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SECOND TRISTICHOPTERID (SARCOPTERYGII, OSTEOLEPIFORMES) FROM THE UPPER DEVONIAN OF CANOWINDRA, NEW SOUTH WALES, AUSTRALIA, AND PHYLOGENY OF THE TRISTICHOPTERIDAE

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ABSTRACT—A new tristichopterid, *Cabonnichthys burnsi* gen. et sp. nov. from the Upper Devonian Mandagery Sandstone near Canowindra, New South Wales, Australia, is the second tristichopterid to be described from this locality. The first, *Mandageria fairfaxi*, was interpreted as the sister group of the Laurussian taxon *Eusthenodon*. *Cabonnichthys burnsi* gen. et sp. nov. is similar to these two taxa in possessing a posterior supraorbital extending ventrally behind the orbit to exclude the postorbital from the orbital margin, a posteriorly positioned pineal surrounded by kite or teardrop shaped bones, and an enlarged fang-like tooth at the anterior end of the premaxillary tooth row. *Cabonnichthys burnsi* differs from *Mandageria* and *Eusthenodon* in retaining a contact between the intertemporal and posterior supraorbital, and in possessing “horn-like” processes on the postparietal shield that notch into the posterior margin of the postorbital. The Tristichopteridae is a clade characterized inter alia by the possession of postspiracular bones. A phylogenetic analysis of the Tristichopteridae yields the topology [*Tristichopterus* [*Eusthenopteron* [*Jarvikina* [*Platycephalichthys* [*Cabonnichthys* [*Mandageria* + *Eusthenodon*]]]]]]]. This topology is consistent with the biostratigraphy of the group, and with a number of morphological trends including size increase and elaboration of the anterior dentition. It also suggests that the group has a northern origin and dispersed into Gondwana during the Upper Devonian.

INTRODUCTION

The Famennian fish fauna from the Mandagery Sandstone, near Canowindra, New South Wales (Fig. 1), is at present known from approximately 100 blocks containing well-preserved placoderms and sarcopterygians. These fishes are preserved in a single stratigraphic horizon, representing part of a single community of fish that apparently became trapped in a drying pool of water which concentrated and eventually killed them. Of the nearly 3000 fish collected, the most common are the antiarchs *Bothriolepis* von Eichwald, 1840 and *Remigolepis* Stensiö, 1931, while the arthrodire *Groenlandaspis* Heintz, 1932 and the sarcopterygians are rarer. Four genera of sarcopterygians are recognized at Canowindra thus far, two of which have already been described, *Canowindra grossi* Thompson, 1973 and *Mandageria fairfaxi* Johanson and Ahlberg (1997). *Canowindra grossi*, known from a single specimen, was shown to be an osteolepiform by Long (1985a) and assigned to the Gondwanan family Canowindridae by Young et al. (1992), along with *Koharalepis* Young et al., 1992 from Antarctica and *Beelarongia* Long, 1987 from Victoria, Australia.

Mandageria fairfaxi belongs to the Tristichopteridae (= Eusthenopteridae, Cloutier and Ahlberg, 1996), a group which also includes *Tristichopterus* Egerton, 1861 from the Givetian of Scotland, *Eusthenopteron* Whiteaves, 1881, from the Frasnian of Canada, Latvia and Russia, *Platycephalichthys* Vorobyeva, 1959 and *Jarvikina* Vorobyeva, 1977 from the Frasnian of the Baltic region, *Eusthenodon* Jarvik, 1952 from the Famennian of Greenland and Russia, and possibly *Spodichthys* Jarvik, 1985 (Upper Devonian of Greenland) and *Hyneria* Thomson, 1968 (Famennian of Pennsylvania). The Australian taxon *Marsdenichthys longioccipitus* Long, 1985c was originally assigned to the Tristichopteridae; however, *Marsdenichthys* is now believed to be a rhizodontid (J. A. Long, pers. comm., 1995). Although sarcopterygian bones from Grenfell, New South Wales, have been tentatively attributed to *Eusthenodon* (Young, 1993), *Mandageria* and the materials described below are the only unambiguous tristichopterids described from

Australia. The present materials, assigned to *Cabonnichthys burnsi* gen. et sp. nov., represent the third sarcopterygian described from Canowindra.

Institutional abbreviations—AMF, Australian Museum, Sydney; BMNH, Natural History Museum, London.

SYSTEMATIC PALEONTOLOGY

Class SARCOPTERYGII Romer, 1955

Order OSTEOLEPIFORMES Berg, 1937

Family TRISTICHOPTERIDAE Cope, 1889

Remarks—The family Tristichopteridae is uniquely characterized by the possession of postspiracular bones (Jarvik, 1980; Cloutier and Ahlberg, 1996). Known members also have a characteristic trifurcate tail, round scales with a boss on the inner surface, absence of cosmine, and vomers with long posterior processes which clasp the sides of the parasphenoid. However, some of these characters are also shared with other groups; the scale morphology, for example, is shared with rhizodonts (Andrews, 1985). Absence of contact between the anterior supraorbital and lateral rostral, suggested as a tristichopterid synapomorphy by Young et al. (1992), is in fact variable within the Tristichopteridae. The full significance of these character distributions has yet to be elucidated. Few attempts have been made to resolve the phylogenetic relationships of taxa assigned to the Tristichopteridae.

Genus *CABONNICHTHYS* gen. nov.

Type Species—*Cabonnichthys burnsi*, sp. nov.

Etymology—For Cabonne Shire Council, incorporating the town of Canowindra, which provided invaluable help during the excavation of the locality.

Known Distribution—Mandagery Sandstone, Famennian, New South Wales, Australia.

Diagnosis—As for type and only known species.

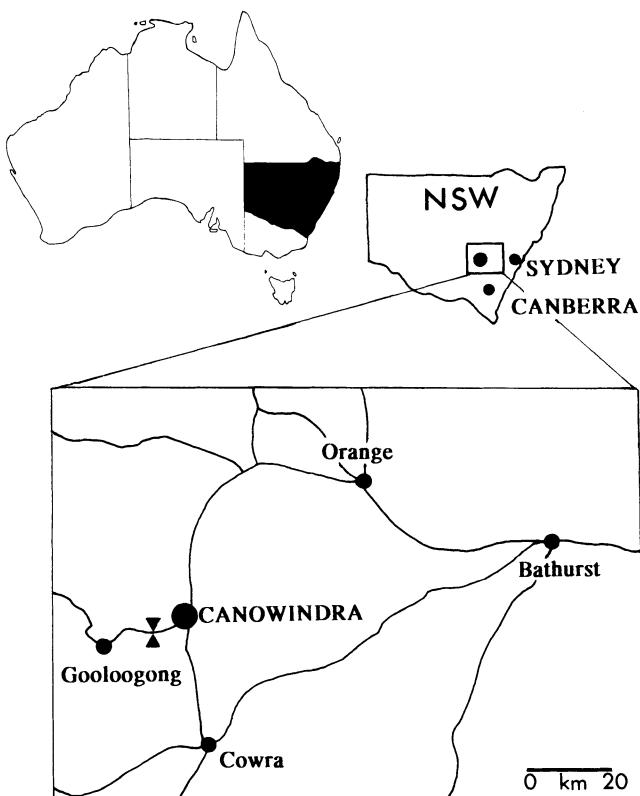


FIGURE 1. Locality map of Upper Devonian (Famennian) fish fauna, near Canowindra, New South Wales, Australia. Fossil fish locality indicated by opposing triangles on road between Canowindra and Gooloogong. Adapted from Johanson and Ahlberg, 1997.

CABONNICHTHYS BURNSI sp. nov.
(Figs. 2–15)

"Second Canowindra tristichopterid" Johanson and Ahlberg, 1997.

Holotype—Australian Museum AMF96858a, dorsolateral view of skull, right pectoral fin and anterior part of body; AMF96858b, associated posterior part of body with second dorsal, anal and caudal fins.

Referred Specimens—AMF96856a–c, dorsal skull, partial palate, partial gular region, postcranial skeleton; AMF96856, dorsal skull, postcranial skeleton; AMF96863, ventral view of skull, including gulars and submandibulars, postcranial skeleton; AMF96898, internal dorsal view of lower jaws, premaxillary fangs, partial right cheek and upper jaw, gular plates, right clavicle, cleithrum and scapulocoracoid, and ventral surface of body from pectoral fin to poorly preserved caudal fin; AMF96900, postcranial skeleton with second dorsal, anal and caudal fins; AMF96901, posterior skull roof, partial left pectoral fin with lepidotrichia, scales; AMF96902, dorsal skull and body; AMF98037, internal surface of skull roof, right cheek and lower jaw, cleithrum, poorly preserved pectoral fin, small portion of body; AMF98038, palate; AMF98390, pectoral fin endoskeleton with scapulocoracoid and some lepidotrichia in lateral view.

Etymology—For Dr Bruce Burns, who made it possible for Alex Ritchie to relocate and excavate the Canowindra locality.

Horizon and Type Locality—10 km SW of Canowindra, N.S.W., on the road to Gooloogong. Mandagery Sandstone, Upper Devonian (Famennian).

Diagnosis—Medium-sized tristichopterid approximately

0.74 m in length. Differs from other known tristichopterids in the following combination of characters: pineal bones kite- or teardrop-shaped, pineal opening relatively close to posterior parietal margin; contact between intertemporal and posterior supraorbital; supratemporals with small rounded "horn" on lateral margin, fitting into notch on posterodorsal margin of the postorbital; Lateral extrascapulars approximately triangular with slightly indented medial margin, widely separated by median extrascapular; postorbital excluded from orbital margin by contact between posterior supraorbital and jugal; enlarged tooth at anterior end of premaxilla; dentary fang pair present; coronoids entirely without marginal teeth; caudal fin homocercal, and diamond-shaped rather than trilobed.

Description

Cabonnichthys burnsi is a medium-sized tristichopterid; the most complete specimen, AMF96858 a,b (Figs. 2, 3) is estimated to be 74 cm long. The head is broad (breadth/length ratio approximately 0.74), with a blunt snout and a proportionately wider postparietal shield.

Parietal Shield and Snout—The sutures between the bones in the snout region cannot be traced in external view except for the posterior margin of the median postrostral, which is V-shaped as in other osteolepiforms, and some of the margins of the supraorbitals, tectal and most posterior nasal (Figs. 2A, 3A, 4, 5). AMF98037 shows the median postrostral and nasal series in mesial view (Figs. 8A, 9A). There are four nasal bones on the right side of the skull, the most posterior bone being much the largest. The left and right nasal series do not appear to meet in the midline anteriorly, but it is unclear how many rostral bones are present.

In *Cabonnichthys*, only one specimen shows the lateral rostral clearly. This individual, AMF98037, preserves the internal surfaces of the lateral bones of the skull roof and cheek. Here (Figs. 8A, 9A) the narial opening is clearly visible, as are the two bones surrounding it dorsally and ventrally. Unfortunately the tectal is incomplete posterodorsally, but both tectal and lateral rostral resemble the corresponding bones in *Eusthenopteron*. AMF98037 does not show the relationship between the lateral rostral and anterior supraorbital, as the latter bone is incomplete. However, two specimens, AMF96902 and AMF96856, show the relationship between the anterior supraorbital and the tectal in external view. In AMF96856 (Figs. 4B, 5B) the two bones meet, although the contact is proportionately much shorter than in *Eusthenopteron*. Lateral to the contact, part of a third bone can be seen; if this is the lacrimal, as seems most likely, there is no contact between the anterior supraorbital and lateral rostral. AMF96902 shows a slightly different pattern (Figs. 4A, 5A). Here, a gap of about 3 mm separates the anterior supraorbital from the tectal. This permits the lacrimal to suture with the posteriormost nasal, and unquestionably precludes any contact between the supraorbital and lateral rostral.

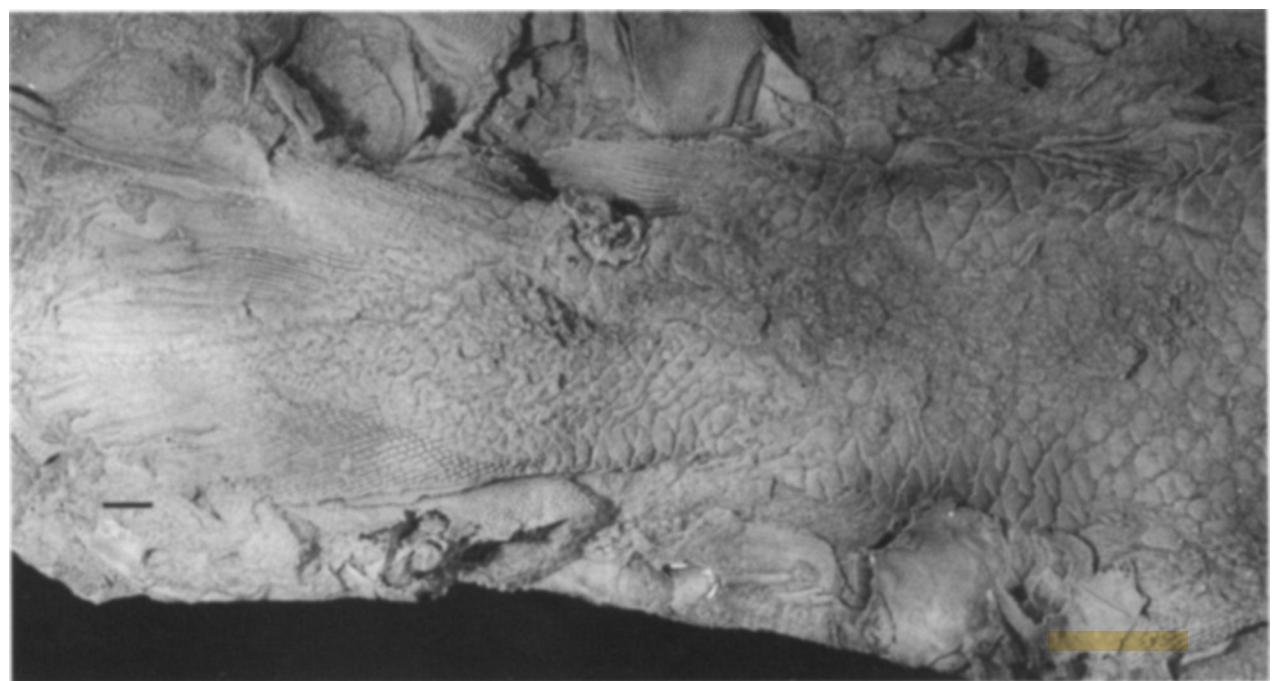
The parietals (approximately 1.3 times longer than the postparietals) have the long and narrow shape characteristic of tristichopterids (Figs. 4, 5). They are proportionately rather large, reaching forwards beyond the level of the orbits. The pineal region of *Cabonnichthys* is positioned near the posterior parietal margin. The pineal series of bones is kite- or teardrop-shaped with a distinct posterior point.

