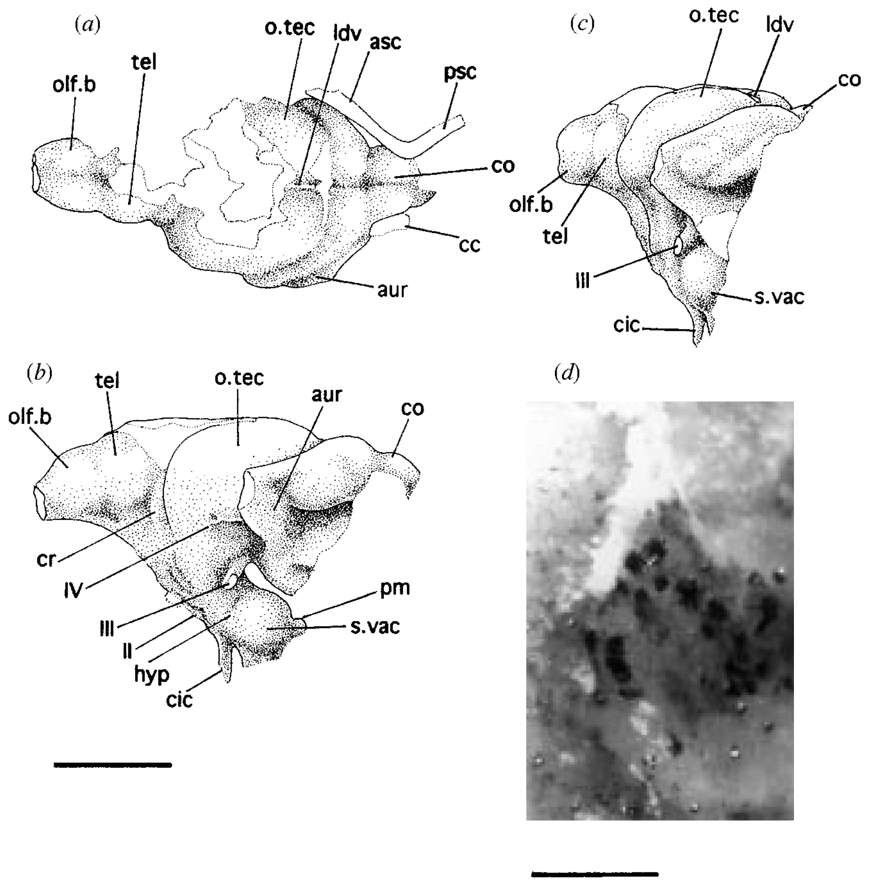

Figure 6. *Mesopoma planti* NHM P11656. Cast of endocranial cavity showing external morphology of brain: (*a*) dorsal view; (*b*) lateral view; (*c*) posterolateral view. Scale bar, 2 mm. (*d*) Detail showing melanocytes in dorsal roof. Scale bar, 200 µm. For a list of abbreviations, see Appendix A.

polypterid condition, where the anterior margin of the olfactory bulb lies in front of the anteriormost extent of the eyeball (Senn 1976). Comparison with *Acipenser* is less clear because of the derived anteroventral position of the orbit and reduced eye size (Marinelli & Strenger 1973).

MM W1146 has the base of a dorsally directed canal emerging from the top of the left side of the telencephalic region (figure 5*a–c*, acv). This resembles an identically positioned, left-side stub on the endocranial cast of *Kansasiella* interpreted as the path of the anterior cerebral vein (Poplin 1974, fig. 22, v.cer.ant). Another example is present in *Mimia* (Gardiner 1984, fig. 33, cotel.), although this canal lies more anteriorly so that it communicates with the left, anterodorsal myodome, through which the anterior cerebral vein is thought to have drained into the supraorbital vein. Similar examples of this canal are present in *Osorioichthys* (Taverne 1997), *Pteronisculus* (Nielsen 1942) and the stem-teleost *Pholidophorus bechei* (Patterson 1975, fig. 61 & 65, acv.), but in none of these taxa is the canal known to be restricted to the left side. Furthermore, in *P. bechei* the likely homologue of this canal is positioned much more posteriorly, lying caudally relative to the foramen for the trochlear (IV) nerve.

The optic tectum of *M. planti* is the most prominent part of the endocranial cast (figure 6, o.tec): the maximum anteroposterior and lateral dimensions of the tectum are approximately double those of the olfactory bulb and telencephalon combined. These proportions resemble those of teleost brains such as *Salmo gairdneri* (figure 7*i*,*j*; Nieuwenhuys 1982). A well-defined median groove divides the optic tectum into distinct bilateral lobes (figure 6*a*). This clear division of the tectum is absent in *Acipenser* (figure 7*c*; Marinelli & Strenger 1973; Nieuwenhuys & Pouwels 1983) but is present in polypterids and neopterygians (figure 7). Although Nieuwenhuys (1982) illustrates *Erpetoichthys calabaricus* with a posteriorly incompletely divided tectum, Bjerring (1991) shows the same species with an anteroposteriorly complete division, and R. G. Northcutt (personal communication) confirms the presence of this division in *Polypterus*. In NHM P.11656, a low, central crest lying within the posterior part of this groove (figure 6, ldv) probably marks the course of the longitudinal dorsal vein (Zwehl 1961). In lateral view (figure 6*b*, cr), another crest lies within the recess dividing the optic tectum from the telencephalon. The significance of this is unclear, but it probably also relates to the anterior cerebral venous network. The posterior of the optic tectum is flanked by the cerebellum, from which it is divided by a well-marked groove. A natural mould of the trochlear (IV) nerve (figure 6*b*, IV) emerges from this recess and extends anteriorly for a short distance just beneath the most laterally prominent apart of the tectum.

The diencephalic region is strongly developed, with the hypophyseal space directed ventrally and slightly posteriorly (figure 6*b*, hyp). This orientation resembles more closely that of *Acipenser* (figure 7*d*; Marinelli & Strenger 1973) or *Polypterus* (figure 6*b*; Senn 1976) rather than *Lepisosteus* (figure 7*f*; Balfour & Parker 1882) and *Amia* (figure 7*h*; McCormick 1983), in which the orientation is anteroventral. The root of the optic (II) nerve is indicated by close association with the black (retinal–choroid pigment?) layer at the rear of the scleral cup (figures 4*b* and 6*b*, II). The ventralmost extent of the hypophysis is

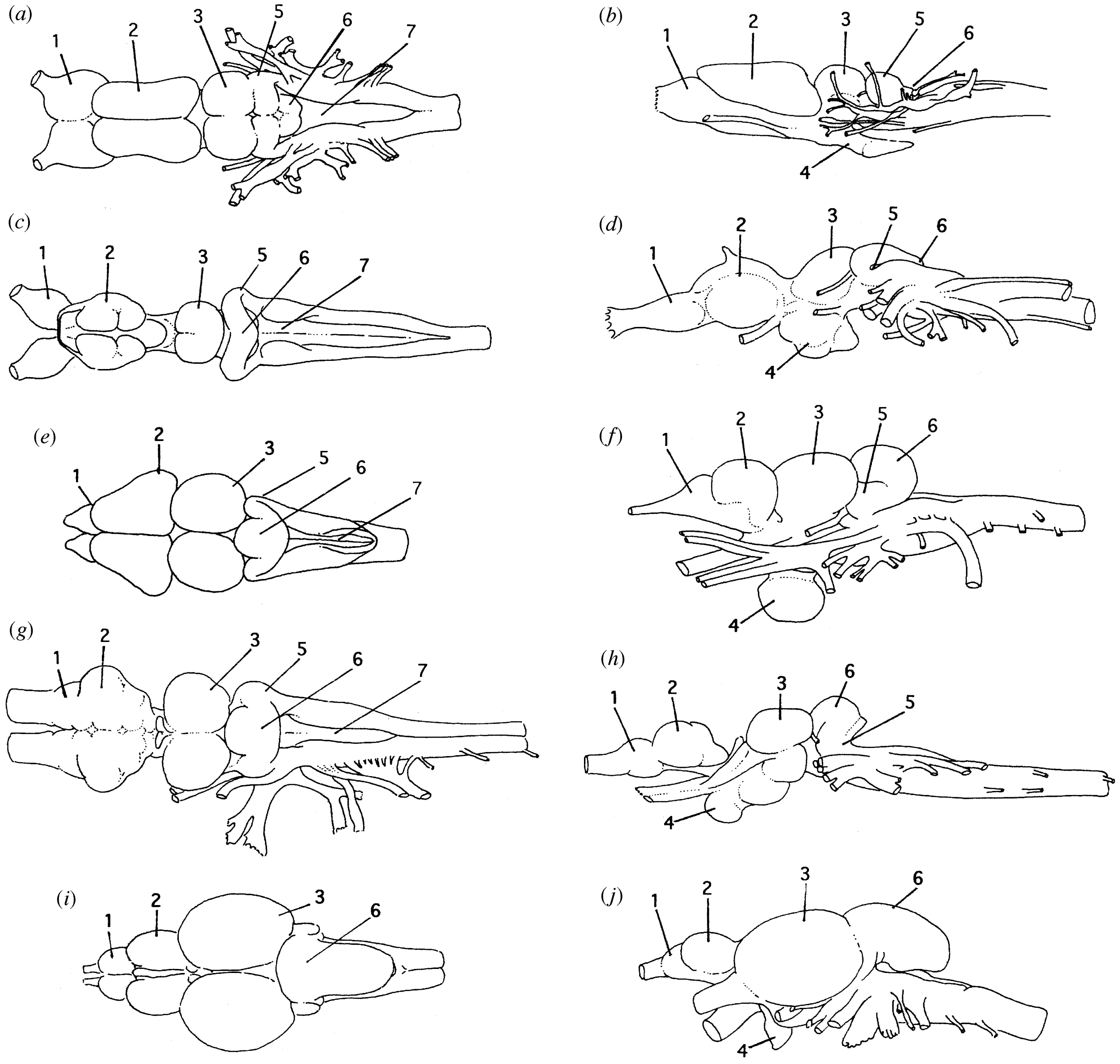

Figure 7. External morphology of actinopterygian brains. *Polypterus* in (*a*) dorsal and (*b*) lateral views (after Senn 1976; Nieuwenhuys 1982; Bjerring 1991); *Acipenser* in (*c*) dorsal and (*d*) lateral views (after Marinelli & Strenger 1973; Nieuwenhuys & Pouwells 1983); *Lepisosteus* in (*e*) dorsal view (optic tectum and posterior region; after Balfour & Parker 1882; telencephalon and anterior region; after Herrick 1891; Scharrer 1944) and (*f*) lateral view (after Balfour & Parker 1882; Herrick 1891; Northcutt & Butler 1976); *Amia* in (*g*) dorsal and (*h*) lateral views (after McCormick 1983); *Salmo* in (*i*) dorsal and (*j*) lateral views (after Nieuwenhuys 1982). Not drawn to scale; key to arab numerals listed in Appendix A.

obscured in NHM P11656. The cast of this region divides ventrally to produce, anteriorly, a narrow vertical canal for the internal carotid artery (figure 6*b*, cic), like that of *Kentuckia* (Rayner 1951) or *Kansasiella* (Poplin 1974). The posterodorsal bulge in the hypophyseal space probably represents a recess for the saccus vasculosus (figure 6*b*,*c*, s.vac), although the division of this area from that enclosing the pituitary body is unclear. The posterior extent of this bulge is much less than that of *Kansasiella*. Anterodorsal to this recess, and directly below the broadest part of the optic tectum, lies the root of the oculomotor (III) nerve.

