



Taylor & Francis
Taylor & Francis Group

New Information on the Enigmatic Tetrapodomorph Fish *Marsdenichthys longioccipitus* (Long, 1985)

Author(s): Timothy Holland, John Long and Daniel Snitting

Source: *Journal of Vertebrate Paleontology*, Vol. 30, No. 1 (Jan., 2010), pp. 68-77

Published by: [Taylor & Francis, Ltd.](#) on behalf of [The Society of Vertebrate Paleontology](#)

Stable URL: <http://www.jstor.org/stable/20627155>

Accessed: 21-08-2014 18:15 UTC

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at
<http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



The Society of Vertebrate Paleontology and Taylor & Francis, Ltd. are collaborating with JSTOR to digitize, preserve and extend access to *Journal of Vertebrate Paleontology*.

<http://www.jstor.org>

NEW INFORMATION ON THE ENIGMATIC TETRAPODOMORPH FISH *MASDENICHTHYS LONGIOCCIPITUS* (LONG, 1985)

TIMOTHY HOLLAND,^{*1,2} JOHN LONG,^{1,2} and DANIEL SNITTING³

¹School of Geosciences, Monash University, Clayton, Victoria, 3800, Australia, tholland@museum.vic.gov.au;

²Museum Victoria, Melbourne, Victoria 3001, Australia;

³Sub-Department of Evolutionary Organismal Biology, Department of Physiology and Developmental Biology, Uppsala University, Uppsala, Sweden

ABSTRACT—The tetrapodomorph fish *Marsdenichthys longioccipitus* from the Givetian-Frasnian of Mt. Howitt, Victoria, Australia, occupies an uncertain phylogenetic position. *Marsdenichthys* has been linked to the base of the Tristichopteridae, as well as to the poorly known Northern Hemisphere form *Rhizodopsis*, based on the presence of rounded scales bearing a median boss on the internal surface. However, its affinities to these taxa are ambiguous, due to the incomplete preservation of the two *Marsdenichthys* specimens initially described. For the first time, we present significant information regarding the cheek and palate of *Marsdenichthys*, based on the descriptions of two new specimens from Mt. Howitt. New autapomorphies for *Marsdenichthys* are proposed, including the presence of a bar-like maxilla being approximately equal in depth to the dentary, and a rectangular anterior termination of the lacrimal. Several plesiomorphic features are described from the palate, including rounded vomer morphology lacking a posterior process, a relatively short, broad parasphenoid, and a dermopalatine approximately equal in length to the ectopterygoid. No synapomorphies are shared between *Marsdenichthys* and tristichopterids. Scale morphology is redescribed, and shown to exhibit concentric rings on the external surface, as in *Rhizodopsis*. However, differences in skull morphology, such as the lack of an external opening for the pineal foramen in *Rhizodopsis*, suggest that this scale morphology may have evolved independently.

INTRODUCTION

Recent work from the Late Devonian Mt. Howitt fish site of Victoria has significantly increased the record of tetrapodomorph fishes in Australia. The discovery of *Beelarongia patrichae* Long, 1987, contributed to the erection of an endemic Gondwanan group, the Canowindridae, whereas the description of *Howittichthys warrenae* Long and Holland, 2008, encompasses a number of ‘elpistostegid’-like features, including an elongate pectoral fin-lobe, long unbranched basal lepidotrichia, and rhombic-cut, reticulate scales. A third form, *Marsdenichthys longioccipitus* Long, 1985a, was initially described as a “eusthenopterid” (= tristichopterid), a group previously known only from the Northern Hemisphere. Subsequent discoveries of Late Devonian tristichopterids from Australia include *Cabonnichthys* Ahlberg and Johanson, 1997, and *Mandageria* Johanson and Ahlberg, 1997, from the Mandagery Sandstone of Canowindra, New South Wales (NSW), and *Eusthenodon* (Johanson and Ritchie, 2000; Johanson, 2004) from the Hunter Siltstone of Grenfell, NSW.

The phylogenetic position of *Marsdenichthys* is of particular interest, as it was placed at the base of the Tristichopteridae (Cope, 1889) by Long (1985a). Taxa within this group, most notably *Eusthenopteron*, have received extensive study as they are considered as exhibiting intermediate morphology between basal tetrapodomorph fishes and tetrapods (Jarvik, 1980; Clack, 2002). However, the placement of *Marsdenichthys* within the Tristichopteridae was made without reference to any known tristichopterid apomorphies, i.e., postspiracular bones. Long (1985a) proposed that the absence of some derived tristichopterid characters, concerning the size and shape of the parasymphysial dental plate and the direction of the crista parotica, were due to

the incomplete nature of the two *Marsdenichthys* specimens. In addition, several features typical of basal tetrapodomorph morphology were described in *Marsdenichthys*, i.e., the presence of extratemporal bones and the size ratio between parietals and postparietals. In regard to these primitive character states, *Marsdenichthys* was placed as the most basal member of the Tristichopteridae, based on the presence of rounded scales with an internal median boss (Long, 1985a). Long justified this resolution on the assumption that only tristichopterids evolved this character within the ‘Osteolepiformes’, but cautioned that if other ‘osteolepidids’ displayed similar scale morphology, *Marsdenichthys* could be a specialized ‘osteolepidid’. Since that time, both the ‘Osteolepiformes’ and ‘Osteolepididae’ have been shown to be paraphyletic (Ahlberg and Johanson, 1998), with several ‘non-tristichopterid’ former constituents of the ‘Osteolepiformes’ exhibiting rounded scales with a median boss, including *Medovia* Lebedev, 1995 from the Upper Famennian of Russia, the canowindrid *Canowindra* Thomson, 1973, from the Famennian of NSW, Australia, and *Rhizodopsis* from the Carboniferous of Illinois, USA (Schultze, 1974), Ireland (Andrews and Westoll, 1970; Wyse Jackson and Monaghan, 1995), England (Williamson, 1837), Spain (Iwaniw, 1984), Silesia (Roemer, 1865), France (Leriche, 1908), Belgium (Cloutier and Caudillier, 1995), Russia (Vorobyeva and Obruchev, 1964) and the Lower Permian SW-Germany (Schultze and Heidtke, 1986). Long (1999) tentatively placed *Marsdenichthys* within the ill-defined group, the Rhizodopsidae (Berg, 1940), based on similar scale ornamentation. To compound the matter, Coates and Friedman (in press) place *Rhizodopsis* within a clade comprising members of the Megalichthyidae, based on characters such as the closure of the vestibular fontanelles and the pineal foramen and the presence of ring centra. *Marsdenichthys* has been excluded from most major phylogenetic analyses involving the Tetrapodomorpha (e.g. Johanson and Ahlberg, 1997; Johanson, 2004), with the taxon

*Corresponding author.

only included within Cloutier and Ahlberg (1995), in a clade with *Eusthenopteron* (inside a monophyletic ‘Osteolepiformes’); Long et al. (2006), in a polytomy with *Eusthenopteron*, basal to *Megalichthys*; and Holland and Long (2009) in a polytomy with *Megalichthys*, basal to *Medoëvia* and *Gogonasus*.