A small pitline is visible near the middle of each parietal in *Cabonnichthys*, but the sensory canals cannot be traced. The parietal is flanked by the posterior supraorbital and an elongate intertemporal. The posterior supraorbital has a long and pointed posterior process which is overlapped laterally by the intertemporal.

Postparietal Shield—The anterior border of the postparietal shield is considerably shorter than the posterior border. The midline suture between the postparietals is easy to trace, but



A



B

FIGURE 2. *Cabonnichthys burnsi* gen. et sp. nov. A, AMF96858a, dorsal skull, right pectoral fin, partial postcranial; B, AMF96858b, associated posterior part of body with second dorsal, anal, and caudal fins. In this and all subsequent Figures, scale = 1 cm, unless otherwise noted.

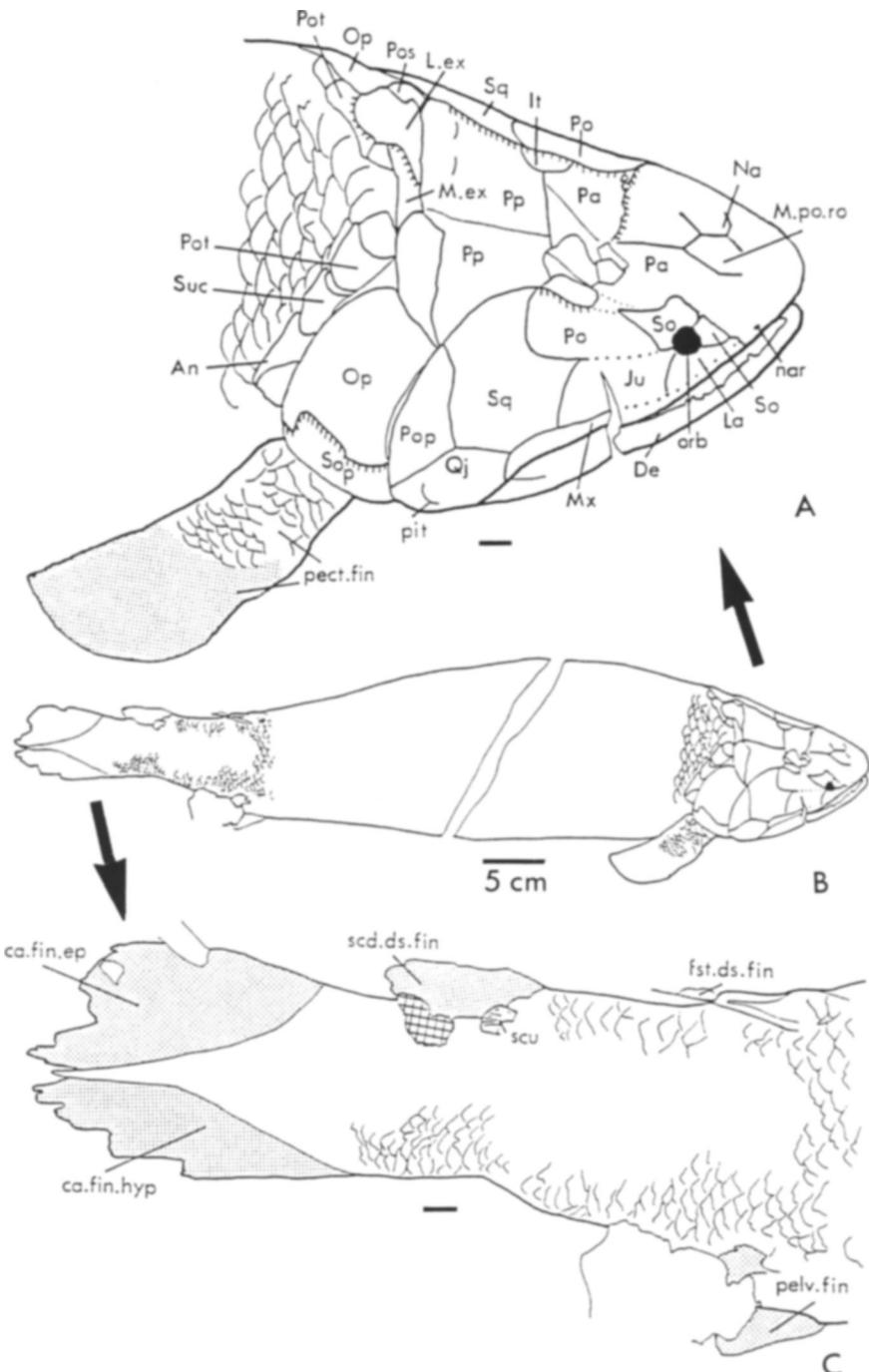


FIGURE 3. *Carbonichthys burnsii*, AMF96858a,b. A, head region, B, associated anterior and posterior halves of AMF96858, C, caudal region. Abbreviations: An, anocleithrum; ca.fin.ep, epichordal lobe of caudal fin; ca.fin.hyp, hypochordal lobe of caudal fin; De, dentary; fst.ds.fin, first dorsal fin; It, intertemporal; Ju, jugal; La, lacrimal; L.ex, lateral extrascapular; M.ex, median extrascapular; M.po.ro, median postrostral; Mx, maxilla; Na, nasal; nar, naris; Op, opercular; orb, orbit; Pa, parietal; pect.fin, pectoral fin; pelv.fin, pelvic fin; pit, pitline; Po, postorbital; Pop, preopercular; Pos, postspiracular; Pot, posttemporal; Pp, postparietal; Qj, quadratejugal; scd.ds.fin, second dorsal fin; scu, basal scute; So, supr orbital; Sop, subopercular; Sq, squamosal; Suc, supracleithrum.

only one small specimen (AMF96902, Figs. 4A, 5A) shows the tabular and supratemporal sutures clearly. In this specimen, the two bones appear to be of similar size, separated by an oblique margin. In larger specimens these bones are superficially fused with the postparietals, a characteristic which may reflect reworking of the bone surface in older individuals. The extratem poral is absent, as in all tristichopterids. A most characteristic

feature is the development of the anterolateral corner of the supratemporal into a hooked process which fits into a concavity in the posterior margin of the postorbital (Fig. 4, 5).

Extrascapulars and Postspiracular—The lateral extrascapulars of *Carbonichthys* are smaller than the median extrascapular, and are three-sided bones with smoothly curved lateral margins, and slightly indented medial margins (Figs. 4, 5). The

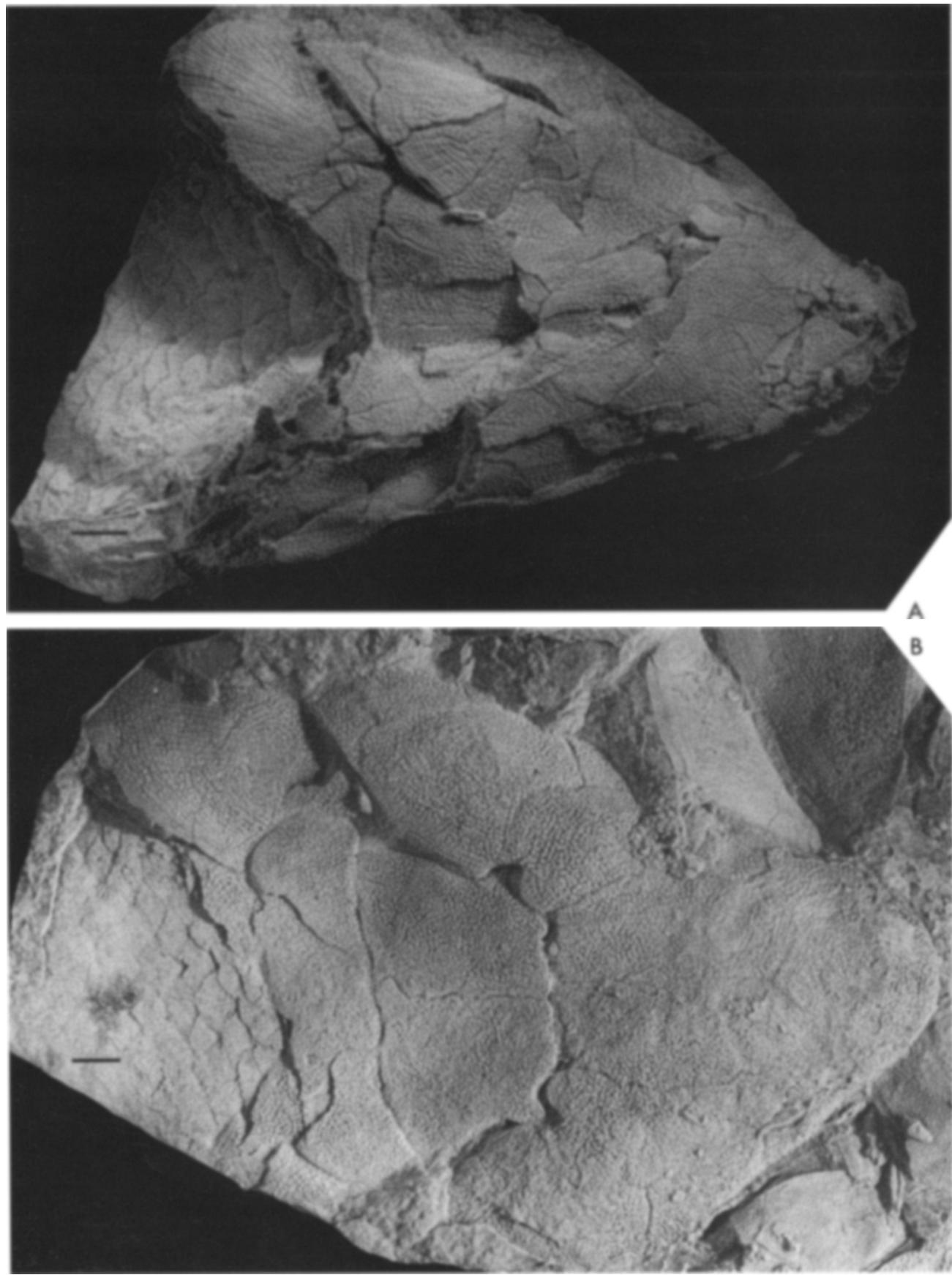


FIGURE 4. *Cabonnichthys burnsi*. A, dorsal skull roof and body, AMF96902; B, dorsal skull roof, AMF96856.

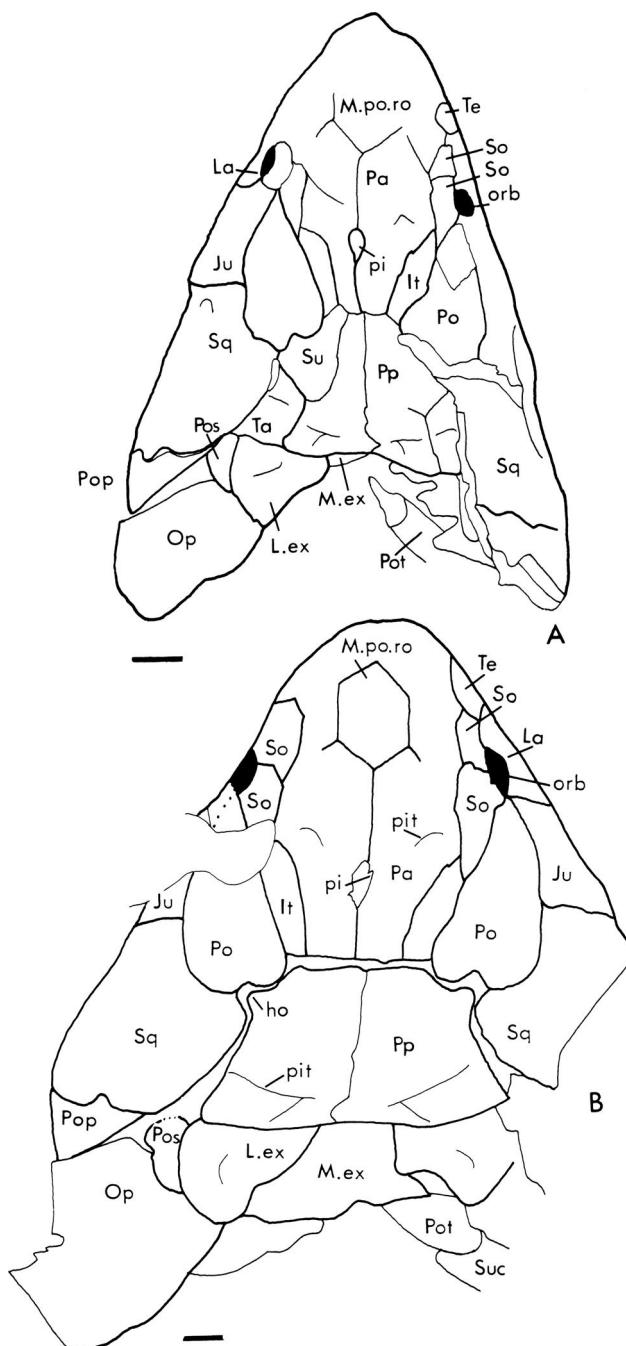


FIGURE 5. *Cabonnichthys burnsi*. A, AMF96902; B, AMF96856. Abbreviations as in Figure 3 plus: ho, horn on lateral corner of parietal shield; pi, pineal plates; Su, supratemporal; Ta, tabular; Te, tectal.

lateral extrascapulars are well separated anteriorly by the median extrascapular. Because of the anterior separation of the lateral extrascapulars, the median extrascapular of *Cabonnichthys* is trapezoidal rather than triangular. Lateral to the lateral extrascapular, most specimens of *Cabonnichthys* show a well-preserved crescentic postspiracular bone (Figs. 4, 5). This is a tristichopterid synapomorphy (Jarvik, 1980; Long, 1985b; Cloutier and Ahlberg, in press).

Postorbital—The orbits of *Cabonnichthys burnsi* are relatively small and situated in the anterior third of the headshield, and are visible dorsally. Posterior to the orbit, the postorbital

of *C. burnsi* is anteroposteriorly elongate, wider posteriorly and narrowing anteriorly. The postorbital contacts the lateral edge of the intertemporal and the dorsal margins of the squamosal and jugal. The anterior end of the postorbital is excluded from the orbital margin by a contact between the posterior supraorbital and the jugal.