The cerebellar region includes casts of the corpus and vestibulolateral lobes. Unlike *Kansasiella* (Poplin 1974), *Pteroniscula*s, *Boreosomus* (Nielsen 1942), *Australosomus* (Nielsen 1949) or the semionotid *Tetragonolepis* (Thies 1989), this region is not obscured by infillings of the lateral occipital fissure and dorsal fontanelle, or diverticula extending from the cavum cranii. The morphology of such diverticula in *Pteroniscula*s *magnus*, and the likelihood of such spaces housing lymph forming organs (cf. Thies (1989) on *Tetragonolepis*) is discussed in detail elsewhere (Coates 1998). As in all non-teleostean actinopterygians, the vestibulolateral lobes are directed rostrolaterally as a pair of auriculae (figure 6*a*,*b*, aur; Nieuwenhuys 1982). The corpus is divided medially by an anteroposterior groove (figure 6*a*, co) as in *Polypterus*, *Erpetoichthys* (figure 7*a*; Nieuwenhuys 1982), and, to a lesser extent, *Acipenser* (Stensiö 1963, Marinelli & Strenger 1973; Nieuwenhuys & Pouwels 1983). As in polypterids and *Acipenser* the corpus protrudes posteriorly and probably extends ventrally into the fourth ventricle. There is no indication that this portion of the corpus arched above the ventricle as it does in *Amia* (Nieuwenhuys 1982;

McCormick 1983), *Lepisosteus* (Northcutt & Butler 1976) and more advanced actinopterygians; neither is there any suggestion of an anteromedial prominence to the corpus, as present in each of these taxa (figure 7*e–j*).

The region enclosing the rhombencephalon is obscured by other structures in NHM P11656, including the infilled otic capsules. The left side preserves the basal part of the crus commune and the origin of anterior, posterior and horizontal semicircular canals (figures 4*b* and 6*a*). The ampulla for the posterior semicircular canal is especially well preserved (figure 4*b*, amp.psc). Ventral to these, a broken surface sections through the *pars inferior*, revealing the apparent profile of a large statolith. Only the dorsalmost parts of the semicircular canals are visible from the right otic capsule.

Finally, the roof of the optic tectum and telencephalon in NHM P11656 is capped with a further layer, consisting of the same material as other cavity infills in this specimen, lying beneath the edges of the remaining dermal bone (edges of the frontals remain visible, mostly within the nodular matrix). The edges of this layer are broken at an oblique angle relative to the dorsal surfaces, so that only a small area of uninterrupted dorsal surface is available for inspection. Unlike the subjacent surface of the 'brain cast', this layer is speckled with small, black, stellate shapes resembling melanocytes (figure 6*d*). These are mostly about 50 μm across (although there is considerable variation), and arranged in near-linear rows radiating from a posteromedial focus. This layer is probably equivalent to that which Moodie (1920) misidentified as the meningeal space in *Kentuckia deani*. In which case, following Rayner (1951), this is probably the mineralized, highly cancellar endochondral roof of the neurocranium. The melanocytes lie within the topmost layer of this material, suggesting that it may incorporate basal laminae of the dermal skull roof. This is corroborated by the presence of similar stellate bodies beneath the surface of other dermal bones (notably the post-temporal and operculum) in NHM P11656.

7. DISCUSSION

Morphological data covered in this description include several new characters which inform questions about patterns of primitive actinopterygian evolution. These can be used to test Gardiner & Schaeffer's (1989) phylogeny (the only large-scale, computer-based cladistic analysis of primitive actinopterygians) and reassess the relationships of palaeoniscid-grade genera to the origins of extant groups. Accordingly, the phylogenetic analysis presented here concerns an expanded and revised version of Gardiner & Schaeffer's data matrix. The number of characters is raised from 32 to 64, and the number of taxa is increased from 13 to 23. Of the genera included within Gardiner & Schaeffer's matrix, *Cheirolepis* characters are recoded following a new description of *C. canadensis* (Arratia & Cloutier 1996). Genera added to the data set include the Devonian *Howqualepis* (Long 1988) and *Osorioichthys* (Taverne 1997), both of which display combinations of features that may be intermediate to *Cheirolepis* and all other actinopterygians. Gardiner & Schaeffer (1989) did not include *Howqualepis* in their full phylogenetic analysis, but placed it in their '*Moythomasia*' group, whereas Gardiner (1993) placed it in the Mimiidae. *Woodichthys* (Coates 1998) is a newly described, Lower Carboniferous taxon from the Bearsden fauna, Glasgow, preserved in detail equivalent to that of *Howqualepis*, and may occupy a similar stem-actinopteran position. *Cosmoptychius* (after Schaeffer 1971), *Kansasiella* (Poplin 1974, 1975) and *Coccocephalus* (after the redescription by Poplin & Véran (1996)) are included for their neurocranial information, and the parasemionotid *Watsonulus* (Olsen 1984) because it illustrates character conditions close to the presumed divergence of the major living neopterygian clades. Primitive teleost conditions are scored from Patterson's (1968, 1973, 1975) description of *Pholidophorus* unless stated otherwise.

New characters in the data matrix include several which relate directly to the preceding description of *M. planti*. These include a series concerning large-scale neuroanatomical features which may be inferred directly or indirectly from neurocranial endocasts and related material. Other new characters describe the condition of the anterior and posterior myodomes, and patterns of dorsal aortic canal development. Certain characters used in previous analyses, such as the presence or absence of (pseudo-) prismatic ganoin (Ørvig 1967, 1978), have been revised thoroughly in the light of new data (e.g. Richter & Smith 1995). Characters are also included from recent non-computer-based analyses of primitive actinopterygians, most notably those by Long (1988) and Taverne (1997).

Gardiner & Schaeffer (1989) used PAUP software to analyse a data matrix of 32 characters and 13 taxa (*Cheirolepis*, *Polypterus*, *Mimia*, *Moythomasia*, *Pteronisculus*, *Boreosomus*, *Acipenser*, *Saurichthys*, *Birgeria*, *Australosomus*, *Perleidus*, *Lepisosteus* and *Amia*). *Cheirolepis* was used as an outgroup, and their results included two trees of 54 steps, with a consistency index 0.63. *Acipenser*, and by implication the phyletic divergence of chondrostean from neopterygian lineages, emerges at two alternative nodes: either above or below *Pteronisculus* and *Boreosomus*. For the basis of subsequent discussion, Gardiner & Schaeffer interpreted *Acipenser* as more derived than *Pteronisculus* and *Boreosomus*, because it requires fewer independent derivations of a dermopterotic in the temporal series. *Mesopoma* and most other palaeoniscid-grade genera are therefore excluded from the neopterygian total group, and appear as plesion stem-lineage actinopterans (*sensu* Patterson 1982). Gardiner & Schaeffer's (1989) cladogram, with genera from the present analysis inserted according to their conclusions, is shown in figure 8.

As an initial test of Gardiner & Schaeffer's (1989) phylogeny, their data matrix was reanalysed using PAUP version 3.0 (Swofford 1990). The results differ slightly from Gardiner & Schaeffer's, and include four trees of only 51 steps, although retaining the same consistency index of 0.63. An Adams consensus of these includes two polytomies (Gardiner & Schaeffer's Adams consensus includes only one polytomy): (i) between *Polypterus*, *Mimia* and *Moythomasia* plus more derived genera; and (ii) between *Acipenser*, *Pteronisculus*, *Boreosomus* and *Saurichthys* plus more derived genera. However, with successive weighting, the resultant tree is consistent with their selected result.

(a) *Characters used in analysis*

Capital letters in brackets refer to source of character: BG, Gardiner 1984; G & S, Gardiner & Schaeffer 1989;

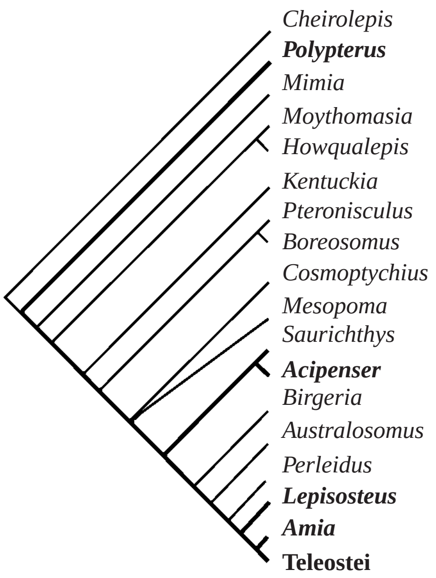

Figure 8. Gardiner & Schaeffer's (1989) cladogram, with genera from the present analysis installed to enable simple comparison with results presented in figure 9.

L, Long 1988; P, Patterson 1982; P & R, Patterson & Rosen 1977; T, Taverne 1997.

Unless stated otherwise, justification of character selection and coding is considered sufficiently well discussed in earlier publications, as listed.

(i) *Histology*

1. Acrodin toothcaps: absent 0; present 1 (BG; G & S; P; T).
2. Prismatic ganoine on scales (G & S; P). Gardiner & Schaeffer (1989) used this as synapomorphy for *Pteroniscidus* plus higher actinopterygians, but Richter & Smith (1995) argue that 'prismatic ganoine' (Ørvig 1978) or 'pseudoprismatic ganoine' (Ørvig 1967) is not a well-defined feature of enamel structure. Ganoine itself is a poorly defined term which is used to describe actinopterygian enamel (Sire *et al.* 1987; Sire 1994). In primitive actinopterygians, enamel is deposited incrementally leaving a series of growth lines, and the terms 'prismatic' and 'pseudoprismatic' refer to arrangements of the constituent crystallites. In *Cheirolepis* the enamel crystallites are too small to be resolved. In *Polypterus* the crystallites are resolvable: at deeper levels they are rod-like and perpendicular to the outer surface, but become increasingly twisted superficially. In *Mimia*, *Moythomasia*, *Acrolepis* (which Hutchinson, in Gardiner & Schaeffer (1989), reconstructed as resembling *Pteroniscidus*), *Colobodus* (a member of the Perleididae, Lehman 1966) and more advanced actinopterans, the crystallites are resolvable and consistently perpendicular to, or arranged into groups which are slightly divergent to, the outer scale surface. Richter & Smith (1995) identify an apparent reversal to enamel with small, irresolvable crystallites, in *Watsonichthys*, while *Palaeoniscum* and *Lepisosteus* display a 'criss-cross' crystallite pattern.

For the purposes of the present study ganoine is regarded as absent in *Acipenser*. However, in an uncatalogued specimen of *Acipenser* in the teaching collections of the Zoology Museum, University College London, scales from the ventral edge of the caudal peduncle bear prominent denticles with apices consisting of enamel-like, translucent material.

Revised characterization: enamel with irresolvable crystallite structure 0; crystallites resolvable 1; crystallites resolvable and mostly perpendicular to the scale surface 2 (sometimes in fan-shaped groups expanding distally); enamel crystallites crossed 3; enamel absent 4.

(ii) *Dermal skeleton—general*

3. Rhomboidal scales, anterior to caudal region, with anterodorsal angle plus peg and socket articulation. Absent 0; present 1 (BG; G & S; P).
4. Intertemporal: short 0; long, contacting nasal 1; absent 2 (G & S; T). The intertemporal has probably been lost on several occasions within actinopterygian phylogeny, linked to the repeated evolution of a dermopterotic (character 5). The Devonian *Dialipina* may exemplify an early example of such loss (Schultze 1992; Schultze & Cumbaa 1996). Likewise, there appears to be no intertemporal in *Cheirolepis canadensis* (Arratia & Cloutier 1996), although a short intertemporal is clearly present in *C. trailli* (Pearson & Westoll 1979, Gardiner & Schaeffer 1989), and is coded as such in the matrix. Outgroup comparison with primitive sarcopterygians suggests that a canal-bearing intertemporal is primitively present (Jessen 1980). Therefore, although *Dialipina* is the earliest known example of an actinopterygian skull roof, it remains more parsimonious to consider the condition of *Cheirolepis trailli* as representative of the primitive pattern.
5. Supratemporal: no frontal contact 0; contacting frontals 1; apparent fusion with intertemporal, forming dermopterotic 2; dermopterotic meets midline 3. States 0 and 1 of this character are used to define a threshold within the gradual transition from primitively short frontals and long parietals to long frontals and short parietals (see discussion in Pearson (1982)), because supratemporal–frontal contact is established as parietal length is reduced. However, although the extremely primitive *Dialipina* is described as having short frontals (parietals) and long parietals (postparietals), the 'supratemporal' reaches the mid-lateral level of the frontal (Schultze 1992; Schultze & Cumbaa 1996). This either represents an early, apomorphic exception to the general trend or, as no intertemporal is present (character 4), it is equally likely that this supratemporal represents a dermopterotic (state 2).