This paper describes two new specimens of *Marsdenichthys* from Mt. Howitt, Victoria. The specimens include previously undescribed elements from *Marsdenichthys*, including regions of the snout, cheek, and palate. This new information will aid future phylogenetic analyses of *Marsdenichthys* within the Tetrapodomorpha.

Institutional Abbreviations—NMV, Museum Victoria, Melbourne; AMF, Australian Museum.

Anatomical Abbreviations—**a.** so, anterior supraorbital; **a.** te, anterior tectal; **ana.** fin, anal fin; **ano**, anocleithrum; **ant**, anterior; **bos**, median boss; **cl**, clavicle; **clth**, cleithrum; **cor**, coronoid; **de**, dentary; **dor.** fin, dorsal fin; **dpt**, dermopalatine; **ect**, ectopterygoid; **ent**, entopterygoid; **esc**, exposed part of external scale surface; **ex.** con, concentric lines on the exposed external scale surface; **ext**, extratemporal; **f.** cor, coronoid fang; **f.** dpt, dermopalatine fang; **f.** ect, ectopterygoid fang; **f.** vom, vomerine fang; **gul**, gular; **id**, infradentaries one-four; **in.** con, concentric lines on the internal scale surface; **it**, intertemporal; **ju**, jugal; **la**, lacrimal; **l.** ex, lateral extrascapular; **l.** ro, lateral rostral; **m.** ex, median extrascapular; **m.** po. ro, median post rostral; **mx**, maxilla; **na**, nasal; **nar**, naris; **op**, opercular; **orb**, orbit; **osc**, overlapped part of external scale surface; **p.** so, posterior supraorbital; **p.** te, posterior tectal; **pa**, parietal; **pect.** fin, pectoral fin; **pelv.** fin, pelvic fin; **pit**, pit-line; **pmx**, premaxilla; **po**, postorbital; **pop**, preopercular; **pos**, posterior; **pot**, posttemporal; **pp**, postparietal; **pr.** ar, prearticular; **ssp**, parasphenoid; **qj**, quadratojugal; **rid**, ridge on entopterygoid; **sop**, subopercular; **sq**, squamosal; **st**, supratemporal; **suc**, supraclieithrum; **tab**, tabular; **vom**, vomer.

MATERIALS AND METHODS

All known material of *Marsdenichthys* was collected by Jim Warren and field party (1970–1971), with Long (1985a) describing the taxon based on two specimens. Long later uncovered two undescribed specimens amongst the collections of Museum Victoria, consisting of a complete skull and palate. Both specimens were found from lower mudstone outcrops along the Howqua River track, at the base of Mt. Howitt, Victoria (Fig. 1). Specimens were prepared in 15 to 20 diluted HCl solution for 24 hours to dissolve bone from the matrix. Additional bone was

removed with a mounted carbide needle. Specimens were cast with black latex and coated with ammonium chloride sublimate. Photographs of the specimens were undertaken with a Panasonic Lumix DMC-FZ20 camera and a Canon EOS 5D with a 65-mm macro lens, with drawings produced based on the photographs. Terminology for describing general morphology will follow Ahlberg and Johanson (1997), whereas scale morphology follows Andrews (1985).

SYSTEMATIC PALEONTOLOGY

SARCOPTERYGII Romer, 1955
TETRAPODOMORPHA Ahlberg, 1991
MASDENICHTHYS LONGIOCIPITUS Long, 1985a

Type Horizon—Avon River Group (Cas et al., 2003).

Age—Givetian–Frasnian (Cas et al., 2003).

Referred Material—NMV P160871, partially complete skull, palatoquadrate, pectoral girdle elements, and indeterminate fins (holotype); AMF65494, poorly preserved skull; NMV P179619, near complete skull; NMV P186572, palatal elements and pectoral girdle and fin.

Revised Diagnosis—*Marsdenichthys* can be differentiated from all other basal tetrapodomorph fishes by the presence of a bar-like maxilla, being approximately equal in depth to the dentary, and a rectangular anterior termination of the lacrimal. In addition, *Marsdenichthys* differs from all tetrapodomorph fishes that possess scales with a central boss (except *Rhizodopsis*) by exhibiting parallel ridges on the exposed external surface of the scale that are intersected by concentric rings, and by the presence of both round and rhombic scales. *Marsdenichthys* differs from tristichopterids by the lack of postspiracular bones; a short parietal shield length relative to postparietal shield; a relatively short snout; short denticulate field on the parasphenoid; and a dermopalatine of near equal length to the ectopterygoid. *Marsdenichthys* additionally differs from *Rhizodopsis* by possessing an external opening for the pineal foramen and unfused semicircular vertebrae.

Comments—Long (1985a) noted two distinct size differences in the material (two almost complete skulls) assigned to *Marsdenichthys*, with the holotype (NMV P160871) estimated to reach approximately 25 cm in length and AMF 65494 measuring over 100 cm. Long (1985a) regarded this difference in size as a result of ontogeny, with the juvenile form representing the holotype. The two new specimens of *Marsdenichthys* are of similar size to the holotype, and do not permit a further opportunity to assess a possible growth series. Comparisons between *Marsdenichthys* and *Rhizodopsis* should be regarded with caution, due to the few available specimens of both genera.

New data concerning the shape of the maxilla and the lacrimal comes from one side of the flattened specimen NMV P179619. Although the relation of these bones has been splayed out relative to the skull roof during preservation, there is nothing to suggest that they have been crushed or highly distorted.