In internal view, as shown by specimens AMF98037 (Figs. 8A, 9A) and AMF98865, the postorbital is surprisingly broad. It "underlaps" the lateral edge of the parietal shield to such an extent that it achieves a broad contact with the parietal and completely obscures the suture between the posterior supraorbital and intertemporal.

Jugal, Squamosal, Preopercular and Quadratojugal—The jugal is rectangular in shape, and is larger than the lacrimal (Figs. 2A, 3A), but has only a limited contribution to the orbital margin. The squamosal is roughly six-sided, with a concave anterodorsal margin where it meets the ventral lobe of the postorbital (Figs. 2A, 3A). The dorsal margin, which touches but does not suture with the supratemporal, tabular and postspiracular, is smoothly convex. This squamosal morphology is not substantially different from that in other osteolepiforms, which Long (1987:840) regarded as a derived feature characterizing the group.

The sutural margins of the preopercular and quadratojugal are generally difficult to trace, but they can be seen fairly clearly in the holotype AMF96858a (Figs. 2A, 3A). They agree in all essentials with the corresponding bones of *Eusthenopteron* (Jarvik, 1980).

Premaxilla and Maxilla—The premaxilla is preserved in most specimens of *Cabonnichthys*. The facial lamina of the premaxilla is always superficially fused with neighbouring bones, so that it is impossible to determine its precise extent in external view. However, the lamina can be seen in internal view in AMF98037 (Figs. 8A, 9A); it closely resembles that of *Eusthenopteron*. A dorsally directed ridge can be seen on the anterior part of the facial lamina in this specimen. It is comparable in position to the ridge housing the supraorbital sensory canal in *Eusthenopteron* (Jarvik, 1980:fig. 117B), and can probably be identified with it.

In palatal view, the most striking feature of the premaxilla is the presence of an enlarged tooth at the anterior end that abuts the midline of the snout (Figs. 8A, 9A, 10, 11). The area just posterior to this, the apical fossa, is not well preserved. The maxilla is not well displayed in external view in any specimen. However, AMF96898 shows a well-preserved internal view (Figs. 10A, 11A). In general terms the maxilla compares well with that of *Eusthenopteron*, but the posterodorsal process (ventral to the jugal-squamosal junction) is proportionately lower.

Operculo-Gular Series—Some of these elements can be seen in most specimens of *Cabonnichthys*, although no one individual preserves the entire series (Figs. 2A, 3A, 4, 5, 8A, 9A). The subopercular is not shown well by any specimen, and the median gular has not been observed at all, but there is nothing to suggest that the operculo-gular series differs significantly from that of *Eusthenopteron* (Jarvik, 1980).

Palate—The palatal region is only preserved on three specimens of *Cabonnichthys*, AMF96856, 98038 and 98865; the preservation in the latter is rather poor. Small portions of the palate are also visible on AMF96898 (vomerine and dermopalatine fangs) and AMF98037 (dermopalatine fangs). On AMF98038 (Figs. 6A, 7C), the palatal area is well preserved. The dermopalatine and ectopterygoid carry complete marginal tooth rows as well as the standard tristichopterid complement of fangs (one pair on the dermopalatine, two pairs on the ectopterygoid). There is no palatoquadrate exposure at the suture between dermopalatine and ectopterygoid. The entopterygoids reach forward to a point just posterior to the anterior tip of the denticulated field of the parasphenoid. The parasphenoid itself

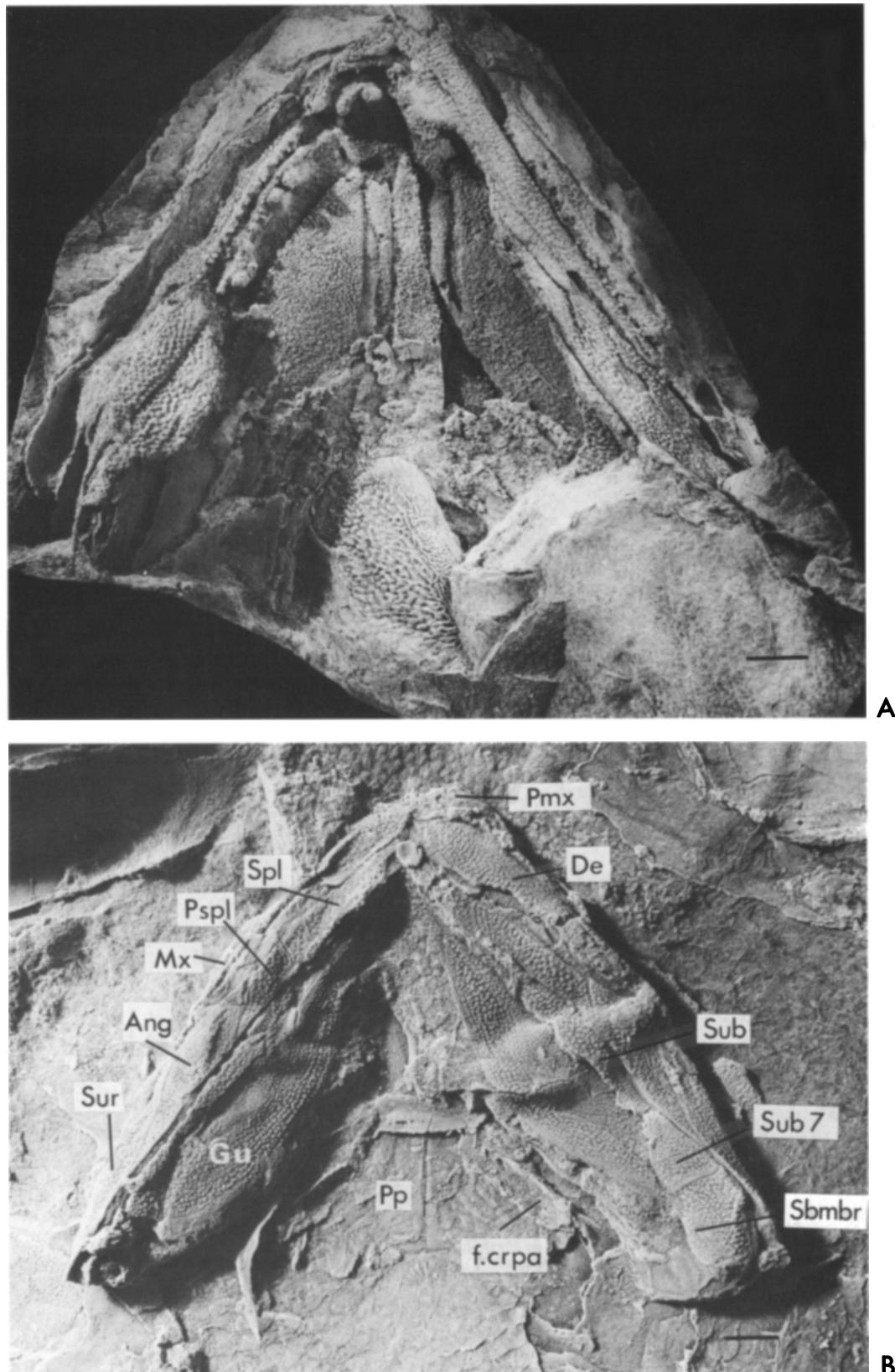


FIGURE 6. *Cabonichthys burnsi*. A, palatal, ventral view of lower jaws, dorsal portion of cleithrum, AMF98038; B, ventral view of lower jaws, AMF96863. Abbreviations as in Figure 3, plus: Ang, angular; f.crpa, fossa for crista parotica; Gu, gular plate; Pmx, premaxilla; Pspl, presplenial; Sbmbr, submandibulobranchiostegal; Spl, splenial; Sub, submandibular; Sub7, submandibular 7; Sur, surangular.

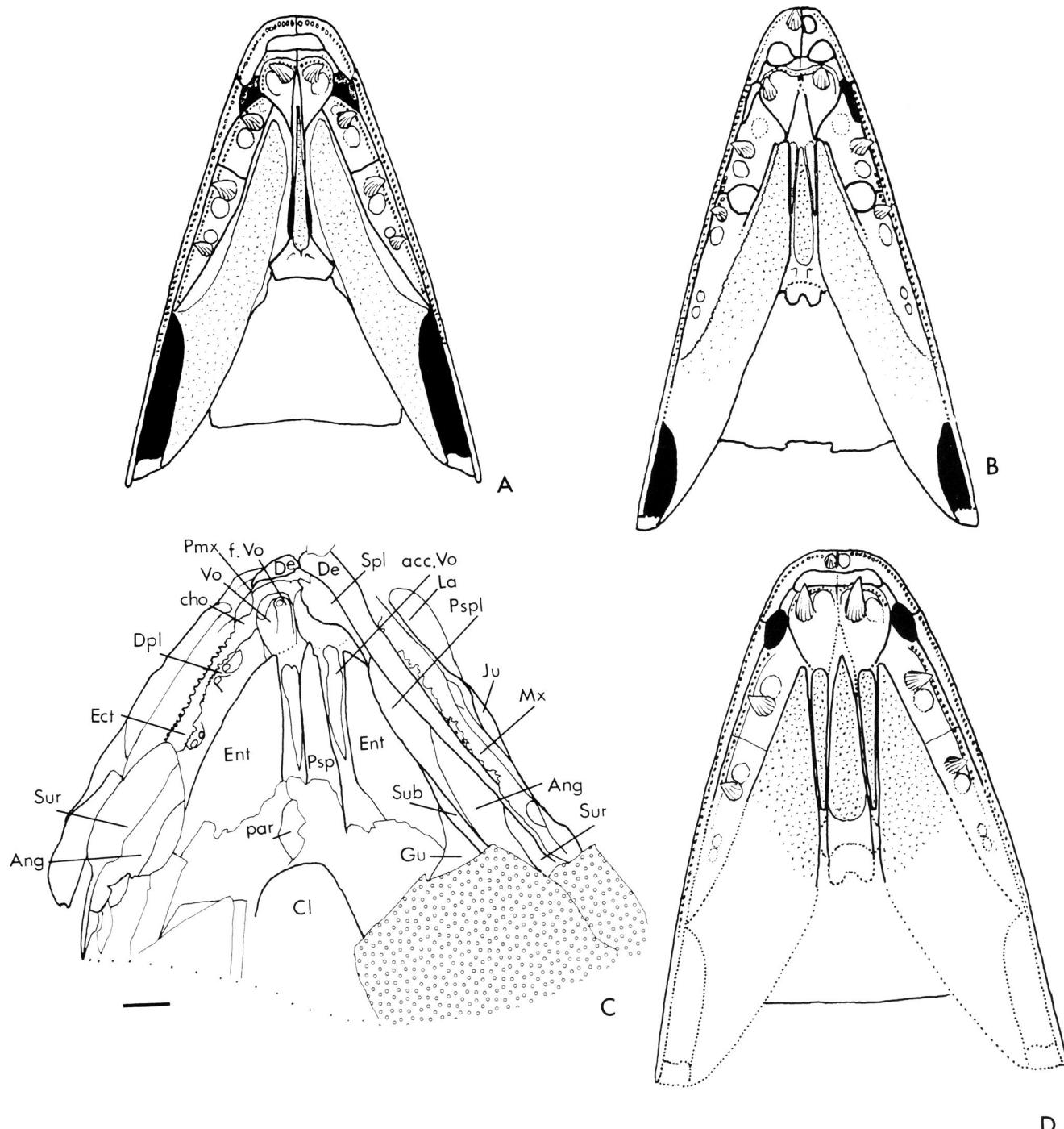


FIGURE 7. A, *Eusthenopteron*, palatal reconstruction. B, *Mandageria*, palatal reconstruction. C, *Cabonnichthys burnsi*, AMF98038. D, *Cabonnichthys*, palatal reconstruction. Abbreviations as in Figure 3 and 6, plus: acc.Vo, accessory vomer; cho, choana; Cl, cleithrum; Dpl, dermopalatine; Ect, ectopterygoid; Ent, entopterygoid; f.Vo, vomerine fang; par, parotic dental plate; Psp, parasphenoid; Vo, vomer.

is broad throughout most of its length, only narrowing at the anteriormost tip. The vomers are rounded and meet in the midline. Just posterior to the vomers, between the parasphenoid and entopterygoid, lies a long, narrow denticulated dermal bone. This element is broadest anteriorly, where it overlies the posterior part of the vomer, and tapers posteriorly to a point. This bone most closely resembles the so-called accessory vomer of primitive actinopterygians (Gardiner, 1984:fig. 53). We will apply the term 'accessory vomers' to these palatal bones, but re-

gard them on parsimony criteria as homoplastic with the accessory vomers of actinopterygians. A well-defined right choana can be seen in AMF98038, and the same specimen also preserves an incomplete paraotic dental plate (compare Jarvik, 1980:fig. 124).