Although intertemporal–parietal contact occludes supratemporal–frontal contact in *Kentuckia deani* (Rayner 1951) and *K. hlavini* (Dunkle 1964), in this instance the condition is considered derived (scored as 1), because: (i) the supratemporal extends anteriorly level with the posterior end of the frontal; and (ii) uniquely derived processes of the intertemporal and parietal maintain their mutual contact.

Gardiner & Schaeffer (1989) follow Pehrson (1922, 1944, 1947) and Jollie (1984*a*,*b*), who note that in *Polypterus*, *Acipenser*, *Polyodon*, *Lepisosteus* and *Amia*, two major primordia form a single bone in the temporal region. As in Gardiner & Schaeffer's analysis, this bone is identified as a dermopterotic (state 2). In each case, an anterior (intertemporal) primordium includes neuromasts innervated by the ramus oticus of the facial nerve (VII), and a posterior (supratemporal) primordium includes neuromasts innervated by a branch of the glossopharyngeal nerve (IX). Pehrson and Jollie both describe the dermopterotic as an 'intertemporo-supratemporal', show the joint innervation of the enclosed stretch of canal, and show how, in *Polypterus*, this bone also replaces an early, weakly developed parietal, so that the dermopterotic now meets the midline (state 3). Haplolepids, and perhaps porolepids and coelacanths, probably exhibit a similar condition (Jollie 1984*a*). No extant actinopterygian displays convincing evidence of separate intertemporal and supratemporal bones, although in *Polyodon* only large specimens fuse anterior and posterior precursors of the dermopterotic (Grande & Bemis 1991).

As acknowledged by Gardiner & Schaeffer (1989), it appears that a dermopterotic has evolved on several independent occasions in actinopterygian evolution. The systematic value of this character at deep nodes in actinopterygian phylogeny is therefore reduced.

The supratemporal in *Watsonulus* (Olsen 1984) is interpreted here as an extrascapular.

6. Dermosphenotic contacts nasal 0; separate from nasal 1 (G & S).
7. Supraorbitals: absent 0; present 1 (G & S). These are difficult to identify in *Coccocephalus* (M. I. Coates, personal observation), but are scored as present in the current analysis (cf. Poplin & Véran 1996). In *Saurichthys*, supraorbitals are scored as absent, after Rieppel (1985); *contra* Stensiö (1921) and Gardiner & Schaeffer (1989).
8. Suborbitals: absent 0; present 1 (G & S).
9. Dermohyal fused to hyomandibula 0; separate from hyomandibula 1. *Polypterus* is the only living actinopterygian in which the dermohyal is fused to the hyomandibula. Jollie (1984*a*, fig. 8*b*) illustrates the full extent of this dermal bone in *Polypterus*, where it is mostly concealed from external view by overgrowth of the posterior edge of the preoperculum. Hyomandibula–dermohyal fusion is present in several primitive actinopterygians, including *Howqualepis* (Long 1988), *Mimia* and *Moythomasia* (Gardiner 1984). From Pearson & Westoll's (1979, p. 362) description, it appears that *Cheirolepis* also exhibits this condition, but the condition in *Osorioichthys* (Taverne 1997) is unknown. Such fusion is therefore assumed to be a primitive characteristic of actinopterygians, although outgroup comparison indicates that this is apomorphic relative to other osteichthyans. Presence of a narrow, subtriangular dermal bone between the dorsal limb of the squamosal–preopercular complex and the operculum is not, however, unique to actinopterygians. A dermohyal-like bone is also present in the cheek of onychodonts (Jessen 1966), but the relation to an underlying hyomandibula is unclear. In all other genera included within the present analysis, the hyomandibula, where known, is detached from the dermohyal, which could otherwise be decribed as an accessory opercular bone.
10. Interoperculum: absent 0; present 1 (BG; G & S).
11. Lateral gulars large, with rounded posterolateral profile 0; lateral gulars equivalent to area of three branchiostegals or less, with posterior and lateral angles 1; all gulars absent 2; lateral gulars absent, median gular present 3; lateral gulars absent, median gular paired 4. Large, rounded lateral gulars are present in *Cheirolepis* (Pearson & Westoll 1979), *Osorioichthys* (Taverne 1997) and *Polypterus*. Similarly large lateral gulars covering most of the throat are also present in all (non-tetrapod) Palaeozoic sarcopterygians, indicating that this condition is primitive for osteichthyans. Actinopterygians exhibit several patterns of gular evolution, most of which involve reduction and/or loss of the lateral gulars. This trend contrasts strongly with the cladistian condition, in which the median gular is absent (this likely apomorphy is uncoded in the present analysis), but the lateral gulars are extremely large. Chondrosteans lack all gulars (Marinelli & Strenger 1973; Grande & Bemis 1981), paralleling the condition in *Lepisosteus* (Jollie 1984*b*; Olsen 1984), while *Boreosomus* lacks lateral gulars but has paired median gulars (Nielsen 1942), and *Amia* plus primitive teleosts retain only a median gular. As noted by Taverne (1997), the lateral gulars in most 'palaeoniscids' are reduced in size and resemble little more than enlarged branchiostegal plates. However, the ontogenetic and phylogenetic relation between gulars and branchiostegals is unclear. Evolutionary trends indicate a degree of mutual independence between these adjacent sets of dermal bones, thus corroborating Jollie's (1984*a*) ontogeny-based speculation that gulars should be considered as distinct from the branchiostegal series.
12. Fewer than 12–13 branchiostegal plates or rays: absent 0; present 1 (G & S).

(iii) *Dermal jaws*

13. Premaxilla and antorbital: fused 0; separate 1 (BG; G & S; T).
14. Premaxilla with nasal process: absent 0; present 1 (BG; G & S).
15. Maxilla free of preoperculum: absent 0; present 1 (BG; G & S).
16. Mobile maxilla in cheek: absent 0; present 1 (P & R; BG; G & S).
17. Supramaxilla: absent 0; present 1 (BG; G & S).
18. Lower jaw with surangular: absent 0; present 1 (BG; G & S; P; T). Scored as uncertain for *Kentuckia*, because it appears to be absent in *K. hlavini* (Dunkle 1964; personal observation); scored as present in *Cheirolepis* after Arratia & Cloutier (1996) and Pearson & Westoll (1989), *contra* Gardiner & Schaeffer (1989).
19. Coronoid process derived from dentary and surangular: absent 0; present 1 (BG; G & S).

(iv) *Pharyngeal skeleton*

20. Quadratojugal fused with, and forming brace for, quadrate: absent 0; present 1 (P & R; BG; G & S).
21. Symplectic: absent 0; present 1 (BG; G & S). Definition of symplectic after Patterson (1982), rather than

Véran (1988). The 'symplectic' of *Coccocephalus* (Poplin & Véran 1996) is therefore interpreted as an interhyal, and the 'interhyal' as a posterior ceratohyal.

22. Hyomandibula with canal for the hyoidean branch of nerve VII and opercular process: absent 0; present 1 (G & S; T).
23. Anterior ossification of ceratohyal subcylindrical 0; with a constricted shaft so that the ossification is hourglass-shaped in lateral aspect 1. From outgroup comparison and conditions in *Mimia* and *Moythomasia* (Gardiner 1984), the primitive state of actinopterygian anterior ceratohyals is to narrow anteriorly. In taxa such as *Pteroniscułus*, *Boreosomus* (Nielsen 1942) and *Kansasiella* (associated material, see Poplin 1974), the anterior ceratohyal has acquired a characteristic hourglass-like shape. So far, this morphology is associated consistently with a sigmoid, anterodorsally directed groove for the afferent hyoidean artery (character 24, state 2), but the extent to which these conditions are linked is uncertain. The condition in *Coccocephalus* is inferred from the profile of the natural cast of this ossification (Poplin & Véran 1996).
24. Anterior ceratohyal with smooth lateral surface (no groove present) 0; with distinct groove for afferent hyoidean artery 1; groove sigmoidal and directed anterodorsally 2. Outgroup comparison with acanthodian (Miles 1973) and sarcopterygian (Jarvik 1980) ceratohyals indicates that absence of this groove is primitive. A grooved anterior ceratohyal is present in a wide variety of actinopterygians including *Mimia*, *Moythomasia* (Gardiner 1984), *Australosomus* (Nielsen 1949) and *Watsonulus* (Olsen 1984). In certain genera this groove is curved sigmoidally, so that the anterior end passes towards the dorsal surface; examples include *Pteroniscułus*, *Boreosomus* (Nielsen 1942), *Mesopoma* and *Kansasiella* (associated material, see Poplin 1974).
25. Epibranchials 1 and 2 with strongly forked ends (uncinate processes): absent 0; present 1 (BG; G & S).
26. Upper pharyngeal dentition consolidated: absent 0; present 1 (P & R).

(v) *Neurocranium*

27. Hyoid facet directed posteroventrally 0; directed ventrally (orientated horizontally) 1 (G & S).
28. Spiracular groove enclosed within canal: absent 0; present 1 (BG; G & S; P; T).
29. Ventral cranial–otic fissure separate from lateral–otico-occipital fissure 0; ventral otic and otico-occipital fissure confluent via vestibular fontanelle 1; fissure pattern obscured by cartilage 2; fissures closed by bone 3. The condition in *Howqualepis* (scored 0) is taken from Long's (1988) figures 15*a*, 16*a* and 23*a*, where the fissures are separated by a broad bony bridge, rather than figure 18, where they are reconstructed as confluent. In *Pteroniscułus* the fissures are confluent in certain specimens and separated in others (Nielsen 1942; Coates 1998; M. I. Coates, personal observation). For the present analysis, *Pteroniscułus* is scored as 1. The condition in *Watsonulus* (scored as 1) is taken from figures 6 and 8 in Olsen 1984. Comparable conditions in *Birgeria* (Nielsen 1949), *Macrepistius* (Schaeffer 1971) and *Heterolepidotes* (Patterson 1975) are obscured by extensive posterolateral expansion of the parasphenoid and bone growth.
30. Canal for dorsal aorta short, with wide anterior opening and exposed point of bifurcation into lateral aortae 0; bifurcation point partly concealed, and canal with median or paired opening for efferent branchial arteries to join dorsal aorta 1; separate anterolaterally directed openings for lateral aortae 2; canal secondarily absent 3. Absence of an aortic canal in outgroups indicates that this character is primitively apomorphic for actinopterygians. The point at which it evolved, however, is uncertain. The condition in *Cheirolepis* is unknown, and in *Polypterus* the canal exhibits an apomorphic condition in which the length is increased by caudal growth of the parasphenoid. However, de Beer (1937, plate 28) shows that in a 76 mm juvenile the aortic canal within the occipital bone is short, situated posteriorly and terminates anteriorly level with the rear of the otic capsules. This is similar to the short canals of *Mimia*, *Moythomasia* (Gardiner 1984) and *Howqualepis* (Long 1988); *Polypterus* is therefore scored as 0. *Polypterus* is not the only living actinopterygian retaining an aortic canal (*contra* Patterson 1975): a short, anteriorly sited canal enclosing the division into lateral aortae persists in *Acipenser* (Marinelli & Strenger 1973). The anterior paired openings of this canal pattern resemble those of *Kansasiella* (Poplin 1974) and *Pteroniscułus* (Nielsen 1942), while canals which enclose the aortic division incompletely are present in *Woodichthys* (Coates 1998) and *Coccocephalus* (Poplin & Véran 1996). These canals also include median openings for efferent branchial arteries, and the condition in *Acipenser* may result from these openings becoming confluent with the occipital aortic foramen. Paired anterior openings for lateral aortae are also present in *Perleidus* (Patterson 1975), but here the canal is short and located posteriorly. This transformed canal pattern is assumed to correlate with posterior migration of the ventral otic fissure and enlargement of the circulus cephalicus (Poplin 1974; Patterson 1975). The *Mimia*-like aortic canal of *Australosomus* (Nielsen 1949) is assumed to represent a reversal.
31. Fossa bridgei: absent 0; present 1 (BG; G & S; T).
32. Lateral cranial canal: absent 0; present 1 (BG; G & S; P; T). This canal displays a variety of topological relations to the otic labyrinth and fossa bridgei; although present in most primitive actinopterygians, its functional significance remains uncertain (Rayner 1948; Patterson 1975; Coates 1998). Gardiner & Schaeffer (1989) code this canal as present in *Acipenser*, but sections through the cavum cranii and otic capsule of *Acipenser ruthenus* show no trace of this cavity (Marinelli & Strenger 1973, fig. 249 and 250), and Findeis (1998) describes it as absent in *Scaphirhynchus*. Similarly, Gardiner & Schaeffer code the canal as present in *Birgeria*, although it appears to be unknown in Nielsen's (1949) description. In the present analysis this character is scored as absent for both of these genera.