DESCRIPTION: NEW MATERIAL OF *MASDENICHTHYS*

The description of NMV P179619 and NMV P186572 will consist of previously unknown morphological characters (Long, 1985a). The scales of *Marsdenichthys* will be redescribed in order to further differentiate scale morphology from other tetrapodomorph fish taxa.

Premaxilla and Maxilla—The premaxilla (Figs. 2, 3) of *Marsdenichthys* compares well with that of other tetrapodomorph fishes, in being anteriorly deep and having a posterior process that extends ventral to the lateral rostral and anterior tectal to contact the maxilla. The dorsal margin of the premaxilla contacts the first bone in the tectal series and the lateral rostral. It is

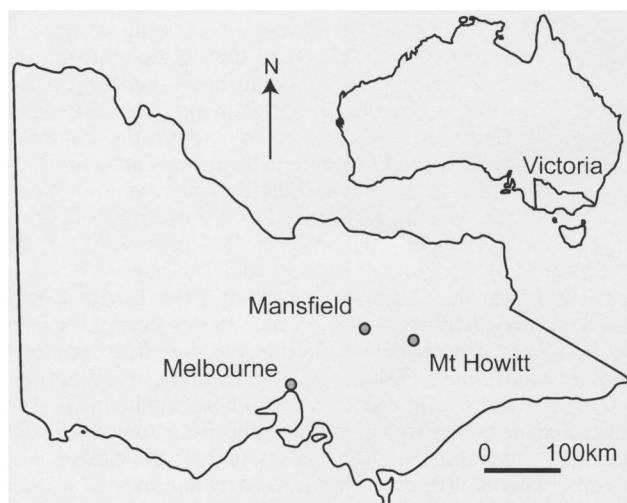


FIGURE 1. Position of Mt. Howitt fossil site, Victoria, Australia. Shaded area represents the Alpine National Park.

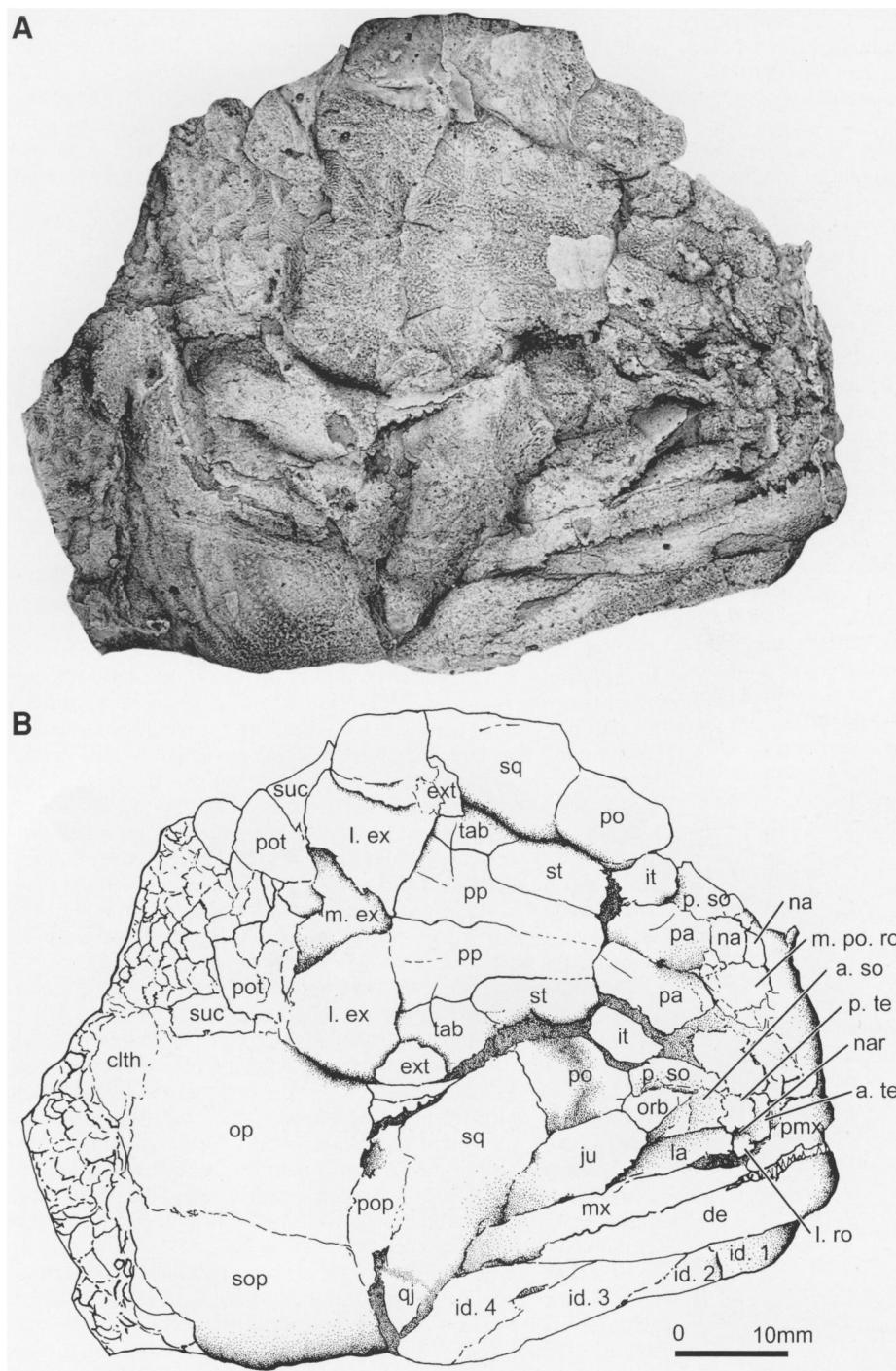


FIGURE 2. Skull of *Marsdenichthys longicippitus* NMV P179619. A, photograph of specimen; B, interpretive drawing of specimen.

difficult to discern the presence of a premaxillary pseudofang, although several marginal teeth are observable.

The maxilla (Figs. 2, 3) is long and bar-like, being equal in depth to the dentary. It tapers slightly towards its anterior, but not to the extent in *Megalichthys* (Miall, 1885), *Rhizodopsis* (Traquair, 1881), *Eusthenopteron* (Jarvik, 1980), and *Osteolepis* (Jarvik, 1950a). The posterior border of the maxilla is diagonal, as opposed to the markedly convex posterior border on the maxilla of *Latvius* (Jessen, 1973). Several marginal teeth are present.