Mandible—The external face of the mandible is quite well preserved in AMF96863; it presents no significant differences from *Eusthenopteron* (Jarvik, 1980). The internal face is also well preserved. AMF96898 (Figs. 10, 11) is particularly infor-

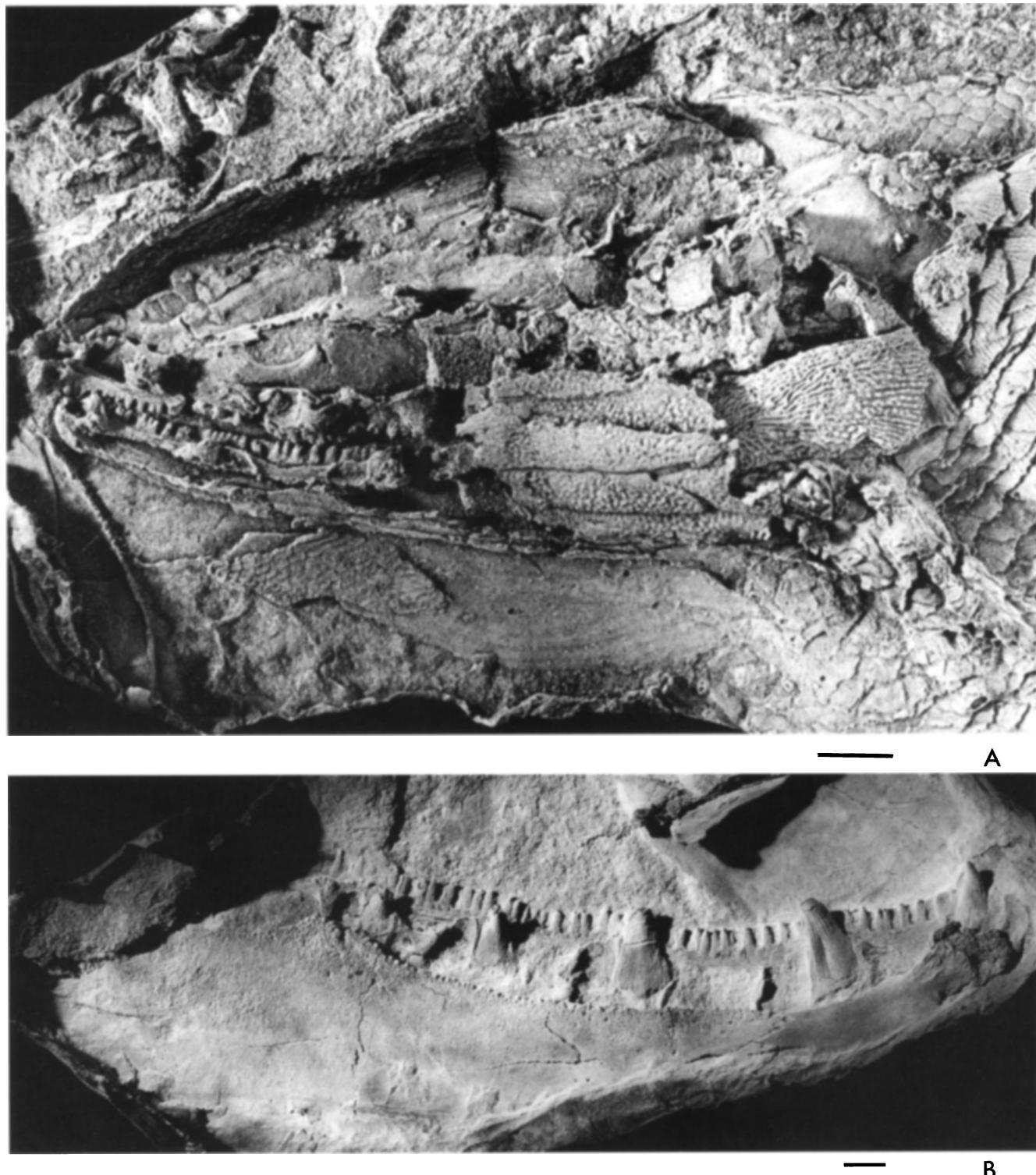


FIGURE 8. A, *Cabonnichthys burnsi*. Internal surface of skull roof, right cheek and lower jaw, cleithrum, poorly preserved pectoral fin, small portion of body, AMF 98037. B, internal view of lower jaw of *Eusthenodon*, BMNH P64121.

mative, and additional details are provided by AMF98037 (Figs. 8A, 9A). The dentary is long and slender, with a single row of small teeth present laterally. At the anterior end the dentary carries a pair of large fangs. Three coronoids are present in the lower jaw. The anterior and middle coronoids carry

one fang pair each, whereas the posterior coronoid carries two. Marginal coronoid teeth are absent.

As in other osteolepiforms and porolepiforms, the coronoids are separated by deep fossae. In AMF96898, some of the fangs of the palate are preserved in articulation with the lower jaw

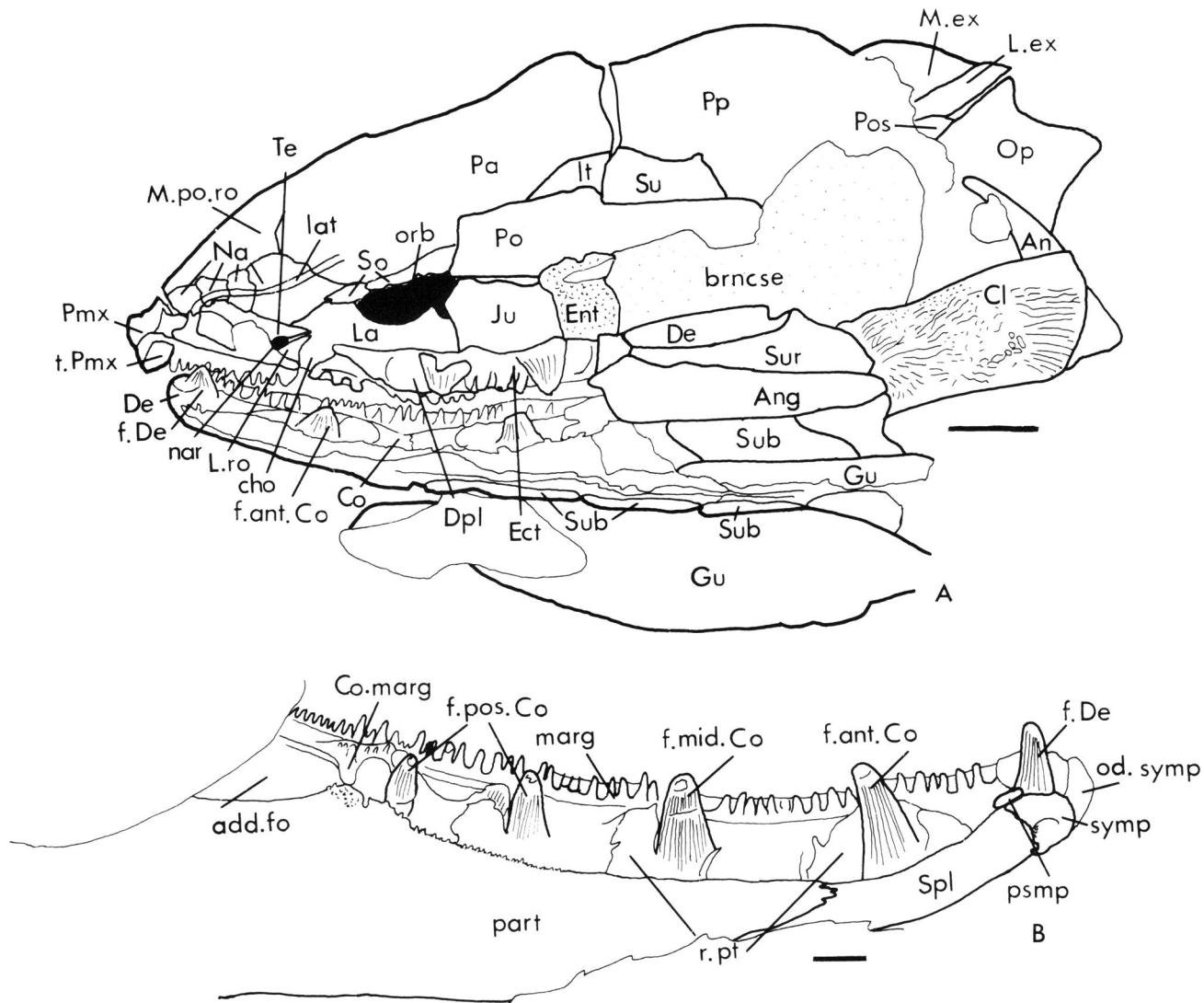


FIGURE 9. *Cabonnichthys burnsii*. A, AMF98037. B, BMNH P64121. Abbreviations as in Figures 3, 5, 6 and 7, plus: **add.fo**, adductor fossa; **brncse**, braincase; **Co**, coronoid; **Co.marg**, marginal coronoid dentition; **f.ant.Co**, anterior coronoid fang; **f.mid.Co**, middle coronoid fang; **f.pos.Co**, posterior coronoid fang; **marg**, marginal dentition; **f.De**, dentary fang; **lat**, lateral line canal; **L.ro**, lateral rostral; **od.symp**, overlap area of symphysis; **part**, prearticular; **psmp**, parasymphysial plate; **r.pt**, replacement pit for coronoid fang; **symp**, symphysis; **t.Pmx**, enlarged tooth on premaxilla.

(Figs. 10, 11). The vomerine fangs bite into the precoronoid fossa, while the dermopalatine fangs fit snugly into the intercoronoid fossa between the anterior and middle coronoids. The dentary fangs can be seen to fit into the apical fossa (just posterior to the enlarged premaxillary teeth, Fig. 11), and the posterior fang of the fang pair on the anterior coronoid fits into a hole in the anterior part of the dermopalatine. Contrary to Rosen et al.'s (1981) interpretation of *Eusthenopteron*, no lower jaw fang fits into the choana; the fangs are all more mesial in position.

Mesial to the dentary and coronoids, the internal face of the lower jaw displays a large prearticular which is sutured anteriorly to the mesial lamina of the splenial. The parasymphysial plate is not preserved in any specimen that we have been able to examine, but a small attachment area for this bone can be seen at the anterior end of the mesial lamina of the splenial (Figs. 10, 11). It is apparent that the parasymphysial plate was small, and that it did not extend posteriorly along the mesial face of the dentary.

Scales—*Cabonnichthys* has typical tristichopterid scales: round, cosmine-free and with a teardrop-shaped boss in the middle of the internal face (Figs. 2, 8A, 12A). The scale ornament consists mainly of quite deep and widely spaced (approximately 1 mm apart) anteroposterior grooves. However, the areas between these grooves are not quite smooth; their edges are slightly raised, and these raised edges are connected by irregular but quite closely spaced faint transverse ridges.

Pectoral Girdle—The external surfaces of the clavicle and cleithrum are not well preserved in any specimen. However, the internal faces of these bones, together with the scapulocoracoid, are nicely exposed in AMF96898 (Fig. 12A, 13A). A complete series of posttemporal, supracleithrum and anocleithrum can be seen in the holotype, AMF96858a (Figs. 2A, 3A). We have not observed an interclavicle.

The clavicle is generally similar to that of *Eusthenopteron* (Jarvik, 1980; pers. obs., PEA). However, its ventral blade appears slightly broader, with a less acute anteroventral angle, and the ascending process is somewhat shorter. A ridge running

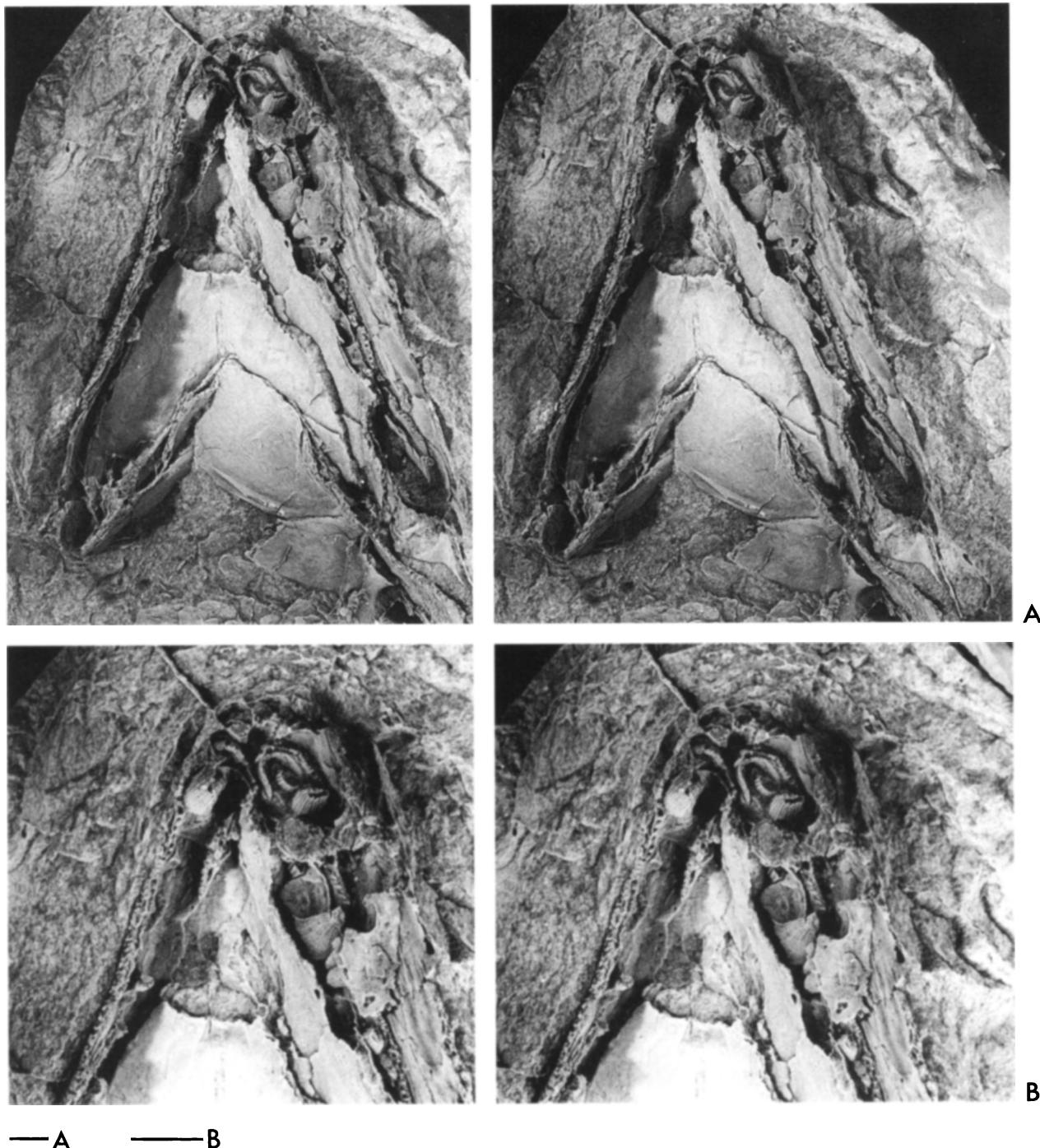


FIGURE 10. *Cabonichthys burnsii*, stereopairs of AMF96898. A, internal dorsal view of lower jaws, premaxillary fangs, partial right cheek and upper jaw, gular plates. B, closeup of anterior lower jaws and premaxillary fangs.

parallel to the posterior margin of the ventral blade forms the contact area for the ventral process of the cleithrum. The cleithrum of AMF96898 is more damaged than the clavicle; it has lost most of its ventral process and a good deal of the anterior margin. However, the general impression is once again one of close similarity to *Eusthenopteron*.

This is also true of the more dorsal shoulder girdle elements preserved in AMF96858a. The ornamented portion of the posttemporal is nearly identical in shape and size to that of the supracleithrum. The ornamented area of the anocleithrum is of approximately similar length to the supracleithrum, although it

has an extended posteroventral process and overall a more elongate shape (Fig. 2A).

The scapulocoracoid is preserved in different views in two specimens. AMF96898 (Figs. 12A, 13A) shows a complete scapulocoracoid in mesial view, still attached to the cleithrum. AMF98390, a detached pectoral fin skeleton which can be attributed to *Cabonichthys* with reasonable confidence because of its size and the appearance of the attached lepidotrichia, is accompanied by a scapulocoracoid which is exposed in lateral view. This specimen gives an unusual view of the three buttresses which would have attached to the cleithrum in life (Figs.