33. Post-temporal fossa: absent 0; present 1 (BG; G & S). Gardiner & Schaeffer (1989) score this as present in *Birgeria*, suggesting that the fossa opened laterally, somewhat like the condition in *Watsonulus* (Olsen 1984). However, Nielsen's (1949) description does not include a post-temporal fossa, and shows the relevant neurocranial material as too poorly preserved for such a reconstruction. This character is therefore coded as uncertain. Gardiner & Schaeffer also interpret a post-temporal fossa as present in *Acipenser*, but Findeis (1998) refutes this because (i) in *Amia*, pholidophorids, leptolepds and extant teleosts, the post-temporal fossa is continuous with the anterodorsal roof of the neurocranium, whereas in acipenserids it is restricted to the occiput; and (ii) the acipenserid post-temporal fossa forms secondarily as multiple vertebral segments merge into the rear of the neurocranium. Topographic and ontogenetic criteria therefore lead to the coding of this character as absent in *Acipenser*; functional similarity (housing anterior trunk musculature) provides insufficient basis to support coding this character as present.
34. Dilatator fossa: absent 0; present 1 (BG; G & S).
35. Parasphenoid with ascending process crossing the ventral otico-sphenoidal fissure to the lateral commissure: absent 0; present 1; reaches spiracular canal 2 (secondarily reduced in more derived taxa) (BG; G & S; P; T). The ascending process in *Polypterus* does not appear to be homologous with those of actinopteran parasphenoids, whereas the ascending process in *Acipenser* is considered homologous with that of *Amia* (as discussed in Gardiner 1984). Mayhew (1924) and Rayner (1948) each figure *Lepisosteus* without any ascending process, and the parasphenoid condition in larval specimens is ambiguous with respect to this character (Jollie 1984*b*). However, Gardiner (1984) and Gardiner & Schaeffer (1989) code this process as present in *Lepisosteus*, identifying it as mostly obscured by the large basipterygoid process (B. Gardiner, personal communication). In *Perleidus*, this character is scored as 2, after the condition in *P. madagascariensis* (Lehman 1952).
36. Parasphenoid posterior edge lies anterior to ventral otic fissure 0; parasphenoid posterior expanded to cover ventral otic fissure 1; posterior expanded region encloses canal for dorsal aorta 2. State 2 of this character is apomorphic for *Polypterus* (see discussion of character 28).
37. Dermal basipterygoid process: absent 0; present 1 (BG; G & S; T).

(vi) *Posterior myodome*

Previous studies (including Schaeffer & Dalquest 1978; Gardiner 1984; Gardiner & Schaeffer 1989) have characterized posterior myodome conditions as absent, paired, or single, but the present analysis uses a four-character series to improve discrimination between primitive stages of structural organization. In the absence of information on *Cheirolepis*, and the derived conditions of *Polypterus* and living chondrosteans, the myodome-less and actinopterygian-like proportioned braincase of the sarcopterygian *Youngolepis* (Chang 1982) provides an alternative outgroup perspective on the likely polarity of these characters. When applied to *Youngolepis*, the following characters are scored as: 38–0; 39–0; 40–0; 41–unknown. This corroborates the interpretation of corresponding conditions in *Mimia* as primitive.

38. Canal for pituitary vein: present 0; enlarged 1; obliterated 2. Pituitary vein canal enlargement and eventual obliteration is linked to progressive invasion by the insertion of the external rectus muscle (Schaeffer & Dalquest 1978). Differences between *Mimia* and *Moythomasia* (Gardiner 1984) probably illustrate stages in this transformation (Coates 1998). In *Mimia*, the dorsal surface of the basisphenoid bears a bolster posteromedial to the pituitary vein canal, whereas *Moythomasia*, in common with more derived actinopterygians, lacks this bolster and the canal space is enlarged.

Gardiner & Schaeffer (1989) argue that *Polyodon* retains traces of a secondarily reduced posterior myodome as an orbital depression housing all four rectus muscle insertions. This interpretation is regarded as unlikely, because (i) the muscle insertion pattern would be unique among non-teleosts (patterns of rectus muscle insertion are summarized in Patterson (1975)); and (ii) it requires secondary loss of characters 38–41. Reinterpretation of this orbital pit as a feature arising late in ontogeny is considered more parsimonious.

The condition in *Mesopoma* is coded as 2 (canal obliterated), from the appearance of a large, infilled space immediately behind the pituitary–hypophyseal pillar. In *Woodichthys* (Coates 1998) the condition is coded as uncertain, although the position of the ventral fissure suggests that it was at least similar to that of *Moythomasia* (canal enlarged). Obliteration of the canal in *Cosmoptychius* is apparent from Schaeffer's (1971) redescription of the neurocranium, including the dorsal surface of the basisphenoid.

39. Roof of posterior myodome perforated by ventrally directed canal for palatine branch of facial nerve (VII): absent 0; present 1. Presence of this canal provides a way of characterizing the presence of a distinct anterodorsal boundary or roof to the posterior myodome. Like character 38, this is present in *Moythomasia* but absent in *Mimia*. Absence of this feature in *Kentuckia* is consistent with Rayner's (1951) description of the myodome as 'so open dorsally as to scarcely be said to have a roof'.
40. Anterior boundary to posterior myodome marked by ridge from basisphenoid pillar to basipterygoid process: absent 0; present 1.
41. Abducens (VI) foramen in dorsal position, level with dorsoventral midpoint of optic foramen (II): absent 0; present 1. The ventral position of the abducens foramen in *Mimia* contrasts strongly with genera such as *Moythomasia* and *Pteronisculus* in which it is elevated to a significantly more dorsal position. The condition in *Acipenser* (Marinelli & Strenger 1973) is scored as uncertain because of the derived anteroventral displacement of the eye and optic nerve foramen.

(vii) *Anterior myodome*

42. Anterodorsal myodome: paired 0; single 1; absent 2.

43. Distinct dorsal and ventral anterior myodomes, i.e. superior and inferior oblique muscles with separate insertions 0; with shared–convergent insertion 1.

In *Polypterus* the superior oblique muscle originates above the inferior oblique, and penetrates the canal for the profundus and superficial ophthalmic nerves (Schaeffer 1971; Patterson 1975). Patterson (1975) describes living chondrosteans as lacking anterior myodomes, but Findeis (1998) describes separate anterior dorsal and ventral myodomes in the postnasal wall of *Acipenser*. The condition of *Osorioichthys* (Taverne 1997), *Mimia*, *Moythomasia* (Gardiner 1984) and probably *Coccocephalus* (Poplin & Véran 1996, text–fig. 6; M. I. Coates, personal observation) matches those of the Chondrostei, with separate dorsal and ventral myodomes. Like the posterior myodome, outgroup comparison with *Youngolepis* (Chang 1982) supports the interpretation of these conditions as primitive. Although undescribed in *Youngolepis*, the postnasal wall includes dorsal and ventral depressions, of which the dorsal is associated with a large profundus foramen (Chang 1982, fig. 12). More advanced taxa exhibit patterns of increasingly convergent oblique muscle insertions. *Kansasiella* (Poplin 1974), *Lawrenciella* (Poplin 1984), *Boreosomus* (Nielsen 1942) and *Mesopoma* have laterally confluent, but dorsoventrally separate, anterior myodomes which may be synapomorphic for a discrete cluster of 'palaeoniscid' genera. Dorsoventrally shared oblique muscle insertions characterize more advanced stem-neopterygians. In *Lepisosteus*, anterior myodomes are absent but, as in *Amia*, both oblique muscles converge and pass through the orbitonasal canal and originate on the nasal septum (Schaeffer 1971; Jarvik 1980). *Australosomus* has a single large anterior myodome (Nielsen 1949); in *Watsonulus* (Olsen 1984), the anterior myodome resembles the condition in *Amia*. In pholidophorids, leptolepids and extant teleosts, a median canal houses olfactory nerves and both pairs of oblique eye muscles, with the insertion extending into the nasal septum (Patterson 1975). Gardiner *et al.* (1996) include an alternative coding of anterior myodome conditions.

(viii) *Brain morphology*

Outgroup comparison for the following characters is provided by chondrichthyans (e.g. *Squalus*, Stensiö 1963) and living and fossil sarcopterygians (*Latimeria*, Nieuwenhuys 1969; *Lepidosiren*, Thors & Nieuwenhuys 1979; *Eusthenopteron*, Jarvik 1980; *Youngolepis*, Chang 1982). Because gross brain morphology is unknown in any stem-lineage teleost, relevant states for characters 44–52 are scored from conditions in *Salmo* (after Nieuwenhuys 1982). Further detailed comparisons are provided in the descriptive section, and conditions in extant actinopterygian genera with references are summarized in figure 7.

44. Brain morphology linear and elongate with diencephalon exposed clearly in dorsal view; divergent nervous connections between olfactory bulb and nasal sac 0; compact, with anteriorly directed, parallel olfactory nerves 1. Compaction of the gross brain morphology refers to the combined effects of tectal and telencephalic reorganization which, in dorsal view, completely obscure the diencephalon in neopterygians. *Amia* appears to represent a partial reversal of this character: scored as 0. The identity of parallel olfactory tracts or nerves is unclear in the poor quality endocast of *Saurichthys hamiltoni* (Stensiö 1925), but the region interpreted as the diencephalon was probably overlapped by the optic tectum: scored as 1.
45. Olfactory bulb extends beyond anterior level of orbit 0; orbit extends anteriorly relative to olfactory bulb 1. For many genera in which the anterior extent of the endocranial cavity is reasonably clear, e.g. *Mimia* or *Moythomasia* (Gardiner 1984), this character can be scored without reference to a detailed endocranial cast. However, for primitive forms with small orbits (e.g. *Cheirolepis*, Pearson & Westoll 1979; Arratia & Cloutier 1996; *Howqualepis*, Long 1988) relative to those of more derived actinopterygians, this character is scored as uncertain.
46. Optic tectum of equal or smaller size than telencephalon 0; optic tectum larger than telencephalon 1.
47. Olfactory bulb shorter than telencephalon 0; of similar size 1. Unclear in *Kentuckia* endocast (Moodie 1915) and *Saurichthys* (Stensiö 1925); both scored as uncertain.
48. Optic tectum divided into bilateral halves: absent 0; present 1. Unclear in *Kentuckia* endocast (Moodie 1915); scored as uncertain. Faint suggestion of posterior division in *Boreosomus* (Nielsen 1942); indiscernible in *Australosomus* (Nielsen 1949): both scored as uncertain. Optic tectal halves are apparently well removed from one another in *Saurichthys* (Stensiö 1925): scored as 1.
49. Hypophyseal body, or cast of enclosing chamber, projects posteroventrally 0; projects ventrally or anteroventrally 1. While this character is intended to describe reorganization of the brain and surrounding tissues, it also distinguishes between superficial and deep patterns of suspensorial angle change relative to the neurocranium. *Polypterus* illustrates the superficial pattern, in which the suspensorium is directed anteriorly (Bjerring 1991), but the hypophyseal body remains strongly directed posteriorly (Senn 1976; Nieuwenhuys 1982).
50. Cerebellar corpus divided into bilateral halves 0; undivided 1. *Boreosomus* bears only faint evidence of this division (Nielsen 1942), and the cerebellum is unidentifiable in *Australosomus* (Nielsen 1949) and *Saurichthys* (Stensiö 1925); each is scored as uncertain.
51. Cerebellar corpus enters fourth ventricle 0; arches above 1. Unless endocasts show evidence of a significant prominence above the rhombencephalon, the corpus is assumed to have primitively entered the fourth ventricle.
52. Cerebellar corpus with median anteriorly directed portion; absent 0; present 1.