Lacrimal and Jugal—The lacrimal (Figs. 2, 3) is elongate, being longer than deep. The dorsal margin is sunken inside the orbit, most likely during postmortem depression. There is an abrupt, rectangular termination at the anterior border of the bone, where the lacrimal abuts the lateral rostral and the

Jugal—The jugal (Figs. 2, 3) is elongate, being longer than deep. The dorsal margin is sunken inside the orbit, most likely during postmortem depression. There is an abrupt, rectangular termination at the anterior border of the bone, where the lacrimal abuts the lateral rostral and the

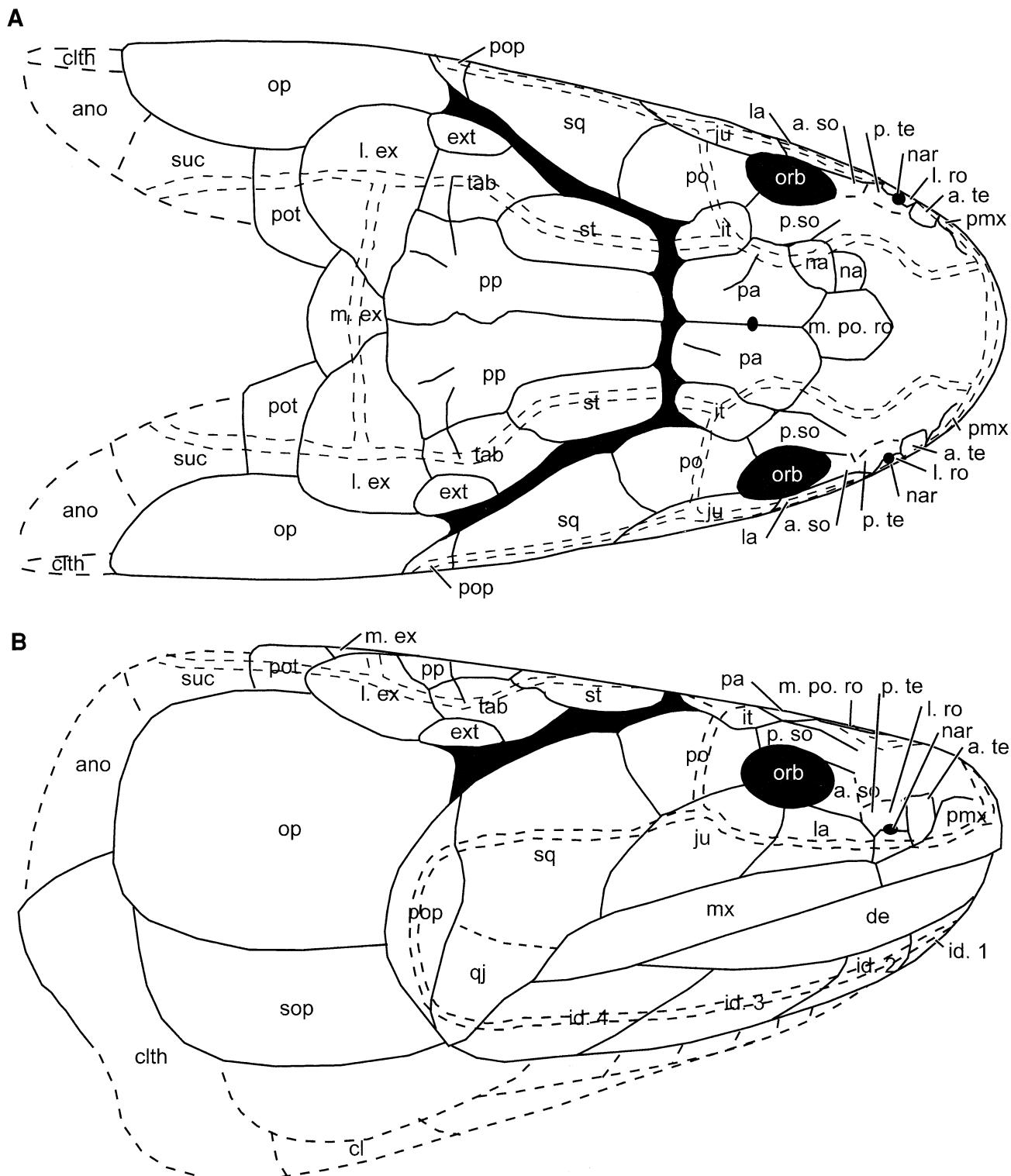


FIGURE 3. Reconstruction of *Marsdenichthys longioccipitus*. **A**, dorsal view; **B**, right lateral view. Broken lines represent unknown skeletal morphology.

posterior tectal. This is in contrast to the condition in other tetrapodomorph fishes, where there is a gradual, dorsoventrally directed slope delineating the anterior margin of the lacrimal. A dorsoventrally directed diagonal border is present between the anterior portion of the jugal and the lacrimal, sim-

ilar to the condition in *Glyptopomus* (Jarvik, 1950b) and the canowindrids *Canowindra* (Long, 1985b) and *Beelarongia* (Long, 1987).

The jugal (Figs. 2, 3) is sub-rectangular and approximately the same length as the lacrimal, but deeper. It is bordered

posteroventrally by the squamosal. The anterior border contributes to the margin of the orbit, unlike the condition in *Mandageria* (Johanson and Ahlberg, 1997) and *Eusthenodon* Jarvik, 1952, where the jugal is excluded from the orbit.

Postorbital—Although the right postorbital (Figs. 2, 3) is badly crushed, the left postorbital is well preserved. It is shorter and deeper than the jugal, but tapers anteriorly where it contacts the posterior supraorbital (dorsally) and orbit (ventrally) along their posterior margins.

Squamosal and Preopercular—The squamosal (Figs. 2, 3) is a relatively large bone, appearing equal in length to the jugal and postorbital. Although the suture between the squamosal and quadratojugal is not discernable, the ventral margin of the squamosal appears to contact the posteroventral margin of the maxilla. The posterior border of the squamosal is concave where it abuts the preopercular.

The preopercular (Figs. 2, 3) is bar-like and is approximately one-third the size of the squamosal, which it contacts anteriorly. Slight contact is made between the ventral margin of the preopercular and the dorsal margin of the quadratojugal.