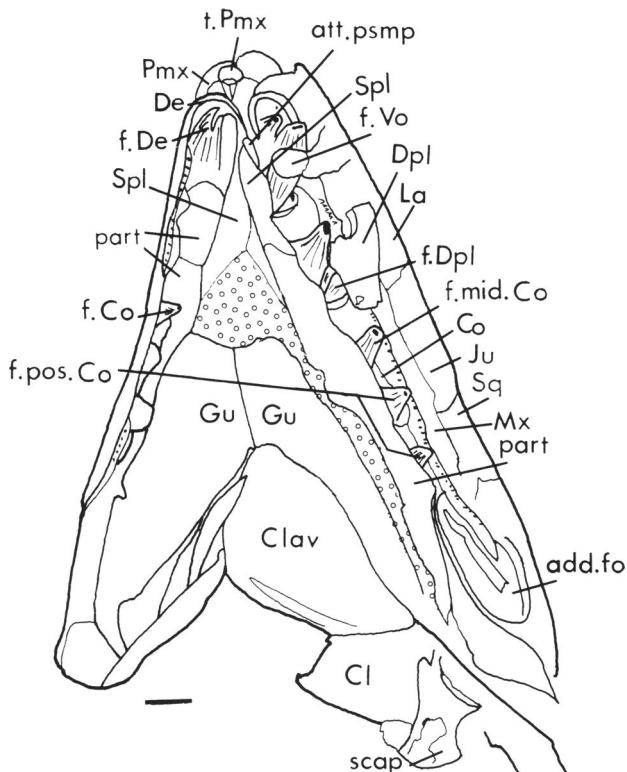


FIGURE 11. *Cabonnichthys burnsi*, AMF96898. Abbreviations as in Figures 3, 7 and 9, plus: att.psmp, attachment for the parasymphysial plate; Clav, clavicle; f.Dpl, dermopalatine fang; scap, scapulocoracoid.

12C, 13B). The scapulocoracoid is similar to that of *Eusthenopteron* (Andrews and Westoll, 1970a; Jarvik, 1980) in construction. The three buttresses are separated by foramina which meet in a central open space under the middle of the bone. This is the general pattern for the Osteolepiformes (Janvier, 1980; Lebedev, 1995; but see below), and is also present in the lungfish *Chirodipterus* (Janvier, 1980). The glenoid fossa, which is carried on the posterior buttress, is large and of a rounded trapezoid shape; the long axis is perpendicular to the cleithrum, and the broadest part of the trapezoid is that closest to the cleithrum. This is the inverse of the situation in *Eusthenopteron* (Andrews and Westoll, 1970a) and *Medoevia* (Lebedev, 1995), where the glenoid fossa widens mesially, away from the cleithrum.

Overall, the scapulocoracoid of *Cabonnichthys* is robustly constructed, and with the correspondingly small size of the foramina between the buttresses, the tripodal nature of the scapulocoracoid of *Cabonnichthys* is not immediately apparent in mesial view (Fig. 12A). Interestingly, both the supraglenoid and infraglenoid buttresses of AMF96898 have abrupt anterior ends with unfinished bone surfaces. It looks as though the footplates of these buttresses were continued (respectively) anterodorsally and anteroventrally by cartilage. The size of the cartilage extensions is unknown, as there are no attachment scars on the cleithrum.

The mesial face of the main body of the scapulocoracoid has a strongly concave dorsal margin, but is otherwise convex and lacks sharp demarcating edges. It might reasonably be described as "saddle-shaped". The mesial face bears a glenoid foramen posteroventrally.

Pectoral Fin—In external view, the pectoral fin of *Cabonnichthys* presents the standard osteolepiform appearance with an extensive lepidotrichial web and fairly short fleshy lobe (Fig.

2A). Unlike *Eusthenopteron* and *Mandageria*, the fin has no distinct posterolateral corner.

The best preserved pectoral fin skeleton which can be attributed to *Cabonnichthys* is the detached fin AMF98390 (Figs. 12C, 13B). The humerus, seen in dorsal view on this specimen, possesses a broad, triangular entepicondyle with a straight posterior margin that is level with (and in fact appears as a continuation of) the ulnar facet. We have not been able to locate an entepicondylar foramen in *Cabonnichthys*, and there is no humeral process. The caput humeri is gently convex. The arrangement of the deltoid and supinator processes matches the *Eusthenopteron* pattern very closely. The ectepicondyle, on the other hand, differs significantly from that of *Eusthenopteron*; it reaches the distal end of the humerus, and carries a distal concave area which appears to be continuous with the ulnar facet. The ectepicondylar foramen is represented by an unroofed canal between the ectepicondyle and supinator process.

The distal parts of the fin skeleton closely resemble those of other known osteolepiforms (Andrews and Westoll, 1970a, b; Jarvik, 1980; Rackoff, 1980; Johanson and Ahlberg, 1997). The radius appears to taper to a point distally, but this unusual feature may simply be due to defective preservation. The ulna is a short, broad element, articulating distally with an elongate intermedium and a proximally broad ulnare. The postaxial portion of the ulnare appears to take the form of a broad flange. Two distal elements articulate with the ulnare.

Posterior Fins—The posterior fins are best preserved on the holotype AMF96858b (Figs. 2B, 3C) and on AMF96900 (Fig. 14). With the exception of the anterior dorsal fin, all have well preserved external morphologies; only the caudal fin, however, reveals part of the internal skeleton.

The caudal fin of *Cabonnichthys* is homocercal and rhomboidal in outline. The body axis extends straight down the middle of the fin, narrowing to a point. The caudal peduncle is deep, and the fin has a low aspect ratio (approximately, the dorsoventral length of fin/mean anteroposterior width). Both epichordal and hypochordal lobes are supported by independent radials, which articulate with the neural and haemal arches, respectively.

The dorsal, anal and pelvic fins fall within the range of known osteolepiform morphologies, but are proportionately smaller than those of *Eusthenopteron* and somewhat different in shape. The posterior dorsal and anal fins carry conspicuous basal scutes ornamented with coarse anteroposterior grooves. The basal scute of the pelvic fin is smaller and not so distinctively ornamented.

DISCUSSION

The most complete specimen of *Cabonnichthys burnsi* is estimated to be 74 cm long. This is less than half the length of *Mandageria* (Johanson and Ahlberg, 1997). The head is broader than in *Mandageria*, with a breadth/length ratio of approximately 74, compared to a B/L ratio of 50 in *Mandageria*. The snout of *Cabonnichthys* is broader and the postparietal shield proportionately wider. However, the position of the intracranial joint is approximately the same in *Cabonnichthys* as in *Mandageria*, as well as *Eusthenodon* (Jarvik, 1952). *Eusthenopteron*, on the other hand, has a more anteriorly placed joint (Jarvik, 1980).

Parietal Shield and Snout—as noted above, the lateral rostral in *Cabonnichthys* does not contact the anterior supraorbital. Young et al. (1992:fig. 47, character G1) recognized only a single synapomorphy of the Eusthenopteridae (=Tristichopteridae): lack of contact between the lateral rostral and the supraorbital=tectal (=anterior supraorbital). Outgroup comparison with osteolepids (Jarvik, 1980) and porolepiforms (pers. obs., PEA) supports their judgement of the character polarity. How-

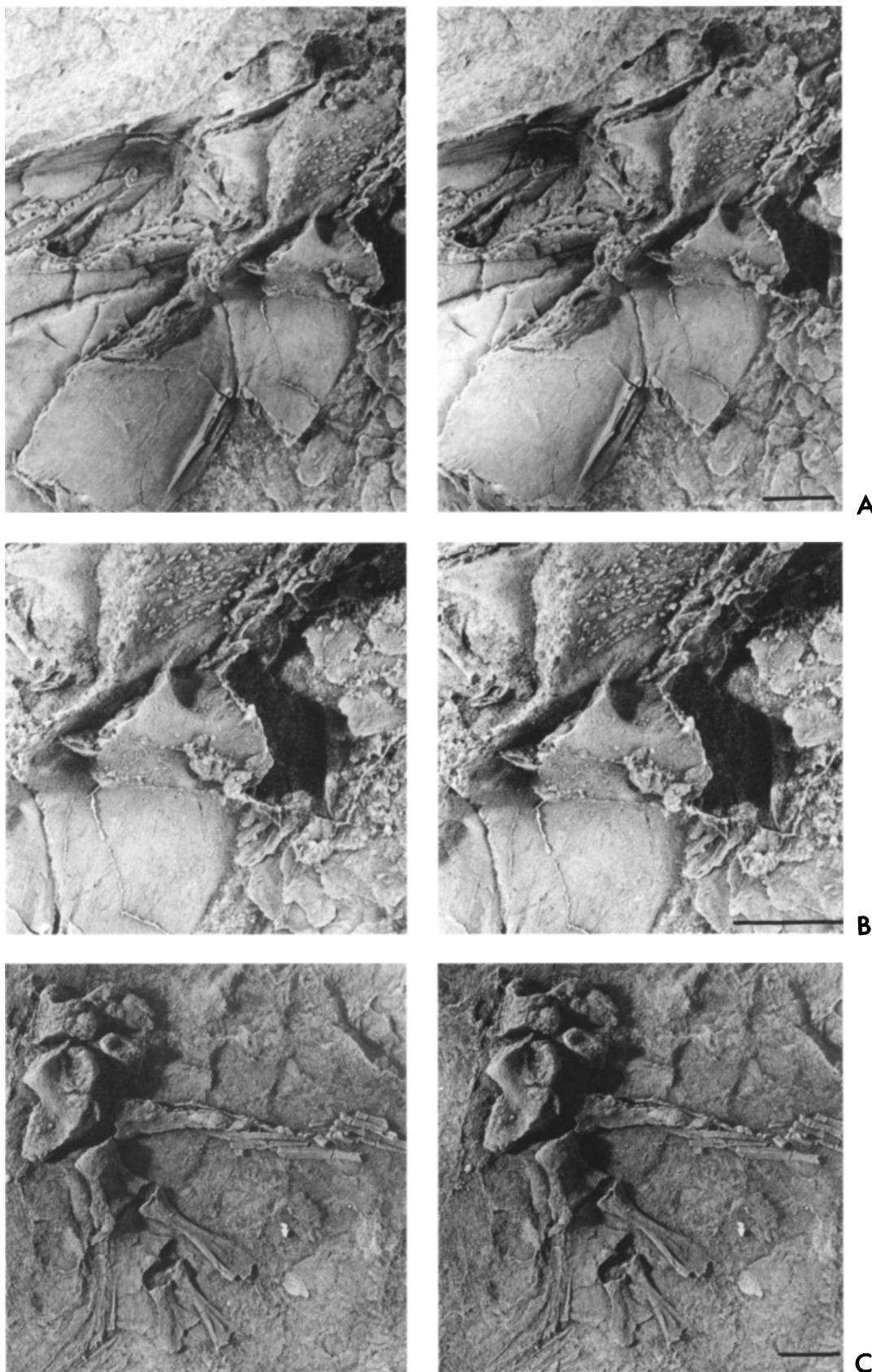


FIGURE 12. *Cabonnichthys burnsi*, stereopairs. A, internal surface of cleithrum with attached scapulocoracoid, AMF96898; B, closeup of scapulocoracoid, AMF96898; C, internal skeleton of pectoral fin, AMF98390.

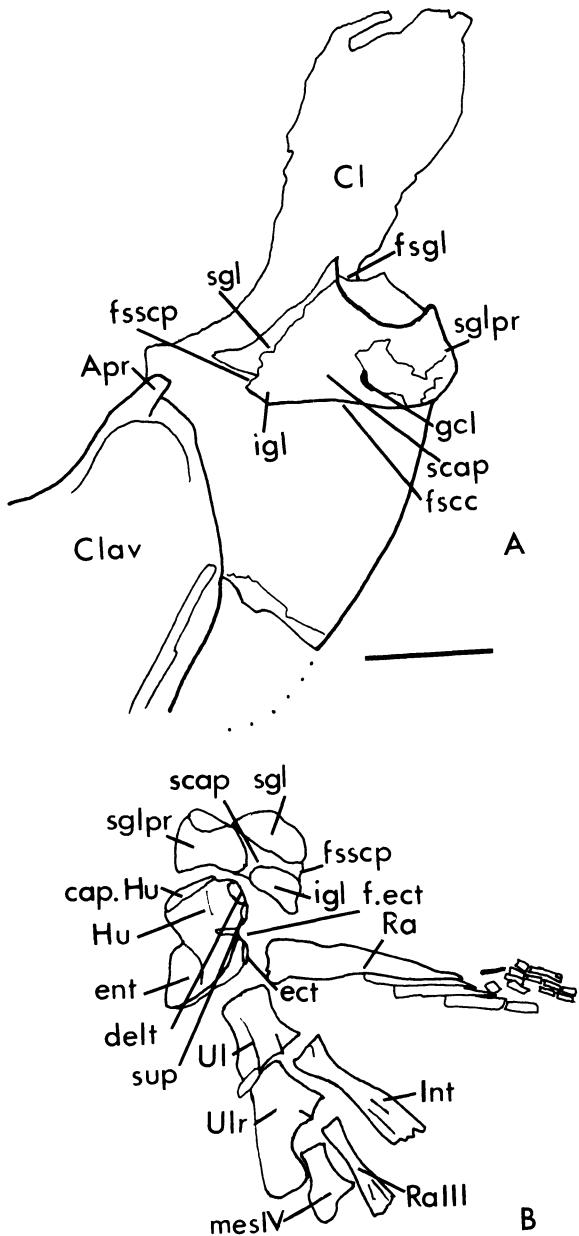


FIGURE 13. *Cabonnichthys burnsi*. A, AMF96898; B, AMF98390. Abbreviations as in Figure 6, 11, plus: **Apr**, ascending process of clavicle; **cap.Hu**, caput humeri; **delt**, deltoid process; **ect**, ectepicondyle; **ent**, entepicondyle; **f.ect**, ectepicondylar foramen; **fscc**, supraceracoid foramen; **fsgl**, supraglenoid fossa; **fsscp**, subscapular fossa; **gcl**, glenoid canal; **Hu**, humerus (first mesomere); **igl**, infraglenoid buttress; **Int**, intermedium (second radial); **mesIV**, fourth mesomere; **Ra**, radius (first radial); **RalIII**, third radial; **sgl**, supraglenoid buttress; **sglpr**, supraglenoid process; **sup**, supinator process; **Ul**, ulna (second mesomere); **Ulr**, ulnare (third mesomere).

ever, the condition in tristichopterids is much less clear-cut than Young et al. imply. In *Mandageria*, these bones are indeed widely separated (Johanson and Ahlberg, 1997). *Eusthenopteron*, the most completely known tristichopterid, shows a point contact between the lateral rostral and anterior supraorbital in external view. However, there is actually an extensive contact between these bones (Jarvik, 1980:fig. 116A), which is concealed by the overlapping lacrimal. A very slight shift in the position of the lacrimal could produce the effect of either sep-

arating the lateral rostral and supraorbital, or revealing a broad contact between them, without actually changing their relationship. In *Eusthenodon* (Jarvik, 1952) there is a short suture between the lateral rostral and supraorbital in external view. The condition in *Jarvikina* is ambiguous (Vorobyeva, 1977:fig. 42A, B) whereas *Platycephalichthys* is reconstructed as lacking any contact, either exposed or hidden, between the two bones (Vorobyeva, 1977:fig. 44B). Interestingly, the tetrapod *Ichthyostega* also has a lateral rostral which is widely separated from the anterior supraorbital ("posterior tectal", Jarvik, 1980:fig. 171). We can thus state that both *Mandageria* and *Cabonnichthys* possess Young et al.'s (1992) derived character, "lateral rostral not in contact with supraorbital," but the status of this character as a tristichopterid synapomorphy must be regarded as doubtful.