(ix) *Girdles and fins*

53. Clavicle lost or reduced to small plate or ossicles lateral to cleithrum: absent 0; present 1 (P & R).
54. Pectoral girdle with middle region and anterior process: absent, 0; present 1 (BG; G & S; P; T).
55. Number of fin rays equals number of dorsal and anal fin supports: absent 0; present 1 (P & R; BG; G & S).
56. Median neural spines in caudal region: absent 0; present 1 (P & R; G & S). Although mostly absent in

primitive actinopterygians, membrane bone median caudal neural spines are reported as present in *Polypterus* (B. Gardiner, personal communication).

57. Upper caudal fin rays elongate: absent 0; present 1 (BG; G & S; P). The caudal fin of *Polypterus* has been shown as intrinsically heterocercal (Bartsch & Gemballa 1992). The elongate upper caudal fin rays originate, ontogenetically, from the ventral side of the caudal axis, and *Polypterus* is therefore scored as 0. However, the extent to which similar ontogenetic transformations result in the presence of elongate upper caudal fin rays in other actinopterygians is unclear. *Saurichthys* is scored as 1 (Rieppel 1985), *contra* Gardiner & Schaeffer (1989, table 2, although this conflicts with their character discussion: p. 157).
58. Lobed base to pectoral fins: present 0; absent 1 (T). Lobed pectoral fins are present in the pre-jawed, osteostracan sister group of gnathostomes (Janvier 1996; Coates 1994). In crown-group gnathostomes, broad, distally well-developed muscular pectoral fins are present in primitive chondrichthyans, and lobed paired fins are characteristic of sarcopterygians (fin structures reviewed in Coates (1994)). The condition in acanthodians is problematic because most pectoral fin bases are proximodistally short and non-lobate, although an apparently lobate pectoral fin is described in the lower Devonian *Kathemacanthus* (Gagnier & Wilson 1996). In actinopterygians, *Cheirolepis* (Pearson & Westoll 1979; Arratia & Cloutier 1996) and *Osorioichthys* (Taverne 1997) have primitively lobed pectorals, and, in the context of present and recent analyses, those of *Polypterus* and *Erpetoichthys* are also considered primitive. Apparent reversals from derived, non-lobate actinopterygian pectorals to a lobed condition occur in *Tarrasius* (Moy-Thomas & Bradley Dyne 1938), *Paratarrasius* (Lund & Melton 1982) and *Cornuboniscus* (White 1939).
59. Anteriormost pectoral fin rays embrace propterygium: absent, 0; present 1 (BG; G & S; P; T).
60. Pectoral fin-ray segmentation: anteriormost pectoral lepidotrichia segmented proximally 0; segmented only distally 1. Patterns of dermal fin-ray segmentation and bifurcation are developmentally regulated (Geraudie *et al.* 1994, 1995) and specific to various levels of actinopterygian phylogeny (*contra* Gardiner & Schaeffer 1989). *Cheirolepis* (Pearson & Westoll 1979) and *Polypterus* both exhibit closely packed pectoral rays which segment at closely spaced intervals throughout their length. Similar patterns in acanthodians and most sarcopterygians (rhizodonts represent a derived exception: Andrews 1985) indicate that this is primitive for osteichthyans. In the vast majority of primitive actinopterygians, this condition is replaced by pectoral fins with anteriormost rays segmented only distally (e.g. *Osorioichthys*, Taverne 1997; *Mimia*, *Moythomasia*, Gardiner 1984; *Mesopoma*). In the present analysis this transformation occurs at the same node as the acquisition of a perforated propterygium (character 61). Taxa exhibiting independent reversals to proximally segmented rays across the entire pectoral fin include *Elonichthys robisoni* (Traquair 1901), *Boreosomus* (Nielsen 1942) and *Birgeria* (Jessen 1972).
61. Fringing fulcra absent 0; fringing fulcra formed by terminal lepidotrichial segments expanded in leading edge of fin 1; fringing fulcra formed by terminal expansion and multiple branching of distal lepidotrichial segments 2 (BG; G & S; P; T). Absent in sarcopterygians, *Polypterus* and *Acipenser*, but present (state 2) in *Lepisosteus* and primitive teleosts (Patterson 1982). Conditions in primitive actinopterygians have been disputed, so that *Cheirolepis trailli* (Pearson & Westoll 1979) is described as lacking fringing fulcra, whereas they are reported as present in *C. canadensis* (Arratia & Cloutier 1996). In fact, both species are described as having enlarged terminal segments of the anterior pectoral fin rays in the leading edge of the fin. This condition seems indistinguishable from that in *Howqualepis*, which is described as having 'no true fringing fulcra' (Long 1988, p. 30). Personal observation of various sarcopterygian fins (fossil and recent) has failed to find any similar lepidotrichial expansion, which is therefore considered to be apomorphic for primitive actinopterygians (state 1). This condition is absent in extant cladistians and chondrosteans. 'True' fringing fulcra appear to result from multiple branching combined with terminal specialization of the lepidotrichial segments (state 2), although few fossil species are sufficiently well preserved to reveal whether these structures are paired, as in *Lepisosteus* (Patterson 1982). In the present analysis *Cheirolepis* and *Howqualepis* are therefore scored as 1, while *Osorioichthys* is scored as 2 (Taverne 1997, fig. 12). Presence of fringing fulcra in *Kentuckia* is scored from the tail in *K. hlavini* (Dunkle 1964).
62. Propterygial canal: absent 0; present 1 (BG; G & S; P; T).
63. Pectoral metapterygium: short, articulating with pair of radials distally 0; elongate, articulating with two or more radials on anterior and distal surface 1; absent 2; resembles two radials joined proximally 3. The metapterygium is usually considered to be an endoskeletal axial structure within the posterior part of the fin or limb bud which, as defined by Shubin & Alberch (1986), segments and bifurcates distally during ontogeny to produce (mostly) preaxial secondary radials. In sarcopterygians and xenacanth chondrichthyans, the paired fin patterns are exclusively metapterygial, while in other gnathostomes two or more radials articulate directly with the girdles. Primitively, all gnathostome pectoral appendages include a metapterygium, but pelvic metapterygia occur much less frequently, and pelvic fins are generally smaller and morphologically simpler (reviewed in Coates 1994; Shubin 1995).

Rosen *et al.* (1981) and Gardiner (1984) considered pectoral–pelvic structural differences to be unique to actinopterygians (see character 64), and suggested that the pelvic metapterygium formed the pelvic girdle within the body wall to explain its absence (after Davidoff 1880). However, metapterygial absence in actinopterygian (and other) pelvic fins is interpreted more simply as the result of temporally reduced and delayed outgrowth relative to pectoral fin development (Sordino *et al.* 1995; Coates 1995). Furthermore, close structural similarity between pectoral and pelvic appendages is interpreted most parsimoniously as apomorphic for sarcopterygians.

Pearson & Westoll (1979) describe *Cheirolepis* as lacking a pectoral metapterygium, but Gardiner (1984) claims that one is present, and it is scored as such (state 0) in the present analysis. Gardiner's interpretation is consistent with the presence of a short pectoral metapterygium in acanthodians (Coates 1994) and *Howqualepis* (M. I. Coates, personal observation NMVP160808; latex peel of specimen shown in Long (1988, fig. 29C)). *Polypterus* and *Erpetoichthys* appear to lack a metapterygial homologue, although Shubin (1995) and others describe the posteriormost (cladistian) pectoral radial as such. Similarly, Gardiner (1984) argues that pectoral fin development in *Polypterus* is fundamentally metapterygial, even though Budgett's (1902) description includes no explicitly metapterygial axis-like features (*sensu* Shubin & Alberch 1986). Instead, a flat prechondrogenic cellular plate is first perforated and then split distally to form an array of distal radials in an anterior to posterior sequence (further information from figures 2 and 5 in Bartsch & Gemballa (1992)). This mode of skeletal pattern development is completely absent from Shubin & Alberch's (1986) review.

This 'perforated plate' is not unique to *Polypterus*: the chondrichthyan *Pristiurus* (Rauther 1940) has a similar pattern of pectoral fin development, and neopterygian examples include *Danio* (Sordino *et al*. 1995), *Amia*, *Anguilla*, *Clupea*, *Gobius* (Kälin 1938) and *Dorosoma* (Arratia 1997). These data suggest that the general properties of appendicular skeletal pattern development which Shubin & Alberch (1986) identified, characterize only tetrapod and perhaps sarcopterygian paired appendages. Shubin & Alberch's definition of the metapterygial axis is insufficient to describe the metapterygia of non-sarcopterygians.

For the purposes of the current study, metapterygial presence is scored solely according to the adult pattern of posteriormost radials, with no implied assumptions about pattern morphogenesis. State 1, which seems to represent enhanced outgrowth of the posterior part of the fin endoskeleton, is widespread among primitive actinopterygians, including *Mimia*, *Moythomasia* (Gardiner 1984), extant chondrosteans and *Amia* (Jarvik 1980). In the present analysis, *Pteronisculus* is scored as '1' after Jessen (1972, plate 22, fig. 2), rather than Nielsen's (1942) description. In Cladistia, *Birgeria* (after Jessen 1972) and teleosts the metapterygium is coded as absent (state 2). Metapterygial presence is not equated with appendicular skeletal anteroposterior asymmetry, which is probably characteristic of all vertebrate paired appendages. *Lepisosteus* is the only genus in the present analysis in which the two posteriormost radials are fused proximally (state 3), but a similar condition is also apparent in *Pachycormus macropterus* (Jessen 1972).

64. Pelvic fin with short base: absent 0; present 1 (L; T). Long-based pelvic fins are present in certain acanthodians, *Cheirolepis* (Pearson & Westoll 1979; Arratia & Cloutier 1996) and *Howqualepis* (Long 1988). This characterization of pelvic fin structure is considered more informative than Gardiner & Schaeffer's (1989), which defines a 'differently constructed' pelvic relative to pectoral fin as apomorphic for actinopterygians. Such 'different' construction is also found in chondrichthyans, placoderms and acanthodians. This character is therefore considered primitive for gnathostomes; structural differences are most conspicuously absent (or reduced) in sarcopterygians (Coates 1994, 1995).

(b) *Results of phylogenetic analysis*

Analysis of these data (using PAUP 3.0; Swofford 1990) initially uses the complete data matrix with characters coded as in Appendix B, then with characters describing brain morphology deleted to test their influence on the branching sequence. Both data matrices were also analysed with extant genera excluded. Unlike previous analyses of primitive actinopterygian interrelationships (Patterson 1982; Gardiner 1984; Long 1988; Gardiner & Schaeffer 1989) *Cheirolepis* was not used as a monophyletic outgroup. Character coding for *Cheirolepis* includes a significant number of missing data: out of 64 characters, 28 are coded as uncertain (and a further two are derived). Moreover, use of *Cheirolepis* as an outgroup prevents direct testing of the phylogenetic position of this genus relative to other potential members of the actinopterygian stem-group, such as *Osorioichthys* and *Howqualepis*. Instead, the outgroup consists of primitive states as discussed in the character list, and is therefore a conjectural series of ancestral conditions. Where possible, these are drawn from primitive sarcopterygians, with supplementary primitive states inferred from acanthodians and chondrichthyans. The delayed transformation option for character optimization was used throughout. Most characters are coded as binary, with only 13 out of 64 coded as multistate. Of these multistate characters, two are treated as ordered: 35 (parasphenoid ascending process) and 38 (expansion of the pituitary vein canal).

Analysis of the complete data matrix produced 54 trees of 170 steps, with a consistency index of 0.50. A strict consensus of these trees (result not shown) includes a large polytomy situated between resolved branching sequences, from *Cheirolepis* to *Osorioichthys*, and from *Australosomus* to Teleostei (these resolved branching patterns are maintained in figure 9*a*). Successive weighting, using rescaled consistency index and best fit options, produced three trees with a consistency index of 0.71, showing alternative branching patterns between *Boreosomus*, *Kansasiella* and *Mesopoma* (figure 9*a*). In comparison with Gardiner & Schaeffer's (1989) result (figure 8), the major differences are threefold. First, *Acipenser* inserts at a lower node, corresponding approximately to the lower alternative which Gardiner & Schaeffer rejected. Second, *Saurichthys* is related more closely to extant neopterygians than *Birgeria*, instead of vice versa. Third, a monophyletic group of 'palaeoniscid' genera branches from the base of the neopterygian stem-lineage. It is probably significant that the content of this clade does not correspond in any simple way with Gardiner & Schaeffer's (1989, fig. 12) polytomy of primitive actinopterans.