Quadratojugal—The quadratojugal (Figs. 2, 3) of NMV P179619 is badly crushed, giving the impression of a subtriangular and relatively small element. This appearance is likely an artefact when compared to the well-preserved quadratojugal of NMV P160871, which is a relatively large and clearly abuts the maxilla posteriorly.

Nasals, Tectals, and Rostrals—Although elements from the snout were previously described in AMF 65494, the new specimen NMV P179619 allows accurate description of the nasal, tectal and rostral bones of *Marsdenichthys* for the first time.

The median postrostral (Figs. 2, 3) is large and near-hexagonal in shape, with a pointed posterior margin that protrudes between the anterior margins of the parietals. Preserved to the left side of the median postrostral are a posterior nasal and a nasal bone (Figs. 3, 4). The anterior nasal is approximately half the size of the posterior nasal, which it contacts posteriorly. Both are subcircular in shape.

The anterior tectal bone (Figs. 2, 3) is present behind the premaxilla. It is small and rectangular, contacting the anterior border of the lateral rostral ventrally and the posterior tectal dorsally. This posterior tectal (Figs. 2, 3) is square and dorsally borders the naris. It is approximately equal in size to the anterior tectal.

The lateral rostral (Figs. 2, 3) is small, and roughly square in dimension, as in *Latvius* (Jessen, 1973), *Mandageria* (Johanson and Ahlberg, 1997), and *Gogonasus* (Long et al., 1997), with a horizontal suture between it and the dorsally positioned posterior tectal including the external naris. There is no secondary lateral rostral, which is present in *Mandageria* (Johanson and Ahlberg, 1997).

Supraorbitals—The anterior supraorbital (Figs. 2, 3) is roughly square and is the smallest bone bordering the orbit (Figs. 3, 4). This is in contrast to *Cladaro-symblerma* (Fox et al., 1995) and *Glyptopomus* (Jarvik, 1950b), which exhibit larger anterior suborbitals than posterior suborbitals.

The shape of the posterior supraorbital (Figs. 2, 3) is difficult to determine, with the left posterior supraorbital sunk within the orbit, whereas the right posterior supraorbital is incomplete. It is longer than the orbit, and varies in depth, being narrow anteriorly and increasing in width where mesial contact is made with the parietal, as in *Eusthenodon* (Jarvik, 1952).

Palate—The palate of *Marsdenichthys* is only preserved in two specimens, NMV P186572 and NMV P160871, although only an incomplete palatoquadrate is preserved in the latter. A parasphenoid, vomers, dermopalatine, ectopterygoid, and a complete palatoquadrate are described for the first time in NMV P186572 (Fig. 4).

In overall morphology, the palate of *Marsdenichthys* closely resembles that of other basal tetrapodomorph fishes. The para-

phenoid (Fig. 4) is relatively short and broad compared to those of tristichopterids (e.g., Jarvik, 1980), exhibits a heavily denticulate region that tapers towards the anterior end, and does not extend beyond the anterior border of the palatoquadrate, as in *Medoevia* (Lebedev, 1995) and *Gogonasus* (Long et al., 1997). This condition is distinct from that of *Eusthenopteron* (Jarvik, 1954), where the parasphenoid is elongate and narrow, exhibiting a pointed denticulate field extending beyond the anterior margin of the palatoquadrate. The surface of the denticulate field in *Marsdenichthys* is slightly concave, as opposed to the convex surface in *Mandageria* and *Jarvikina* (Johanson and Ahlberg, 1997). No accessory vomers are preserved alongside the lateral margin of the parasphenoid, in contrast to *Mandageria* (Johanson and Ahlberg, 1997) and *Cabonichthys* (Ahlberg and Johanson, 1997).

Both vomers (Fig. 4) are preserved, with the right being displaced. They are oval, and lack the long posterior process found on the vomers of *Eusthenodon* (Jarvik, 1952), *Eusthenopteron* (Jarvik, 1980) and *Mandageria* (Johanson and Ahlberg, 1997). A fang is present on each bone, with smaller marginal dentition present on the left vomer.

Both the right dermopalatine and ectopterygoid (Fig. 4) are present in articulation, with the left being unpresevered. Both elements are sub-rectangular, with the ectopterygoid tapering posteriorly. Both are several times greater in length than in width, as opposed to the condition in *Eusthenodon* (Jarvik, 1952), which displays a relatively broad dermopalatine and ectopterygoid. In *Marsdenichthys*, the length of the dermopalatine is slightly less than that of the ectopterygoid, as in *Glyptopomus* (Jarvik, 1950a), *Gyroptychius* (Vorobyeva, 1977), *Medoevia* (Lebedev, 1995), *Gogonasus* (Long et al., 1997), and *Eusthenodon* (Jarvik, 1952). In some tristichopterid taxa, such as *Eusthenopteron* (Jarvik, 1980) and *Mandageria* (Johanson and Ahlberg, 1997), the length of the ectopterygoid far exceeds that of the dermopalatine. The combined length of the dermopalatine and ectopterygoid is under half that of the palatoquadrate complex, as in *Gogonasus* (Long et al., 1997), whereas in *Eusthenopteron* (Jarvik, 1980) and *Mandageria* (Johanson and Ahlberg, 1997), the combined length of the dermopalatine and ectopterygoid is over half that of the palatoquadrate complex. The dermopalatine exhibits one large set of fangs, and several small labial teeth towards the anterior of the bone. This is in contrast to *Eusthenodon* and *Mandageria*, which lack marginal teeth anterior to the dermopalatine fang (Clément, 2002). The ectopterygoid displays one large set of fangs anteriorly, and possibly a second smaller set approaching the posterior. However, it is difficult to tell with certainty if the posterior fang position is situated mesial to the marginal tooth row of the ectopterygoid, or if it is in fact an enlarged tooth in the marginal tooth row. Two pairs of ectopterygoid fangs are present in tristichopterids such as *Eusthenopteron* (Jarvik, 1980) and *Notorhizodon* Young et al. (1992) and the rhizodontid *Barameda* Long, 1989, whereas single fang pair are typical of the ectopterygoids of 'osteolepidids' (e.g., Long et al., 1997). The anterior ectopterygoid fangs are bordered labially by a row of marginal teeth, approximately half the size of the possible posterior ectopterygoid fang set. A number of denticles cover the raised lingual surface of the ectopterygoid.