The parietals of *Cabonnichthys* are proportionately large, extending anteriorly beyond the level of the orbits. This contrasts with the condition in *Mandageria* (Johanson and Ahlberg, 1997), where the parietals reach only to the level of the orbits. Among other tristichopterids, the longest parietals (substantially longer than in *Cabonnichthys*) are seen in *Platycephalichthys* (Vorobyeva, 1977). *Eusthenopteron* resembles *Cabonnichthys* in this respect (Jarvik, 1980; pers. obs., PEA) whereas *Eusthenodon*, like *Mandageria*, has somewhat shorter parietals.

The pineal series of bones is kite- or teardrop-shaped with a distinct posterior point. This condition is also seen in *Eusthenodon* and *Mandageria*, whereas *Eusthenopteron* (Jarvik, 1980) and apparently *Jarvikina* ("*Eusthenodon wenjukovi*"; Vorobyeva, 1962) have an oval pineal series. The kite-shaped pattern is probably derived, although it does occur in the osteolepidid *Gyroptychius milleri* (Jarvik, 1980:fig. 80A). The pineal region of *Cabonnichthys* seems to be more anterior in position than those of *Mandageria* and *Eusthenodon*.

As in *Mandageria* and *Eusthenodon*, but unlike *Eusthenopteron*, the posterior supraorbital of *Cabonnichthys* has a long and pointed posterior process; outgroup comparison with osteolepidids (Jarvik, 1948, 1980) suggests that this is a derived character. However, *Cabonnichthys* retains the primitive contact between posterior supraorbital and intertemporal which has been lost in *Mandageria* and *Eusthenodon*.

Postparietal Shield—An autapomorphy of *Cabonnichthys* is the presence of a hooked process of the supratemporal fitting into a concavity in the postorbital. This "horn" of the postparietal shield corresponds to a slight projection seen in the tristichopterids *Eusthenopteron* (Jarvik, 1980) and *Eusthenodon* (Jarvik, 1952), and the canowindrids *Beelarongia* and *Koharalepis* (Long, 1987; Young et al., 1992).

Extrascapulars and Postspiracular—As in *Eusthenopteron* (Jarvik, 1980), *Eusthenodon* (Jarvik, 1952), and most other osteolepidiforms except the canowindrids (Jarvik, 1948; Young et al., 1992; Fox et al., 1995; Lebedev, 1995) the lateral extrascapulars of *Cabonnichthys* are well separated anteriorly by the median extrascapular. This is a major difference from *Mandageria*, in which the lateral extrascapulars almost meet in the midline anteriorly (Johanson and Ahlberg, 1997). However, in shape, the lateral extrascapulars seem to resemble those of *Mandageria* more than those of *Eusthenopteron* (which are proportionately longer) or *Eusthenodon* (which have strongly convex posteromesial margins and appear almost four-sided).

The median extrascapular of *Cabonnichthys* is trapezoidal rather than triangular. Young et al. (1992:61) noted that a trapezoidal ("equilateral") median extrascapular characterizes the Tristichopteridae, Osteolepidinae, Gyroptychinae and Glyptopominae. They argued that this condition is derived relative to the triangular shape seen in the Rhizodontida and Canowindridae (and, as we now know, in *Mandageria*). However, as outgroup comparison reveals that a median extrascapular with a broad anterior margin occurs in porolepiforms, onychodonts, coelacanths (Young et al., 1992:fig. 46) and lungfishes (Camp-

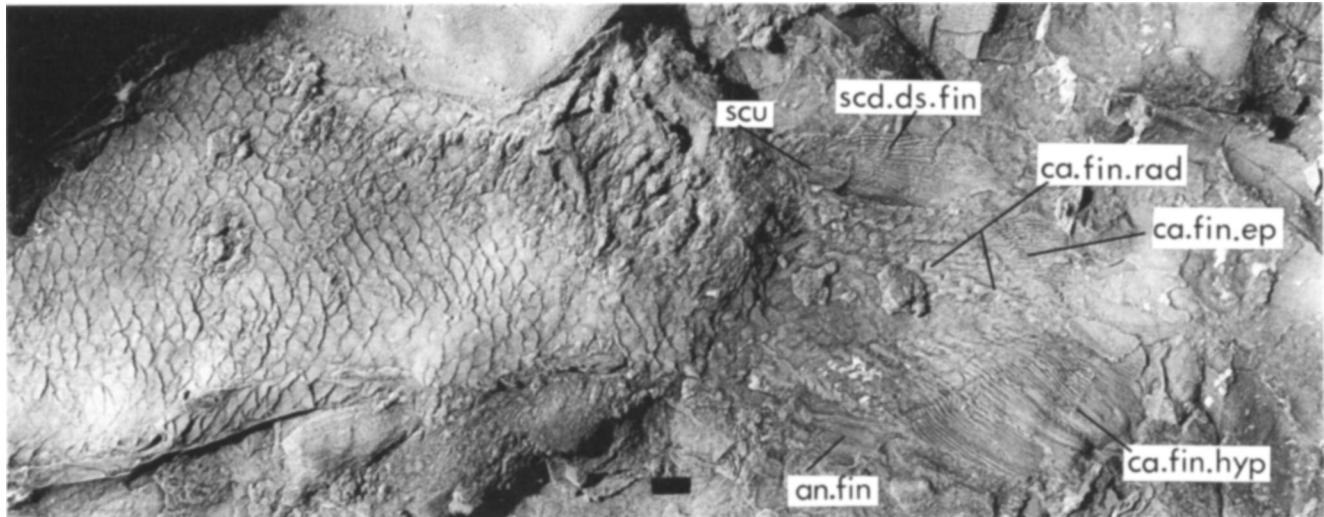


FIGURE 14. *Cabonnichthys burnsi*. AMF96900, caudal region. Abbreviations as in Figure 3, plus: **an.fin**, anal fin; **ca.fin.rad**, caudal fin radial.

bell and Barwick, 1987), it seems much more likely that the trapezoidal pattern is in fact primitive.

Postorbital—In *Cabonnichthys*, the postorbital is excluded from the orbital margin by a contact between the posterior supraorbital and the jugal. Among other tristichopterids, exclusion of the postorbital from the orbit is seen in *Eusthenodon* (Jarvik, 1952:fig. 26A) and *Mandageria* (Johanson and Ahlberg, 1997). However, in these genera it is effected by a contact between the posterior supraorbital and lacrimal. The condition in *Cabonnichthys* seems more primitive, in that it retains a jugal contribution to the orbital margin. The postorbital is also excluded from the orbital margin in the Canowindridae (Young et al., 1992:fig. 44). However, this is most probably homoplastic with the Tristichopteridae.

In internal view, the postorbital ‘underlaps’ the lateral edge of the parietal shield. This is quite different from the pattern in *Eusthenopteron* (Jarvik, 1980). The postorbital also underlaps the parietal shield in *Mandageria* (Johanson and Ahlberg, 1997), but it is unclear whether the condition in that genus is as extreme as in *Cabonnichthys*.

Jugal—The jugal is rectangular in shape, and is larger than the lacrimal. Young et al. (1992:66, fig. 47, character C1) argued that a similar size of the lacrimal, jugal and postorbital was a synapomorphy for the Tristichopteridae, Osteolepididae and Megalichthyidae, while a jugal at least twice as long as high was a synapomorphy of the Canowindridae (character E3). However, in the tristichopterid *Mandageria fairfaxi* (Johanson and Ahlberg, 1997) the jugal is longer than high; furthermore, the lacrimal, jugal and postorbital are dissimilar in size both in that taxon and in *Cabonnichthys*. The taxonomic utility of these “size characters” is questionable because there is a wide range of variation between similar and dissimilar, and these are difficult terms to apply objectively from taxon to taxon.

Premaxilla and Maxilla—An enlarged tooth is present at the anterior end of the premaxilla of *Cabonnichthys*. This tooth is also present in *Eusthenodon* and *Mandageria* (Johanson and Ahlberg, 1997), but it is absent in other known tristichopterids (Vorobyeva, 1977; Jarvik, 1980). Among other sarcopterygians, a similar enlarged tooth is found in rhizodonts (Andrews, 1985; Long, 1989) and megalichthyids (Jarvik, 1966; Fox et al., 1995). The enlarged tooth of *Cabonnichthys* is proportionately somewhat smaller than that of *Mandageria*. In *Mandageria*, the tooth is associated with a backward-pointing process reaching

the vomers, while the situation in *Cabonnichthys* is not clear as this area is not preserved.

The posterodorsal process of the maxilla is proportionately lower in *Cabonnichthys* than *Eusthenopteron*. A lower posterodorsal process is also seen in *Eusthenodon* (Jarvik, 1952, 1985), *Mandageria* (Johanson and Ahlberg, 1997) and *Platycephalichthys* (Vorobyeva, 1962). Further afield, a similar maxillary morphology occurs in tetrapods (Ahlberg et al., 1994; Clack, 1994) and porolepiforms (Jarvik, 1972).

Palate—In most respects the palate of *Cabonnichthys* appears less derived than that of *Mandageria* (Johanson and Ahlberg, 1997) but very similar to that of *Eusthenopteron*. The entopterygoids reach further forward than in *Mandageria*. The vomers are very similar to those of *Eusthenopteron*, but the parasphenoid is slightly broader than in that genus. The ‘accessory vomers’ visible on either side of the parasphenoid in *Cabonnichthys* are also present in *Mandageria* (Johanson and Ahlberg, 1997). Recent work near Eden, NSW, has confirmed the presence of these ‘accessory vomers’ in a large, as yet undescribed tristichopterid (pers. obs., ZJ and PEA).

Mandible—The large fangs present at the anterior end of the dentary in *Cabonnichthys* can be matched in several taxa, including the tristichopterids *Eusthenodon* (Jarvik, 1952), *Platycephalichthys* (Vorobyeva, 1962, 1977) and *Mandageria* (Johanson and Ahlberg, 1997), as well as in megalichthyids (Fox et al., 1995), rhizodonts (Andrews, 1985; Long, 1989; Young et al. 1992), *Panderichthys* (Gross, 1941) and early tetrapods (Jarvik, 1980; Ahlberg et al., 1994). Such fangs are not present in *Eusthenopteron* (Vorobyeva, 1962; Jarvik, 1980) or *Jarvikina* (“*Eusthenodon wenjukovi*”, Vorobyeva, 1962); the polarity of this character within the Tristichopteridae is difficult to determine, as both character states occur among the outgroups.

The anterior and middle coronoids always carry one fang pair each in tristichopterids. The posterior coronoid has two fang pairs in *Cabonnichthys*, *Eusthenodon* (Figs. 8B, 9B), *Eusthenopteron* (Jarvik, 1980:fig. 125) and some individuals of *Platycephalichthys* (Vorobyeva, 1962:pl. XVII); in other *Platycephalichthys* individuals, however, the posterior fang pair on the posterior coronoid is replaced by a row of enlarged teeth. Out-group comparison with porolepiforms (Gross, 1941) and osteolepidids (Fox et al., 1995; Lebedev, 1995) indicates that the posterior coronoid primitively has only one fang pair, arguably with a row of enlarged teeth behind it. Such teeth are present

in *Gogonasus* Long, 1985b (also Long, 1988; Fox et al., 1995) and, less strongly developed, in *Medoevia* (Lebedev, 1995). Apart from the tristichopterids, only the rhizodont *Notorhizodon* Young et al., 1992 has been described as carrying two fang pairs on the posterior coronoid. However, it is difficult to determine whether it really shows this character state, or simply a short row of enlarged posterior teeth. All we can say with confidence for now is that the presence of two fang pairs on the posterior coronoid appears to be a tristichopterid synapomorphy (subject to some individual variation), but that it may in fact define a somewhat more inclusive group.

A more easily interpreted character is the absence of marginal coronoid teeth in *Cabonnichthys*. Although no other tristichopterid is known to lack marginal coronoid teeth altogether, they are absent from the anterior part of the jaw in *Eusthenodon* (Figs. 8B, 9B) and *Mandageria* (Johanson and Ahlberg, 1997). The condition in *Platycephalichthys* is variable (Vorobyeva, 1962, 1977; pers. obs., PEA). By contrast, well-developed marginal teeth are present on the anterior coronoid (as well as more posteriorly) in *Eusthenopteron* (Jarvik, 1980) and *Jarvikina* (Vorobyeva, 1977; pers. obs., PEA). Most other osteolepiforms (Gross, 1941; Vorobyeva, 1962, 1977; Fox et al., 1995; Lebedev, 1995) and porolepiforms (Gross, 1941; Jarvik, 1972) have complete marginal coronoid tooth rows, although these teeth are absent in some megalichthyids (Fox et al., 1995) and holopptychids (pers. obs., PEA). We conclude that the reduction of the marginal coronoid teeth is a derived character within the Tristichopteridae, uniting *Cabonnichthys*, *Mandageria* and *Eusthenodon*.

The parasympathial plate of *Cabonnichthys* is believed to be small, based on the small attachment at the anterior end of the mesial lamina of the splenial. This type of parasympathial plate is also seen in *Eusthenodon* (Figs. 8B, 9B) and is in fact characteristic of the Tristichopteridae as a whole (Vorobyeva, 1962; Jarvik, 1972, 1980; Johanson and Ahlberg, 1997), as well as the elpistostegid *Panderichthys* (Vorobyeva, 1962; Ahlberg, 1991a) and the rhizodont *Notorhizodon* (Young et al., 1992). By contrast, osteolepidids (Jessen, 1966; Jarvik, 1972; Fox et al., 1995; Lebedev, 1995), megalichthyids (Fox et al., 1995) and early tetrapods (Jarvik, 1980; Ahlberg 1991a, 1995; Ahlberg et al., 1994) have elongate parasympathial plates which reach back alongside the dentary to suture with the anterior coronoid.