Removal of extant taxa results in a set of three trees of 111 steps with a consistency index of 0.63. Once again, these show alternative branching patterns between *Boreosomus*, *Kansasiella* and *Mesopoma* (consensus tree: figure 9*b*). This 59-step reduction in tree-length highlights the

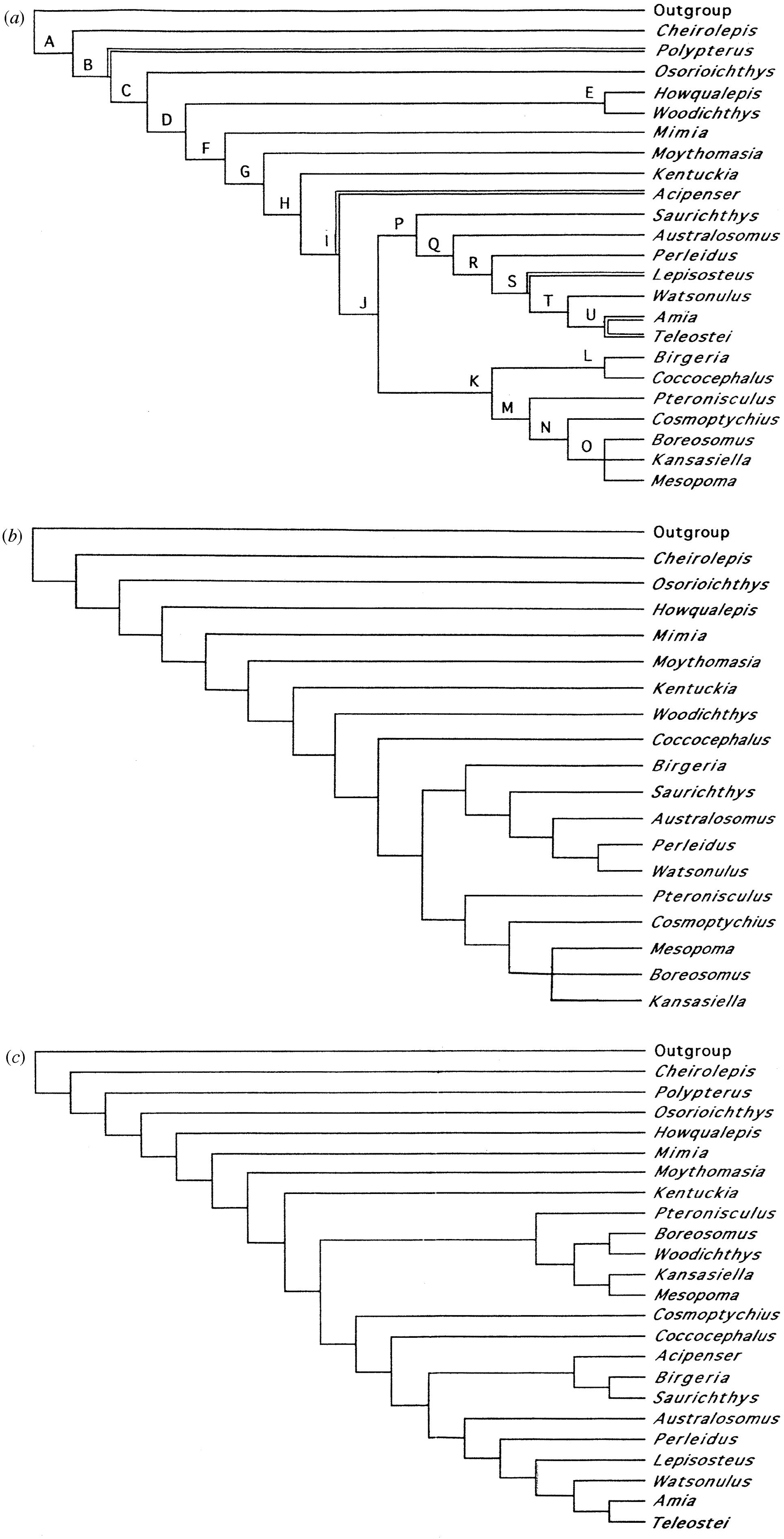

Figure 9. Cladograms resulting from PAUP analyses of the data matrix: (*a*) complete data matrix, with 23 taxa and 64 characters: tree length 170 steps, CI = 0.71 (after reweighting); (*b*) data matrix minus extant taxa (18 genera, 64 characters): tree length 111 steps, CI = 0.86 (after reweighting); (*c*) data matrix minus brain morphology related characters (23 taxa, 55 characters): tree length 151 steps, CI = 0.72 (after reweighting).

considerable demand for character reversals forced by the inclusion of extant genera. Changes to tree topology include the removal of *Coccocephalus* and *Birgeria* from the 'palaeoniscid' clade, and the relocation of *Woodichthys* to a more derived position, indicating that branching patterns in the middle section of the tree are not robust. Reweighting these data, using the same options as before, results in a single tree (not shown) with a consistency index of 0.86. This includes further changes to the branching sequence (Wilkinson & Benton (1996) discuss the effects of successive weighting techniques on tree topologies), in which *Woodichthys* appears as the sister group of *Boreosomus* within the 'palaeoniscid' clade, and *Cosmoptychius* and *Coccocephalus* are successive sister groups of all more derived stem-lineage neopterygians.

Deleting endocast–brain morphology related characters (44–52) removes numerous 'uncertain' scores from the matrix, and improves the relative completeness of the data set. This also makes the data matrix more directly comparable to Gardiner & Schaeffer's (1989). An initial run of this 55-character data set produces 22 trees of 151 steps, with a consistency index of 0.5. Successive weighting reduces the set to a single tree (figure 9*c*), and improves the consistency index to 0.72. The effect of removing these characters is a topology similar to Gardiner & Schaeffer's (1989). *Acipenser* is in a derived position, as sister group to *Saurichthys* (plus *Birgeria*), and this clade is the sister group of *Australosomus* plus more advanced neopterygians. This result shows that the major effect of characters 44–52 on tree topology concerns the phylogenetic insertion of *Acipenser*. Removal of extant taxa from the data set (now reduced to 55 characters and 18 genera) corroborates this interpretation, because the three resultant tree topologies (103 steps; consistency index 0.61) resemble that produced by the complete 64 character set.

(c) *Phylogenetic conclusions*

These results challenge Gardiner & Schaeffer's (1989) hypothesis that the divergence of chondrostean and neopterygian lineages occurred at a node which is more derived than that of groups including *Pteronisculus*, *Boreosomus* or *Mesopoma* (figure 8). Instead, this event appears to have occurred earlier in actinopterygian phylogeny (figure 9*a*), although at a node which is more derived than the nearest equivalent in Gardiner's (1984, fig. 146) previous analysis. In this, *Kentuckia* lies within the actinopteran (Chondrostei plus Neopterygii) crown group, while in the present analysis *Kentuckia* is the most derived plesion of the actinopteran stem-lineage. Of the genera included in figure 9*a*, the presence of *Mesopoma* within the 'palaeoniscid' clade places a minimum date for the chondrostean–neopterygian split within the Lower Carboniferous (*ca*. 339 Myr ago; Harland *et al*. 1989). Chronologically, this is identical to the implications of Gardiner & Schaeffer's result, which has the Chondrostei branching from below their '*Palaeoniscum* group'. Both *Mesopoma* and '*Elonichthys*' *serratus* (the earliest member of the '*Palaeoniscum* group'; Gardiner 1993) are known from the Viséan of Glencartholm (Moy-Thomas & Bradley Dyne 1938). The phylogenetic location of the cladistian–actinopteran divergence, however, is unchanged relative to Gardiner & Schaeffer's and other recent analyses. However, *Howqualepis* is transposed to a more primitive node, as in Long's (1988, fig. 50*b*) alternative hypothesis of Devonian actinopterygian interrelationships. This location, and the entire branching sequence from *Cheirolepis* to *Moythomasia* in figure 9*a*, is identical to that in Taverne's (1997) analysis of the relationships of *Osorioichthys*. A minimum date for the cladistian–actinopteran split may therefore be around 377 Myr ago (Harland *et al*. 1989), as indicated by the Givetian age of the Mount Howitt fauna (source of *Howqualepis*) (Young 1996; note that this includes an alternative date for the Givetian–Frasnian boundary of 367 ± 2 Myr ago).

Character distributions are similarly revised (a list of nodal unambiguous character transformations appears in Appendix A) and present new combinations of apomorphies defining the major monophyletic actinopterygian subdivisions. Accordingly, the actinopteran stem-lineage (figure 9*a*, node C) emerges in the present analysis with the following character set (characters occurring at the equivalent node in Gardiner & Schaeffer's (1989), cladogram are marked with an asterisk): (59) anteriormost pectoral fin rays embrace the propterygium*; (60) pectoral fin rays segmenting only distally; (61) fringing fulcra formed by terminal lepidotrichial expansion and multiple branching*; (62) propterygial canal present*. In comparison with Gardiner & Schaeffer's (1989, fig. 12, table 1) results, nodes D and F in figure 9*a* also specify characters uniting a '*Mimia* group' with more advanced actinopterans. In the present analysis, node D includes the following characters: (11) lateral gulars with posterior and lateral angles, resembling enlarged branchiostegals; (58) non-lobate pectoral fin; and node F includes (2) resolvable enamel crystallites mostly perpendicular to scale surface; (32) lateral cranial canal present*; (45) orbit extends anteriorly relative to olfactory bulb; (54) pectoral girdle with middle region and anterior process*; (63) pectoral metapterygium elongate, articulating with two-plus radials along the anterior surface.

The most striking feature of this assemblage is that 6 out of 11 characters concern paired fin morphology, affecting both endoskeletal and dermal skeletal systems. Thus the origin of a canalized propterygium precedes pectoral fin lobe reduction, and this precedes the origin of the metapterygial morphology which persists in extant chondrosteans. In constrast to this transformation sequence, the dermal character transformations coincide, so that anteriormost dermal fin rays are segmentally repatterned, clasp the propterygium and acquire fringing fulcra, all at node C (figure 9*a*). Whether these associations represent an actual, singular, episode in fin evolution or an artificial coalescence which may be teased apart with the introduction of new data (as is apparent with endoskeletal fin characters) remains to be tested. More complete specimens of *Cheirolepis* and *Dialipina* would be particularly informative about early patterns of actinopterygian fin evolution, while investigations of fin ontogeny in cladistians and chondrosteans comparable to those already completed on *Danio rerio* (Smith *et al*. 1994; Sordino *et al*. 1995; Geraudie *et al*. 1994) would illuminate the likely developmental underpinning of such anatomical transformations.

Although Gardiner & Schaeffer (1989) were particularly concerned with the origin of the Chondrostei, relatively little attention has been paid to the corresponding base of the total-group Neopterygii. Gardiner *et al*. (1996) provide the most recent review of 'basal neopterygians', but their use of 'basal' refers exclusively to taxa branching close to the divergence of *Lepisosteus*, *Amia* and teleosts. *Pteronisculus* is referred to as a 'stem-neopterygian' but this description is undiscussed, despite the fact that it conflicts with Gardiner & Schaeffer's (1989) conclusions. Otherwise, Gardiner *et al*. (1996) do not address the extent of the neopterygian stem-lineage. In the present analysis, stem-neopterygians originate at node J (figure 9*a*), where they are defined by the following apomorphies: (13) antorbital separate from premaxilla; (38) canal for pituitary vein obliterated; (47) olfactory bulb of similar size to telencephalon; (48) optic tectum divided into bilateral halves; (49) hypophyseal space projects ventrally or anteroventrally.

Straightforward comparison of this character set with Gardiner & Schaeffer's (1989) result is complicated by the different points of neopterygian–chondrostean phylogenetic divergence. In Gardiner & Schaeffer's (1989, fig. 12) cladogram, the sole stem-neopterygian apomorphy is 'numerous irregular anamestic supraorbital bones between nasal and keystone-shaped dermosphenotic'. In the present analysis, the equivalent character (7) occurs with others uniting *Perleidus* with more derived neopterygians (node R, figure 9*a*). The location of this character is at a relatively more advanced node than in Gardiner & Schaeffer's cladogram, because *Saurichthys* is scored here as lacking supraorbitals. Alternatively, in Gardiner's (1984) analysis, the chondrostean–neopterygian divergence is defined by the presence of a (paired) posterior myodome. This equates approximately with character 38, state 1, which occurs here at node G (figure 9*a*), and therefore within the actinopteran rather than neopterygian stem-lineage.