The outline of the entopterygoid (Fig. 4) is typical of those in tetrapodomorph fishes. A denticle field is present towards the anterior, to become almost absent towards the posterior. The posteromesial surface of the entopterygoid is concave, whereas an anteroposteriorly directed ridge is present near the lingual border of the entopterygoid. A region of smooth bone is present lateral to this ridge, which borders the margin of the adductor fossa. The quadrate articulation and the adductor fossa are partially obscured by a displaced overlying gular (Fig. 4).

Mandible—Both new specimens of *Marsdenichthys* are preserved with right mandibular elements, with NMV P179619

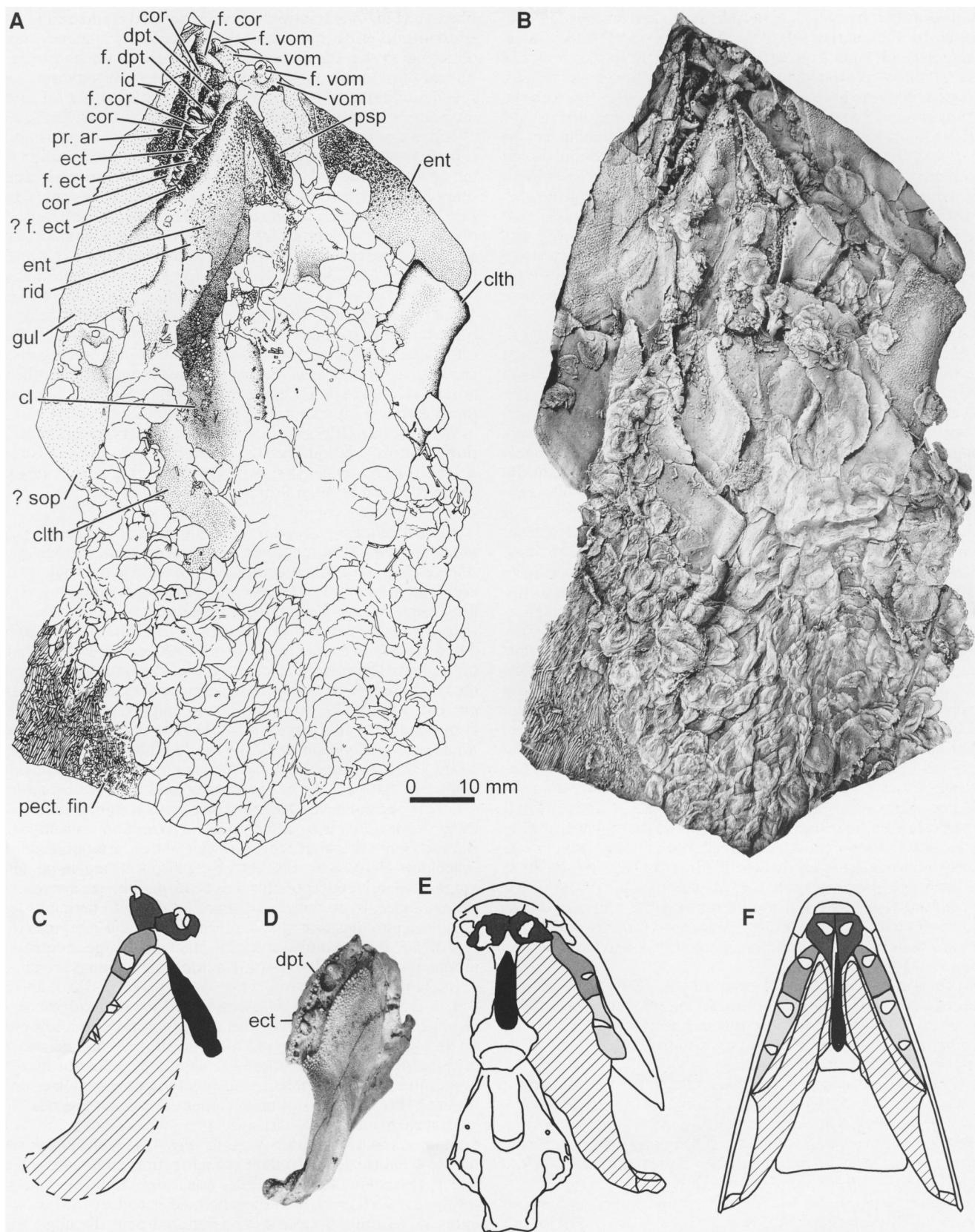


FIGURE 4. Palates of tetrapodomorph fishes. **A**, interpretive drawing of *Marsdenichthys longioccipitus* NMV P186572; **B**, photograph of NMV P186572; **C**, palatal bones of NMV P186572; **D**, palatoquadrate complex of *Gogonasus* specimen NMV P221807; **E**, reconstruction of the palate and endocranum of *Gogonasus* (modified from Long et al., 1997); **F**, reconstruction of the palate and endocranum of *Eusthenopteron* (modified from Jarvik, 1980). Black = parasphenoid; dark grey = vomer; grey = dermopalatine; light grey = ectopterygoid; diagonal lines = entopterygoid and palatoquadrate. Reconstructions not to scale.

including a dentary (Figs. 2, 3) and four infradentaries (Figs. 2, 3) in labial view and NMV P186572 preserving infradentaries, three coronoids, and a prearticular (Fig. 4) in lingual view. In NMV P179619, the position of the first infradentary is slightly displaced, with the anterior end terminating abruptly before the front of dentary. Numerous marginal teeth are preserved.

In NMV P186572, three large fang-bearing elements can be interpreted as coronoids. The length of each coronoid is approximately the same. Each coronoid exhibits a large straight fang, with the second and third coronoids exhibiting a replacement fang in close association. The size of the first coronoid fang is roughly equal to the dermopalatine fang, with the second and third coronoids displaying smaller fangs. A number of small marginal teeth are present on all coronoids, as in *Medoevia* (Lebedev, 1995), *Gogoniasus* (Long et al., 1997), *Cladarosymblesma* (Fox et al., 1995), and *Eusthenopteron* (Jarvik, 1980). An elongate and thin bone, the prearticular, is preserved ventral to the coronoids. The anterior region is level with that of the first coronoid fang, with the surface becoming denticulate adjacent to the suture between the first and second coronoid.