Scales—The scales of *Cabonnichthys* are proportionately much larger than those of *Mandageria*, and lack the posterior corner and constricted “waist” seen in that genus. In both respects, *Mandageria* appears to be derived, while *Cabonnichthys* shows the primitive tristichopterid condition. The scale ornament of *Cabonnichthys* is very similar to that of *Mandageria*, but differs from the *Eusthenopteron* pattern which consists of closely spaced, irregular anteroposterior ridges and tubercles (Jarvik, 1952:fig. 30C; pers. obs., PEA). *Eusthenodon* is described by Jarvik (1952:fig. 30A) as having yet another pattern, consisting of an irregular but essentially anteroposterior network of ridges. Intuitively, this pattern resembles *Mandageria* and *Cabonnichthys* more closely than *Eusthenopteron*, but we have not had the opportunity to examine *Eusthenodon* scales first hand.

Pectoral Girdle—Overall, there is a close similarity between the pectoral girdles of *Cabonnichthys* and *Eusthenopteron*. This is also true of the more dorsal shoulder girdle elements. Interestingly, the relative proportions of the anocleithrum and supracleithrum in AMF96858 are almost perfectly intermediate between those of *Eusthenopteron* and *Mandageria*. In *Eusthenopteron*, the ornamented area of the anocleithrum is substantially longer than that of the supracleithrum (Jarvik, 1980: fig. 126). *Mandageria*, on the other hand, has a strikingly long supracleithrum and an anocleithrum with a very short triangular

area of ornament (Johanson and Ahlberg, 1997). In *Cabonnichthys*, the two ornamented areas are of approximately the same length (Fig. 2A). Outgroup comparison with *Medoevia* (Lebedev, 1995) and *Canowindra* (Long, 1985a) suggests that a long anocleithrum is primitive within the Tristichopteridae, and indeed, Long (1985b) has suggested an elongate anocleithrum is characteristic of the osteolepiforms as a whole.

The scapulocoracoid of *Cabonnichthys* is similar to that of *Eusthenopteron* (Andrews and Westoll, 1970a; Jarvik, 1980) in construction, but the main difference between these scapulocoracoids lies in the proportions of the three buttresses and the spaces between them. In *Eusthenopteron*, the buttresses are tall, slender and widely separated, giving the scapulocoracoid an overtly tripodal appearance. In *Cabonnichthys* they are much more robust and closely spaced. The difference is seen most readily by comparing the lateral view of the scapulocoracoid of *Cabonnichthys* on AMF98390 (Fig. 12C), with the corresponding view from *Eusthenopteron* (Andrews and Westoll, 1970a: fig. 4e).

The main body of the scapulocoracoid of *Cabonnichthys* differs somewhat from that of *Eusthenopteron*. In the latter genus the mesial face is straight-sided and gently concave with raised edges (Andrews and Westoll, 1970a:fig. 4; pers. obs., PEA), while in *Cabonnichthys* the mesial face is “saddle-shaped.” A glenoid foramen is present in a mesial position on the scapulocoracoid of both taxa.

A tripodal scapulocoracoid is characteristic of all known osteolepiforms (though many genera are in fact unknown in this respect), and was viewed as a possible osteolepiform synapomorphy until it was noted that the scapulocoracoid of the diploean *Chirodipterus* also possessed these three attachments (Janvier, 1980). Given the probable sistergroup relationship of the osteolepiform-tetrapod and porolepiform-lungfish clades (Ahlberg, 1991b; Cloutier and Ahlberg, 1995, in press), it seems quite likely that this general scapulocoracoid structure is a synapomorphy of the two clades. Long (1985b: 16) defined a more precise morphological character by noting that the attachment areas were small and of similar size in osteolepiforms, but different sizes in *Chirodipterus*. However, the scapulocoracoid attachments are of different sizes in *Cabonnichthys* and “osteolepid A” from Iran (Janvier, 1980), and also in *Rhizodopsis* (Andrews and Westoll, 1970b:398), *Megalichthys* (Andrews and Westoll, 1970b:409), and *Ectosteorachis nitidius* (Thomson and Rackoff, 1974:fig. 1). The value of this character is questionable. A potentially more interesting character is the glenoid foramen, which is present in *Cabonnichthys*, *Eusthenopteron* and *Medoevia* but absent in Janvier’s (1980) osteolepids “A” and “B” as well as in *Chirodipterus* (Janvier, 1980; pers. obs., PEA) and porolepiforms (Ahlberg, 1989). Unfortunately, the present usefulness of this character is limited by the small number of osteolepiforms in which the scapulocoracoid is adequately known.

Pectoral Fin—The humerus of *Cabonnichthys* differs most obviously from that of *Eusthenopteron* in the shape of the entepicondyle. Unlike in *Eusthenopteron* (and *Mandageria*), where the entepicondyle is finger-shaped and projects distally beyond the level of the radial and ulnar facets, the entepicondyle of *Cabonnichthys* is a broad triangular structure with a straight posterior margin level with the ulnar facet. In shape it resembles the entepicondyle of *Sterropterygion* (Rackoff, 1980), but the orientation of the process is much more like that in *Eusthenopteron* and *Mandageria*. This orientation is also seen in other sarcopterygian groups (Ahlberg, 1991b) and seems to be primitive for the Sarcopterygii as a whole. The caput humeri is gently convex, as in *Eusthenopteron*, *Mandageria* and other known osteolepiforms (Andrews and Westoll, 1970a; Rackoff, 1980; Lebedev, 1995).

It is gradually becoming clear that humeral morphology var-

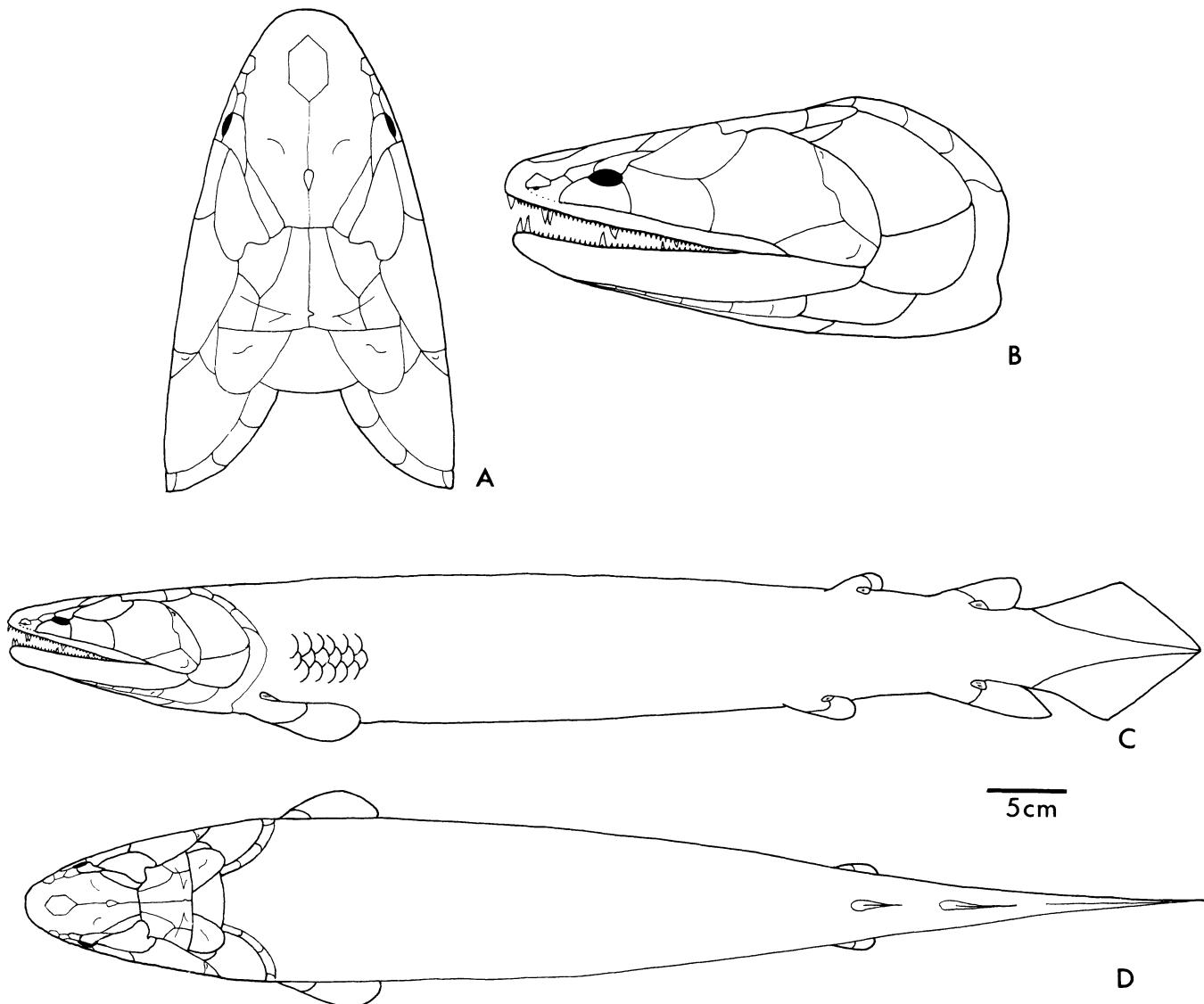


FIGURE 15. *Cabonnichthys burnsi*. Reconstructions. A, B, dorsal and lateral skull. C, D, complete specimen, lateral and dorsal views.

ies among the osteolepiforms. The basic construction is always the same, but there are substantial differences in the shape and position of the processes between *Eusthenopteron*, *Mandageria*, *Cabonnichthys*, *Sterropterygion* and *Beelarongia* (Long, 1987). There are even more striking differences with the humeri of rhizodonts (Andrews and Westoll, 1970b; Long, 1989). These differences in all likelihood reflect variation between genera in the musculature and range of movements of the fin. A few conclusions can be drawn about what these differences might have been; Rackoff (1980) argued that *Sterropterygion* was able to bring its pectoral fin up against the flank with the preaxial edge in a dorsal position, and the bulbous caput humeri of rhizodonts presumably reflects an increased capacity for rotatory movements (Andrews and Westoll, 1970b; Andrews, 1985). The more subtle differences between tristichopterid genera are likely to remain uninterpretable. However, it is interesting simply to note that there *are* differences; they suggest that the pectoral fin was important enough as a locomotory (or maneuvering) organ to be subject to slightly different selection pressures even in closely related forms.

Posterior Fins—The caudal fin of *Cabonnichthys* is homo-

cercal and rhomboidal in outline, not unlike those of *Gyroptychius* and *Glyptopomus*. There is no trace of the three-lobed outline which characterizes *Eusthenopteron* (Andrews and Westoll, 1970a; Jarvik, 1980) and *Tristichopterus* (Egerton, 1861). The presence of independent caudal radials supporting the epichordal and hypochordal lobes is also seen in *Mandageria* (Johanson and Ahlberg, 1997), but in *Eusthenopteron* the epichordal lobe lacks separate radials and is supported by the neural spines. Outgroup comparison with lungfishes and actinopterygians suggests that the latter condition is primitive.

Both *Mandageria* and *Cabonnichthys* differ from *Eusthenopteron* in having proportionately smaller and more posteriorly placed median fins, and tails of a lower aspect ratio (Figs. 15, 16). This probably indicates that they had strong powers of acceleration, but less sustained swimming ability than *Eusthenopteron* (Webb, 1982; Ahlberg, 1992; Belles-Isles, 1992). The relatively smaller caudal fin in *Mandageria* and *Cabonnichthys* as compared to *Eusthenopteron* also suggests these fish were less able swimmers overall. Interestingly, three of the four known sarcopterygians from Canowindra (*Mandageria*, *Cabonnichthys*, and an undescribed rhizodontiform) have postcranial

morphologies which are patently unsuited for sustained swimming. The fourth genus, *Canowindra*, was reconstructed by Thomson (1973) as a more generalised osteolepiform, with a heterocercal tail, and the median fins less strongly bunched at the rear end of the body than in *Mandageria* or *Cabonnichthys*. It may thus have been a more active swimmer. However, some aspects of the reconstruction are conjectural.

PHYLOGENETIC ANALYSIS

Problems

The Tristichopteridae includes seven known genera; *Tristichopterus*, *Eusthenopteron*, *Jarvikina*, *Platycephalichthys*, *Eusthenodon*, *Mandageria* and *Cabonnichthys*. *Spodichthys* and *Hyneria* probably also belong to the group. The Tristichopteridae is conventionally placed within the Osteolepiformes, which is regarded as part of the tetrapod stem group. There is widespread agreement that the Tristichopteridae is a clade (Long, 1985b; Young et al., 1992; Cloutier and Ahlberg, 1996). However, the relationships within the group have only once been assessed cladistically, by Long (1985b), on the basis of three characters. Long's analysis produced the topology [Osteolepididae [Marsdenichthys [Tristichopterus [Eusthenopteron [Eusthenodon + Jarvikina]]]]]]; more recent work suggests that *Marsdenichthys* is not a tristichopterid (see above).

Tristichopterid phylogeny clearly needs to be reexamined. We set about this task by assembling a set of 14 characters, but encountered two significant problems during the data gathering process. The first was strictly practical; several tristichopterid genera (*Tristichopterus*, *Jarvikina*, *Platycephalichthys*, *Spodichthys*, *Hyneria*) are incompletely known or incompletely described. We were able to code most characters for *Tristichopterus* by referring to specimens from the BMNH collections. *Jarvikina* and *Platycephalichthys*, while poorly known in some respects, yield surprisingly good data sets and did not cause problems during the analysis. *Hyneria* and *Spodichthys* proved less tractable, however. *Hyneria* (Thomson, 1968) is so incomplete that it can only be coded for one of our characters (character 11, state (1); see Appendix 1), and we did not include it in our data matrix. *Spodichthys* yielded characters 1–9 and 11, all with state (0); however, because of "spurious apomorphies" generated by PAUP from its unknown characters, its effect in the analysis was always to collapse the *Tristichopterus*—*Eusthenopteron* relationship and increase the number of most parsimonious trees. We therefore removed it from the final data matrix.