Other significant differences between the results of the present analysis and those of Gardiner & Schaeffer (1989) and Gardiner *et al*. (1996) concern the presence of a monophyletic clade of 'palaeoniscids', and the positions of *Birgeria*, *Saurichthys* and *Watsonulus*. The 'palaeoniscid' clade appears in each of the trees shown in figure 9, with a core membership of *Pteronisculus*, *Boreosomus*, *Kansasiella* and *Mesopoma*. Like the membership, the synapomorphies uniting this group vary between trees, but all share a set consisting of: (23) a ceratohyal with a constricted shaft; (24) a sigmoidal ceratohyal groove for the afferent hyoidean artery; and (39) a canal for the palatine branch of the facial nerve piercing the roof of the posterior myodome. None of these characters make promising indicators of further membership of this clade; each is rarely preserved, and for *Kansasiella* characters 23 and 24 are scored from material associated with, rather than articulated with, the cranial remains of this genus. Other synapomorphies of the group, occurring in two out of the three trees in figure 9, are homoplastic, including: (8) presence of suborbitals, and (36) parasphenoid expanded posteriorly to cover the ventral otic fissure. For the present, this result provides insufficient basis to erect (or resurrect) a suprageneric taxon likely to include a large subset of the genera traditionally described as 'palaeoniscids'. Testing the possible monophyly of the collected memberships of all groups associated with these genera (as identified in Gardiner & Schaeffer (1989) and Coates (1993)) is beyond the scope of the current work.

In figure 9*a*, a single character, (8) presence of suborbitals, unites *Birgeria* with the 'palaeoniscid' clade; other synapomorphies at node K are either unknown or reversed. Otherwise, the position of *Birgeria* relative to the chondrostean lineage resembles that in Gardiner & Schaeffer's tree (1989, fig. 12). *Saurichthys* occupies position closer to crown-group neopterygians than *Birgeria* in figure 9*a* (reversing their relative positions in Gardiner & Schaeffer's tree), and is united with higher neopterygians on the basis of characters (12) few branchiostegal rays, and (57) upper caudal rays elongate. This solution follows Findeis (1998) who questions previous phylogenies, such as Gardiner & Schaeffer's, which have associated *Saurichthys* with chondrostean ancestry. Only in figure 9*c* is *Saurichthys* united with the chondrostean lineage, on the basis of characters (3) scale reduction, (36) posterior expansion of the parasphenoid, and (61) absence of fringing fulcra. This result, in the absence of characters 44–52, predictably resembles more closely the synapomorphy distribution in Gardiner & Schaeffer's analysis. In figure 9, *Watsonulus* appears in each tree as the sister group of *Amia* plus teleosts combined, whereas in Gardiner *et al*.'s (1996) recent analysis of neopterygians, *Watsonulus* emerges as a primitive halecomorph. The results presented here are not intended to challenge this conclusion. Gardiner *et al*.'s data achieve far better resolution of the branching sequences in question, while the character states in the current work corroborate the location of *Watsonulus* above node 2 in their figure 1.

(d) *Patterns of evolution in the gross features of actinopterygian brains*

Actinopterygian brain morphology has long been known to include several apomorphic features. These are reviewed in Nieuwenhuys (1982), and include the unique development of the telencephalon (Nieuwenhuys 1962), the presence of a cerebellar valvula (phylogenetic significance discussed in Patterson (1982)) and the torus longitudinalis. The telencephalon in actinopterygians has thickened lateral walls which diverge dorsally, and evert to form solid cerebral hemispheres. In cladistians the dorsal pallium is notably thin, but in other actinopterygians the dorsal pallium is larger than the subpallium (R. G. Northcutt, personal communication). This contrasts strongly with the more familiar pattern of hollow, expanded cerebral hemispheres, as found in tetrapods. Neuroanatomical (rather than gross morphological) changes associated with this specialization, and which follow the phylogenetic trajectory from cladistians to teleosts, include: (i) decreasing olfactory input to the telencephalon; (ii) increasing structural complexity; and (iii) increasing afferent and efferent connections with diencephalic and thalamic centres (Nieuwenhuys (1982) and included references). The apomorphic status of the actinopterygian-pattern telencephalon has been tested and corroborated in a recent review of gnathostome forebrain structure (Northcutt 1995).

The uniquely actinopterygian cerebellar valvula (Nieuwenhuys 1982; Patterson 1982) extends rostrally from the ventral surface of the infolded anteriomedial cerebellar wall and projects into the mesencephalic ventricle. As in telencephalic evolution, increased valvula development correlates positively with closer phylogenetic proximity to the teleosts. Correspondingly weak valvula development in *Polypterus* prompted Jarvik's (1980) conclusion that cladistian and teleostean valvulae are unrelated, but this appears unlikely in the context of other evidence supporting actinopterygian monophyly including cladistians. The third structural apomorphy, presence of the torus longitudinalis, is unique to the Actinopteri (*sensu* Patterson 1982) rather than the Actinopterygii. The torus longitudinalis is formed by the most medial part of each half of the optic tectum, and forms a functional link with the cerebellum. Tori logitudinales are absent in non-actinopterygian vertebrates and cladistians, but are present in teleosts, *Amia*, chondrosteans (Nieuwenhuys 1982) and *Lepisosteus* (Herrick 1891; Collin & Northcutt 1995).

Without a record of ventricular morphology, it is unlikely that any of these characters will be observed in the kind of fossil material included in the present work. The following list presents the minimum likely nodal distribution of coded changes in gross brain morphology (characters 44–52) across the tree in figure 9*a*. *Polypterus*, (48) optic tectum divided bilaterally; node F, (45) olfactory bulb terminates posterior to anterior level of orbit; node H, (44) brain morphology compact with anteriorly directed connections between olfactory bulbs and nasal sacs, (46) optic tectum larger than telencephalon; *Acipenser*, (44) brain morphology reverts to linear, elongate pattern with dorsally exposed diencephalon, (46) optic tectum of equal or smaller size than telencephalon; node J (stem-group Neopterygii), (47) olfactory bulb and telencephalon of similar size, (48) optic tectum divided into bilateral halves, (49) hypophyseal space directed ventrally or anteroventrally; *Mesopoma*, (49) hypophyseal space reverts to a posteroventral orientation; node S (crown-group Neopterygii), (50) cerebellar corpus undivided, (51) cerebellar corpus arches over fourth ventricle, (52) cerebellar corpus with a median anteriorly directed portion; *Lepisosteus*, (46) optic tectum of equal size to telencephalon; *Amia*, (44) diencephalon exposed dorsally, (45) olfactory bulb reverts to extending anteriorly relative to the orbit, (46) optic tectum of equal size to telencephalon.

There are problems with this transformation sequence, because if characters 44 and 46 originate at node H, this suggests that the elongate brain of *Polypterus*, which in this context appears to be primitive, was also present in genera such as *Mimia* and *Moythomasia*. However, the endocranial cavities of *Mimia* and *Moythomasia* (Gardiner 1984) show that this is unlikely, and that in these respects they probably resembled *Kentuckia*. Furthermore, the proportions of the dermal skull of *Cheirolepis*, in contrast to those of extant cladistians, suggest that state 1 for characters 44–46 could be the primitive actinopterygian condition. For this reason, the maximum likely nodal distribution (ACCTRAN option, PAUP 3.0; Swofford 1990) of coded changes in gross brain morphology (characters 44–52) across the tree in figure 9*a* appears significantly more consistent with available data. However, in the absence of adequate fossil morphologies, inferred states for characters 50–52 in *Saurichthys*, *Australosomus* and *Perleidus* must be considered as highly speculative.

Outgroup comparison suggests that the primitive condition of actinopterygian gross brain morphology (node A) includes the following characters: telencephalon everted to form cerebral hemispheres with thin dorsal pallium; weakly developed valvula; (44) elongate brain with diencephalon exposed dorsally and divergent connections between olfactory bulbs and nasal sac; (45) olfactory bulb abutting directly with the telencephalon, extends anteriorly beyond level of orbit; (46) telencephalon larger (more elongate) than optic tectum; (47) olfactory bulb much smaller than telencephalon; (48) optic tectum divided; (49) hypophyseal body directed posteroventrally; (50) cerebellar corpus divided medially, enters fourth ventricle (51), and lacks an anteriorly directed medial portion (52).

By the origin of the actinopteran stem-lineage (node C): (44) brain compact, with anteriorly directed connections between the olfactory bulbs and nasal sacs; (45) olfactory bulb no longer extends beyond anterior level of orbit; (46) optic tectum larger than telencephalon.

By the origin of the actinopteran crown-group (node I), torus longitudinalis present.

Acipenser, exemplifying the Chondrostei, exhibits the following apomorphic transformations: (44) brain morphology reverts to elongate pattern with dorsally exposed diencephalon and divergent olfactory bulbs; (46) optic tectum reverts to equal or smaller size than the telencephalon (but note that the telencephalon remains much shorter than the primitive condition exemplified in cladistians); (48) optic tectum is incompletely divided.

The origin of the neopterygian stem-lineage (node J) is characterized by the following: (47) olfactory bulb and telencephalon of similar size; (49) hypophyseal space directed ventrally or anteroventrally. *Mesopoma* exhibits a reversal of character (49).

The neopterygian stem-lineage above the 'palaeoniscid' clade (node P) is characterized by the following: (50) cerebellar corpus undivided, arches over fourth ventricle (51), and produces a median, anteriorly directed portion (52). Reversals in *Lepisosteus* and *Amia* are as listed previously.

As might be expected, out of the characters describing brain morphologies, those that identify proportional rather than structural changes have the lowest consistency indices. This is reflected in the emergence of *Acipenser* and *Amia* as each being characterized independently by a series of secondary reversals in gross brain proportions. In both taxa, reduced eye size is probably linked to reduced size of the optic tectum. Nieuwenhuys (1982), Collin & Northcutt (1995) and others identify the tectum as the main terminus for retinal fibres, with a significant positive correlation between tectal size and relative contribution of the visual system to total sensory input. Large orbits in primitive actinopterans and neopterygians are therefore consistent with the presence of large optic tecta in fossil endocranial casts. Moreover, Huber *et al.* (1997), in a study of African cichlids, found a close relation between the relative sizes of brain structures and variables related to habitat and prey use, so that species using motile prey were characterized by a well developed optic tectum and large cerebellum.

Early patterns of cranial transformation in the Chondrostei are unknown, because this analysis, like others, fails to identify primitive (i.e. pre-*Chondrosteus*, cf. Gardiner & Schaeffer 1989) members of the stem-lineage.

However, hypotheses of halecomorph phylogeny (preceding *Amia*) include greater detail, and primitive members of the stem-lineage, like other primitive neopterygians, possess a large orbit and short ethmoid region. *Watsonulus* (following Gardiner *et al.*'s (1996) phylogeny) exemplifies this condition, in which the dorsal orbital rim projects above the level of the skull roof midline and the snout is anteroposteriorly short and acute in dorsal and lateral aspects (Olsen 1984). Both of these features contrast strongly with the small orbit and broad, spade-shaped snout of *Amia*. Recognition that these cranial proportions in *Amia* are derived, depends on inclusion of fossil data in comparative analyses and makes phylogenetic sense of the curiously proportioned brain (figure 7*g*,*h*) in which the small tectum and large olfactory lobes are associated with a structurally advanced cerebellum. Functionally, these changes imply a shift in halecomorphs from (primitive) reliance on visual systems to (derived) emphasis on olfaction and acousticolateralis systems. Moreover, if acanthodians (characterized by large orbits and short ethmoid regions) constitute the immediate sister group of osteichthyans (cf. Maisey 1986), it is possible that similar reversals characterize each of the living non-teleostean actinopterygian clades, with the possible exception of gars (Ginglymodi).