Pectoral Girdle—In general morphology, the pectoral girdle of *Marsdenichthys* compares well with that of other tetrapodomorph fishes. Although the clavicle, cleithrum, anocleithrum, supracleithrum, and posttemporal were previously described by Long (1985a), NMV P186572 allows further description of the cleithrum and clavicle. The cleithrum (Figs. 2–4) is broad dorsally and tapers slightly towards the ventral region, although most of this area is obscured by overlying bone. A single clavicle (Figs. 3, 4) may be preserved and is disarticulated from the skeleton. It exhibits a broad ventral blade with a deep concave surface.

Pectoral Fin—A partially preserved pectoral fin (Fig. 4) is present in NMV P186572, with the marginal lepidotrichia fringe being incomplete. The fin element previously described from the holotype, NMV P160871 (Long, 1985a), cannot be verified as a pectoral fin. It is closely associated with a smaller fin element that was excluded from the original description of *Marsdenichthys* (Long, 1985a). It is more parsimonious to regard these elements as either dorsal fins or alternatively as pelvic and anal fins (Fig. 5).

Scales—The scales of *Marsdenichthys* were originally described as round to ovoid and lacking cosmine, comparable to the scales of tristichopterids and rhizodontids (Long, 1985a). New observations from previously described specimen NMV P160871 (Fig. 6A) and new material (Fig. 6B–E), including both circular/oval and rhomboid scales, differentiate the scales of *Marsdenichthys* from tristichopterids and rhizodontids, as well as the rounded scales of *Medoevia* (Lebedev, 1995) and *Canowindra* (Thomson, 1973).

In gross morphology, the scales of *Marsdenichthys* closely resemble those of *Rhizodopsis* (Schultze and Heidtke, 1986).

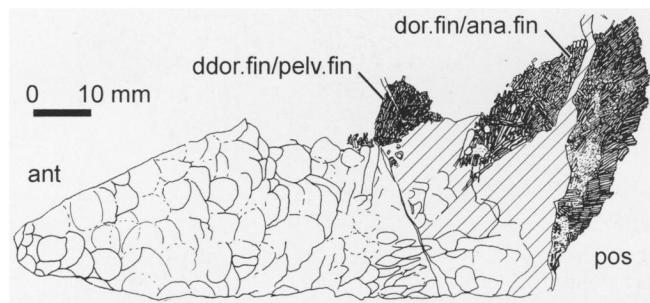


FIGURE 5. Drawing of fin lobes from *Marsdenichthys longioccipitus* NMV P160871. Obscured regions represented by dotted and diagonal lines.

Numerous rounded scales are present on the dorsal and lateral surfaces of the body, whereas rhombic scales are present posterior to the operculogular region. Body scales are large, whereas the scales of the fin lobes are generally narrower and rhombic/rounded (Fig. 6C), similar to those seen in *Rhizodopsis* (Schultze, 1974:fig. 5; Schultze and Heidtke, 1986:figs. 1–2).

The internal scale surface displays concentric growth rings (Fig. 6D), which are generally larger but less conspicuous than the concentric lines of the external surface. A prominent tear-shaped median boss marks the internal surface (Fig. 6D), as in tristichopterids (e.g., Young et al., 1992), rhizodontids (e.g., Andrews, 1985), *Medoevia* (Lebedev, 1995), *Canowindra* (Thomson, 1973), and *Rhizodopsis* (Williamson, 1837; Schultze and Heidtke, 1986:fig. 3b). The exposed region on the external surface (Fig. 5E) of the scale is ornamented with approximately 40 to 50 very fine, parallel straight ridges, which emanate from the center of the scale and terminate posteriorly. These ridges are intersected by between five to seven larger concentric lines (Fig. 6E) and the anterior overlap region of the external surface (Fig. 6E) is marked with fine parallel anteroposteriorly directed, broken lines. These features are also observed in *Rhizodopsis* (Fig. 6F), but absent from tristichopterids and rhizodontids.

DISCUSSION

A phylogenetic analysis of the position of *Marsdenichthys* will not be presented here, but will be published later after character states defining tristichopterids have been further clarified. However, the affinities of *Marsdenichthys* to other tetrapodomorph fish groups will still be briefly summarized.

Johanson and Ahlberg (1997) defined the Tristichopteridae by the possession of postspiracular bones. Other characters shared throughout tristichopterids, but known from other tetrapodomorph fishes, include vomers with a long posterior process that suture to the lateral sides of the parasphenoid, a long ethmosphenoid block, trifurcate tail (all known from *Gyroptychius* and ‘elpistostegid’ fishes: Jarvik, 1948; Vorobyeva, 1977, 1992; Ahlberg et al., 1996), and rounded scales bearing a median boss on the inner surface and absence of cosmine (Ahlberg and Johanson 1997; Johanson and Ahlberg, 1997). Australian tristichopterids such as *Mandageria*, *Cabonichthys* and a form from the Worange Point Formation assignable to *Eusthenodon* (Johanson and Ahlberg, 1997; Ahlberg et al., 2001) are also characterized by the presence of accessory vomers positioned laterally to the parasphenoid. Of these characters, only scale morphology and the absence of cosmine are shared in *Marsdenichthys*. Based on this assessment, it would appear as though the phylogenetic position of *Marsdenichthys* is outside the Tristichopteridae.

The concentric rings intersecting the parallel ridges on the exposed external surface of the scales strongly resemble those of *Rhizodopsis*. However, the phylogenetic relationship of *Rhizodopsis* is poorly understood amongst tetrapodomorph fishes. The only other members previously assigned to the Rhizodontidae include *Callistiopterus clappi* Romer, 1942, a taxon described from a fragmentary juvenile specimen “whose adult form is hypothetical” (Andrews and Westoll, 1970) and *Taeniolepis trautseholdi* Chabakov, 1927, which is known from isolated teeth and scales (Lebedev, 1996). There has never been a detailed modern systematic description and diagnosis published for *Rhizodopsis*, although partially complete skull material (e.g., Traquair, 1881; Säve-Söderbergh, 1936) and complete postcranial skeletons, including pectoral fin elements (e.g., Andrews and Westoll, 1970), are known. Several species have been described based on juvenile specimens (Schultze and Heidtke, 1986, 1993) and isolated scales (e.g., Woodward, 1891; Obruchev, 1955). It is unclear in early depictions of *Rhizodopsis* scales whether internal or