The second problem derives from the fact that tristichopterid phylogeny is nested within a larger conundrum, namely the relationships of the Osteolepiformes. The general location of the Osteolepiformes in the tetrapod stem group, much debated following Rosen et al.'s (1981) controversial paper, is now generally accepted (Holmes, 1985; Maisey, 1986; Panchen and Smithson, 1987; Schultze, 1987; Long, 1989; Ahlberg, 1991b; Cloutier and Ahlberg, 1995, 1996). However, it is not clear how the different osteolepiform groups relate to each other, or whether the Osteolepiformes are monophyletic or paraphyletic relative to the Tetrapoda. Young et al. (1992: fig. 47) attempted the first comprehensive cladistic analysis of the Osteolepiformes on the basis of 38 characters. The stem of their cladogram carries four nodes supporting, from top to bottom: the clade Tetrapoda + Elpistostegalia (=Panderichthyidae); a polychotomy comprising the Tristichopteridae (= Eusthenopteridae), Osteolepididae, Megalichthyidae, Vorobyevaia and Thysanolepis; the clade Canowindriidae; and the clade Rhizodontidae. It thus suggests that the Osteolepiformes are paraphyletic.

We are currently gathering data for a re-examination of osteolepiform interrelationships, but are not yet in a position to put forward even a tentative topology. Thus, while the Tristi-

chopteridae is almost certainly a clade, we cannot identify its sister group. This makes it difficult to polarize characters by outgroup comparison, particularly as a number of the characters which vary within the Tristichopteridae also vary between different osteolepiform groups.

In order to examine the extent of this problem, we decided to run the tristichopterid data matrix with three different outgroups:

- 1) Universal (0) score for all characters. Although this outgroup is strictly speaking a hypothetical construct, it is also the result produced by pooling the scores from the osteolepidids *Osteolepis*, *Gyroptychius* and *Medoevia* using outgroup comparison with porolepiforms to eliminate their respective autapomorphies. In other words, the hypothetical outgroup is probably an accurate representation of the primitive character complex for the Osteolepididae.
- 2) The megalichthyid *Cladarosymblema* (Fox et al., 1995). Because *Cladarosymblema* shares certain derived characters with members of the ingroup, this genus was chosen intentionally as an "unsuitable" outgroup to test its impact on tristichopterid topology.
- 3) A pooled megalichthyid matrix incorporating information from *Megalichthys*, *Ectosteorhachis* and *Cladarosymblema*. This differs from the preceding matrix in scoring character 10 as (0) (the condition in *Ectosteorhachis*, judged to be primitive for the Megalichthyidae) and character 14 as (0) (unknown in *Cladarosymblema*).

We performed analyses using PAUP 3.1.1, not only with the individual outgroups, but also with 1 and 2, and 1 and 3, as joint outgroups. The characters are all binary except for character 14 which is an ordered three-state character (see Appendix 2).

Results

Outgroups 1 and 3 always produced the same result, whether used individually or together; the Tristichopteridae emerged as a fully resolved clade with the topology [Tristichopterus [Eusthenopteron [Jarvikina [Platycephalichthys [Cabonnichthys [Eusthenodon + Mandageria]]]]]] (Fig. 16). When outgroup 1 was used, the resulting tree had a length of 16 steps, a Retention Index of 0.958, and a Rescaled Consistency Index of 0.898. Outgroup 2 on its own produced three equally parsimonious topologies. A semi-strict consensus tree shows a basal trichotomy between *Cabonnichthys*, a clade [*Eusthenodon* + *Mandageria*], and a clade [*Platycephalichthys* [Jarvikina [Eusthenopteron + Tristichopterus]]]. When outgroups 1 and 2 were used together, four topologies were produced. Three of these correspond to those produced by outgroup 2 on its own, except that "outgroup 1" turns up in the ingroup as the sister taxon to *Tristichopterus*. The fourth topology has outgroups 1 and 2 as unresolved joint sister groups to the clade [Tristichopterus [Eusthenopteron [Jarvikina [Platycephalichthys [Cabonnichthys [Eusthenodon + Mandageria]]]]]]. A semi-strict consensus tree of these four topologies is wholly unresolved except for the sister group relationship of *Eusthenodon* and *Mandageria*.

The resolution of tristichopterid phylogeny is clearly very sensitive to the choice of outgroup. Nevertheless, we regard the topology shown in Fig. 16 as substantially better supported than its rivals. Firstly, it is the only one which is completely resolved. Secondly, it provides a perfect stratigraphic fit. By contrast, the clade [*Platycephalichthys* [Jarvikina [Eusthenopteron + Tristichopterus]]] which is generated by outgroup 2 is inverse to the stratigraphic sequence of these taxa, and the problem is exacerbated when outgroup 1 is added to the analysis and becomes the sister group of *Tristichopterus* (see above). Thirdly, the topology in Fig. 16 is consistent with a gradually

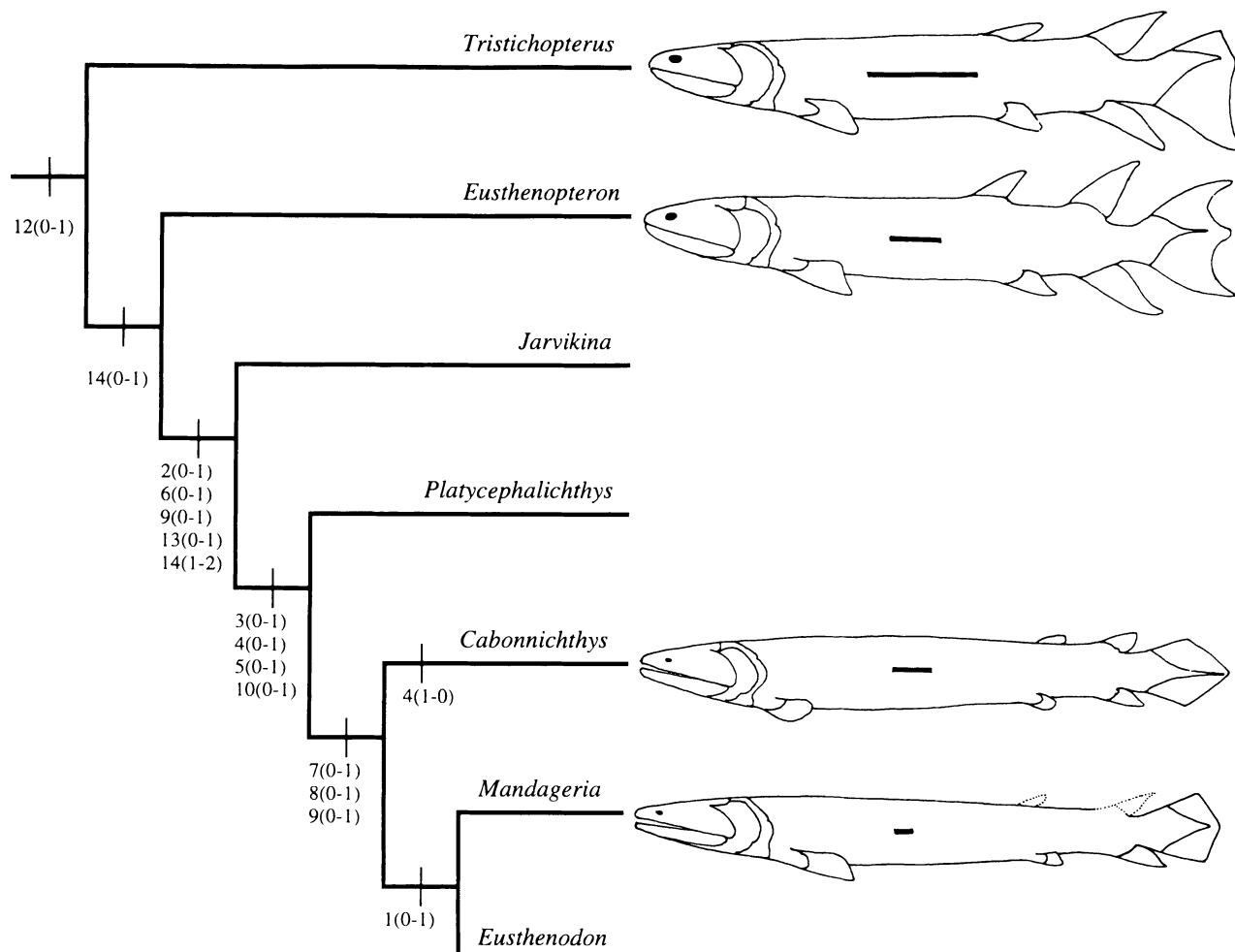


FIGURE 16. Cladogram showing phylogenetic relationships of the Tristichopteridae, with character state distributions mapped on. Scale bar = 5 cm.

lengthening anterior cranial division in the Tristichopteridae. Long (1985b) used this as a multi-state character to resolve the relationships of *Tristichopterus*, *Eusthenopteron*, *Jarvikina* and *Eusthenodon*, and obtained a topology compatible with ours. We thus feel justified in rejecting the topologies generated by outgroup 2, and asserting that the topology [*Tristichopterus* [*Eusthenopteron* [*Jarvikina* [*Platyccephalichthys* [*Cabonnichthys* [*Eusthenodon* + *Mandageria*]]]]]]) is at present the most satisfactory hypothesis of tristichopterid interrelationships. *Spodichthys* is more primitive than *Jarvikina*, and most probably belongs near *Tristichopterus*, whereas *Hyneria* (admittedly on very slender evidence) seems to be at least as derived as *Platyccephalichthys*.

Discussion

A number of inferences can be drawn from this phylogeny. In paleobiogeographical terms, all the more primitive tristichopterids (*Tristichopterus*, *Eusthenopteron*, *Spodichthys*, *Jarvikina*, *Platyccephalichthys*) come from the Laurussian continent. This suggests that the group originated in this region, but that a derived clade within the Tristichopteridae containing *Cabonnichthys*, *Mandageria* and *Eusthenodon* (recently discovered in South Africa, J. A. Long, pers. comm., 1996) achieved a wider distribution including Gondwana. Working from the adequately known tristichopterids, we would be inclined to date

the origin of this derived clade to the late Frasnian or early Famennian. However, this interpretation is thrown into doubt by the presence of an isolated tristichopterid mandible in the *portalenensis* zone of the Aztec Siltstone, Antarctica (Young et al., 1992: fig. 18C). As this mandible carries a large dentary fang pair, it probably represents a genus which is no more primitive than *Platyccephalichthys*; it is thus compatible with the biogeographic pattern outlined above. However, the date of the *portalenensis* zone is probably no later than early Frasnian (Young, 1993), which suggests a considerably earlier dispersal date for the group. It is interesting to note that although *Mandageria* and *Cabonnichthys* are closely related, the sister group of *Mandageria* is the Laurussian genus *Eusthenodon*. This seems to imply that the Gondwana tristichopterids were part of a widely distributed and freely dispersing fauna rather than a geographically isolated radiation.

Morphologically, the Tristichopteridae seems to show quite consistent evolutionary trends. In the first place, there is a striking though not uniform size increase. *Tristichopterus* has a cranial length of up to 7 cm and an overall length of rather less than 40 cm (pers. obs., PEA). In *Eusthenopteron* the corresponding figures are approximately 20 cm and 80 cm (Schultze, 1984). *Jarvikina* is comparable in size to *Eusthenopteron*, but in *Platyccephalichthys* the head must have been nearly 40 cm long (Vorobyeva, 1962). *Cabonnichthys* is again similar to

Eusthenopteron in size, but *Mandageria* is about as large as *Platycephalichthys* (head length 35 cm, overall length 160 cm) and *Eusthenodon* is even larger.

This increase in size correlates with other changes. The anterior cranial division becomes progressively longer (Long, 1985b), while the anterior dentition is augmented first by the appearance of dentary fangs and then by a fang-like tooth on the premaxilla. At the same time, the postcranial morphology is modified. *Tristichopterus* and *Eusthenopteron* both have relatively high aspect-ratio tails with narrow peduncles, and anteriorly placed median fins. The tail is strongly asymmetrical in *Tristichopterus*, less so in *Eusthenopteron*. In *Mandageria* and *Cabonnichthys* the tail is almost completely symmetrical and has a much lower aspect ratio than in the more primitive genera. Furthermore, the median fins are much smaller and positioned closer to the tail. All this suggests a change from a rather active free-swimming mode of life towards an ambush-predator role characterized by acceleration but little sustained swimming (Webb, 1982). The smaller caudal fin in *Mandageria* and *Cabonnichthys*, however, suggests an overall reduced swimming ability. It is worth noting that *Eusthenodon*, which is not known from complete skeletons and has hitherto been reconstructed to resemble *Eusthenopteron* (e.g. Lebedev, 1995), probably looked more like its immediate relatives *Mandageria* and *Cabonnichthys*.

Interestingly, the morphology and dentition of the most derived tristichopterids approaches that of rhizodonts (Andrews, 1985). Our phylogenetic analysis indicates that these similarities are homoplasies, presumably resulting from a similar mode of life.

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APPENDIX 1. Character List.

1. Contact between posterior supraorbital and intertemporal: present (0); absent (1).
2. Shape of posterior supraorbital: posterior process shorter than orbital margin (0); posterior process much longer than orbital margin (1).
3. Relationship of postorbital to orbit: contributes to orbital margin (0); excluded from orbital margin (1).
4. Relationship of jugal to orbit: contributes to orbital margin (0); excluded from orbital margin by lacrimal and posterior supraorbital (1).
5. Shape of pineal series: round or oval (0); kite-shaped with distinct posterior corner (1).
6. Location of pineal series: level with posterior margin of orbits (0); well posterior to orbits (1).
7. Premaxillary dentition: homodont (0); strongly enlarged tooth at anterior end of row (1).
8. Posteromedial process of premaxilla: absent (0); present (1).
9. Posterodorsal process of maxilla: present (0); very weak or absent (1).
10. Marginal coronoid teeth: present on all three coronoids (0); absent on anterior coronoid (1).
11. Dentary fang pair: absent (0); present (1).
12. Postspiracular: absent (0); present (1).
13. Epichordal radials in caudal fin: absent, fin supported by neural spines (0); present (1).
14. Caudal fin shape: strongly asymmetrical (0); slightly asymmetrical (1); symmetrical (2) (ordered three-state character).

APPENDIX 2. Character Matrix.

Taxon	Character													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Tristichopterus</i>	0	0	0	0	0	0	?	?	0	?	0	1	0	0
<i>Eusthenopteron</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	1
<i>Jarvikina</i>	0	1	0	0	0	1	0	0	1	0	0	?	?	?
<i>Platycephalichthys</i>	?	1	1	1	?	1	0	0	1	0	1	?	?	?
<i>Eusthenodon</i>	1	1	1	1	1	1	1	?	1	1	1	1	?	?
<i>Mandageria</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	2
<i>Cabonnichthys</i>	0	1	1	0	1	1	1	1	1	1	1	1	1	2
OG1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
OG2	0	0	0	0	?	?	1	1	0	1	1	0	?	?
OG3	0	0	0	?	?	?	1	1	0	0	1	0	?	0

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