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APPENDIX A

(a) *List of abbreviations used in figures*

acv, foramen of anterior cerebral vein
adm, anterodorsal myodome
amp.asc, ampulla of anterior semicircular canal
an, angular
ano, anterior nostril
asc, anterior semicircular canal
au, cerebellar auricle
avm, anteroventral myodome
br, branchiostegal rays
bsphn, basisphenoid
c.olfn, canal for olfactory nerve
cc, crus commune
chy, ceratohyal
cic, canal for internal carotid artery
co, cerebellar corpus
cr, crest between lateral walls optic tectum and telencephalon
de, dentary
dpt, dermopterotic
dsphn, dermosphenotic
eth.sph, ethmosphenoid
fr, frontal
hsc, horizontal semicircular canal
hyo, hyomandibula
hyp, hypophyseal cavity
ldv, longitudinal dorsal vein
lex, lateral extrascapular
mx, maxilla
na, nasal
olf.b, olfactory bulb
op, operculum
o.tec, optic tectum
pa, parietal
par, prearticular
pm, infilled posterior myodome
pmx, premaxilla
pop, preoperculum
psc, posterior semicircular canal
pt, posttemporal
ptg, pterygoid
q, quadrate
qj, quadratojugal
r/ch, retina/choroid stain
ro, rostral
s.opth.V, canal for twig of superficial ophthalmic nerve V
s.vac, saccus vasculosus
scl, sclerotic cup
sop, suboperculum
sto, statolith
tel, telencephalon
II, foramen of optic nerve II
III, foramen of oculomotor
IV, foramen of trochlear nerve IV
1, olfactory bulb
2, telencephalon
3, optic tectum
4, pituitary body
5, cerebellar auricle
6, cerebellar corpus
7, fourth ventricle

(b) *List of nodal character states for figure 9a*

Node A. 18(0–1). *Cheirolepis*. 61(0–1). Node B. 1(0–1); 2(0–1); 3(0–1); 35(0–1); 64:(0–1). *Polypterus*. 4:(0–2); 5(0–3); 6(0–1); 12(0–1); 18(1–0); 29(0–2); 36(0–2); 48(0–1); 56(0–1); 63(0–2). Node C. 59(0–1); 60(0–1); 61(0–1); 62(0–1). *Osorioichthys*. 8(0–1). Node D. 11(0–1); 58(0–1). Node E. 5(0–1). *Howqualepis*. 61(2–1); 64(1–0). *Woodichthys*. 12(0–1); 30(0–1); 36(0–1); 37(0–1). Node F. 2(0–2); 32(0–1); 45(0–1); 54(0–1); 63(0–1). *Mimia*. 18(1–0); 24(0–1); 35(1–0). Node G. 4(0–1); 28(0–1); 38(0–1); 41(0–1). *Moythomasia*. 24(0–1); 39(0–1). Node H. 5:(0–1); 6(0–1); 9(0–1); 29(0–1); 31(0–1); 44(0–1); 46(0–1). *Kentuckia*. 37(0–1); 40(0–1). Node I. 5(1–2); 12(0–1); 30(0–2); 36(0–1). *Acipenser*. 2(2–4); 3(1–0); 11(1–2); 18(1–0); 29(1–2); 32(1–0); 35(1–2); 38(1–0); 44(1–0); 46(1–0); 61(2–0). Node J. 13(0–1); 38(1–2); 47(0–1); 48(0–1); 49(0–1). Node K. 6(1–0); 8(0–1); 39(0–1); 40(0–1). Node L. 7(0–1). *Birgeria*. 3(1–0); 6(0–1); 56(0–1); 60(1–0); 63(1–2). *Coccocephalus*. 29(1–0); 30(2–1). Node M. 23(0–1); 24(0–2); 35(1–2); 37(0–1). *Pteronisculus*. 4(2–1);

5(2–1). Node N. 13(1–0); 42(0–1). *Cosmoptychius*. 36(1–0). Node O. 12(0–1); 29(1–0). *Boreosomus*. 4(2–1); 5(2–1); 6(0–1); 11(1–4); 30(2–1); 60(1–0). *Kansasiella*.—.*Mesopoma*. 49(1–0). Node P. 12(0–1); 57(0–1). *Saurichthys*. 3(1–0); 61(2–0). Node Q. 22(0–1); 25(0–1); 34(0–1); 42(0–2); 43(0–1); 56(0–1). *Australosomus*. 24(0–1); 30(2–0); 35(1–2); 36(1–0). Node R. 7(0–1); 14(0–1); 33(0–1); 37(0–1); 55(0–1). *Perleidus*. 8(0–1); 35(1–2). Node S. 15(0–1); 19(0–1); 21(0–1); 26(0–1); 27(0–1); 29(1–3); 30(2–3); 50(0–1); 51(0–1); 52(0–1). *Lepisosteus*. 2(2–3); 8(0–1); 11(1–2); 38(2–0); 41(1–0); 46(1–0); 53(0–1); 63(1–3). Node T. 10(0–1); 16(0–1); 17(0–1); 33(0–1); 39(0–1); 40(0–1). *Watsonulus*. 12(1–0); 24(0–1); 29(3–1). Node U. 11(1–3); 20(0–1); 37(1–0); 53(0–1). *Amia*. 2(2–4); 3(1–0); 7(1–0); 35(1–2); 40(1–0); 44(1–0); 45(1–0); 46(1–0); 61(2–0). Teleostei. 8(0–1); 25(1–0); 63(1–2).

APPENDIX B

Character matrix

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acipenser	?	4	0	2	2	1	0	0	1	0	2	1	?	0	?	0	0	0	0	0	0	0
Amia	1	4	0	2	2	1	0	0	1	1	3	1	1	1	1	1	1	1	1	1	1	1
Australosomus	?	?	1	2	2	1	0	0	?	0	1	1	?	0	0	0	0	1	0	0	0	1
Birgeria	1	?	0	2	2	1	1	1	1	0	1	0	1	0	0	0	0	1	0	0	0	0
Boreosomus	?	?	1	1	1	1	0	1	1	0	4	1	0	0	0	0	0	1	0	0	0	0
Cheirolepis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Coccocephalus	1	?	1	2	2	0	1	?	1	0	?	?	1	?	0	0	0	1	0	0	?	0
Cosmoptychius	?	?	1	2	2	0	0	1	?	0	1	0	0	0	0	0	0	1	0	?	0	0
Howqualepis	1	?	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Kansasiella	?	?	1	2	2	0	?	?	1	?	?	?	?	?	?	0	?	?	?	0	?	?
Kentuckia	?	?	1	1	1	1	0	0	1	0	?	0	?	0	0	0	0	?	0	0	?	?
Lepisosteus	1	3	1	2	2	1	1	1	1	0	2	1	1	1	1	0	0	1	1	0	1	1
Mesopoma	?	2	1	2	2	0	0	1	1	0	1	1	0	0	0	0	0	1	0	?	?	?
Mimia	1	2	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Moythomasia	1	2	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Osorioichthys	1	?	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	?	?
Perleidus	1	2	1	2	2	1	1	1	?	0	1	1	1	1	0	0	0	1	0	0	0	1
Polypterus	1	1	1	2	3	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Pteronisculus	?	2	1	1	1	0	0	1	1	0	1	0	1	0	0	0	0	1	0	0	0	0
Saurichthys	1	?	0	2	2	1	0	0	1	0	?	1	1	0	0	0	0	1	0	0	0	0
Teleostei	1	2	1	2	2	1	1	1	1	1	3	1	1	1	1	1	1	1	1	1	1	1
Watsonulus	?	?	1	2	2	1	1	0	1	1	1	0	1	1	1	1	1	1	1	0	1	1
Woodichthys	?	?	1	0	1	0	0	0	?	0	1	1	0	0	0	0	0	1	0	?	?	?

	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acipenser	0	0	0	0	0	1	2	2	1	0	0	0	2	1	0	0	0	0	?	0	0	0
Amia	0	0	1	1	1	1	3	3	1	1	1	1	2	1	0	2	1	0	1	2	1	0
Australosomus	0	1	1	0	0	1	1	0	1	1	0	1	2	0	0	2	0	0	1	2	1	1
Birgeria	?	?	0	?	0	1	?	?	1	?	?	0	1	1	0	2	?	?	?	?	?	?
Boreosomus	1	2	?	0	0	1	0	1	1	1	0	0	2	1	1	2	1	1	?	1	0	1
Cheirolepis	?	?	?	0	?	?	?	?	?	?	?	0	0	0	0	?	?	?	?	?	?	?
Coccocephalus	0	?	?	?	0	1	0	1	?	?	0	0	?	?	?	2	?	1	?	0	0	?
Cosmoptychius	?	?	?	?	0	?	1	2	?	?	?	?	2	0	1	2	?	1	?	?	?	?
Howqualepis	?	?	?	?	0	0	0	0	?	?	?	0	1	0	0	?	?	0	?	?	?	?
Kansasiella	1	2	?	?	0	1	0	2	1	1	0	0	2	1	1	2	1	1	1	1	0	1
Kentuckia	?	?	?	?	0	1	1	0	1	1	0	0	1	0	1	1	0	1	1	0	0	1
Lepisosteus	0	0	1	1	1	1	3	3	1	1	0	1	1	1	1	0	0	0	0	2	1	1
Mesopoma	1	2	?	?	0	?	?	?	?	?	?	?	?	?	?	2	?	?	?	1	0	1
Mimia	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	?
Moythomasia	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	1	1	0	1	0	0	?
Osorioichthys	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?
Perleidus	?	?	1	0	0	?	1	2	1	1	1	1	2	1	1	2	?	?	1	?	?	?
Polypterus	0	0	0	0	0	0	2	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0
Pteronisculus	1	2	0	0	0	1	1	2	1	1	0	0	2	1	1	2	1	1	1	0	0	1
Saurichthys	?	?	0	?	0	1	?	?	1	?	?	0	1	1	0	2	?	?	?	?	?	1
Teleostei	0	0	0	1	1	1	3	3	1	1	1	1	1	1	1	2	1	1	1	2	1	1
Watsonulus	0	1	?	?	1	1	1	3	?	?	1	1	1	1	1	2	1	1	1	2	1	?
Woodichthys	?	?	?	?	0	0	0	1	?	?	0	0	1	1	1	?	?	?	?	?	?	?

	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acipenser	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	1	1	1
Amia	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1
Australosomus	1	1	?	?	1	?	?	?	0	1	0	1	1	1	1	1	2	?	?	1
Birgeria	1	?	?	?	?	?	?	?	0	1	0	1	0	?	?	0	?	1	2	1
Boreosomus	1	1	?	?	1	0	?	0	0	1	0	0	0	1	1	0	2	?	1	1
Cheirolepis	?	?	?	?	?	?	?	?	0	?	?	?	0	0	0	0	1	0	0	0
Coccocephalus	1	?	?	?	1	?	?	?	?	?	?	?	?	1	?	1	?	1	?	?
Cosmoptychius	?	?	?	?	?	?	?	?	0	?	?	?	0	1	?	1	2	?	?	1
Howqualepis	?	?	?	?	?	?	?	?	0	?	?	?	0	1	1	1	1	?	0	0
Kansasiella	1	1	1	1	1	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?
Kentuckia	1	1	?	?	?	0	0	0	?	?	?	?	0	1	?	?	2	?	?	?
Lepisosteus	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	3	1
Mesopoma	1	1	1	1	0	0	0	0	0	?	0	?	0	1	?	1	2	?	?	1
Mimia	1	?	?	?	?	?	?	?	0	1	0	0	0	1	1	1	2	1	1	1
Moythomasia	1	?	?	?	?	?	?	?	0	1	0	0	0	1	1	1	2	1	1	1
Osorioichthys	?	?	?	?	?	?	?	?	0	?	?	?	?	0	1	1	2	1	?	?
Perleidus	1	?	?	?	?	?	?	?	0	?	1	1	1	1	?	1	2	?	?	1
Polypterus	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	1
Pteronisculus	1	1	1	1	1	?	?	0	0	1	0	0	0	1	1	1	2	1	1	1
Saurichtys	1	1	?	1	1	?	?	?	0	?	0	0	1	1	?	1	0	1	?	1
Teleostei	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	2	1
Watsonulus	1	?	?	?	1	?	?	?	0	1	1	?	1	1	1	1	2	?	?	1
Woodichthys	?	?	?	?	?	?	?	?	0	?	0	?	0	1	?	1	2	?	?	1

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