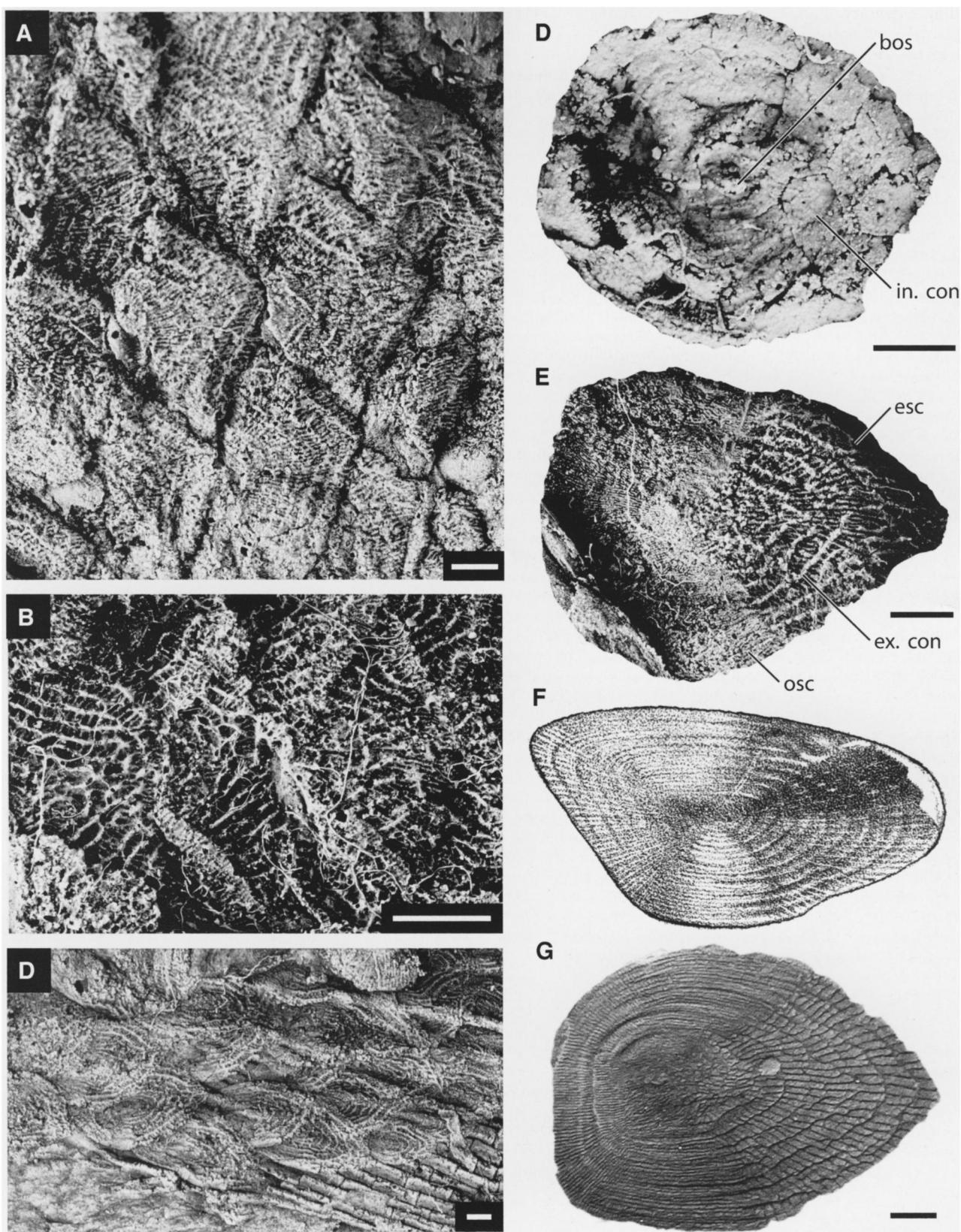


FIGURE 6. Scales of tetrapodomorph fishes. A–E, Scales of *Marsdenichthys longioccipitus*; A, specimen NMV P160871 (holotype) exhibiting rhombic scales on the ventral side of the body; B, specimen NMV P179619 exhibiting rounded scales posterior to extrascapular series; C, specimen NMV P186572 exhibiting narrow rhombic/rounded scales on the pectoral fin lobe; D, isolated scale from NMV P186572 in external view; E, isolated scales from NMV P186572 in internal view; F, isolated scale of *Rhizodopsis* in external view (reproduced from Woodward, 1891); G, cosmine absent scale of cf. *Megalichthys* NMV P203982 in Carboniferous shale from Rothwaltersdorf near Glatz in Schlesien, Germany. Scale bars equal 1 mm.

external scale morphology is shown (i.e., Williamson, 1837; Young, 1866). Despite the need for an extensive revision of the Rhizodopsidae, *Rhizodopsis* has been included within the phylogenetic analysis of Friedman et al. (2007) and Coates and Friedman (in press), with both studies placing the taxon in a clade containing the megalichthyids. However, several possible megalichthyid synapomorphies proposed by Young et al. (1992), such as the enclosure of the nares anteriorly by the lateral rostral and posteriorly by the anterior tectal, are unknown from *Rhizodopsis*, because the bones surrounding the external nostrils have not been described (e.g., Traquair, 1881; Thomson and Hahn, 1968). Other shared features between *Rhizodopsis* and megalichthyids, such as the presence of fused ring centra, are also present in some specimens of *Thursius* (Andrews and Westoll, 1970) (although absent from *Marsdenichthys*). We recommend further study to establish synapomorphies pertaining to *Rhizodopsis* that could clarify any possible relationship between the Rhizodopsidae and the Megalichthyidae. It is worth noting that cosmine-deficient specimens of *Megalichthys* (Fig. 6G) have been misidentified as *Rhizodopsis*, with Andrews and Westoll (1970) noting the two taxa are distinguishable by the presence of the central median boss on the inner surface of the scale in *Rhizodopsis*. Examples of *Megalichthys* specimens showing cosmine-deficient scales with concentric rings on the external surface include NHM P386 and NHM P6607. Jarvik (1948:26) also notes that several typically cosmine-covered tetrapodomorph fish taxa from the Devonian (*Osteolepis*, *Thursius*, and *Gyroptychius*) are occasionally preserved with ornamented scales when "...the superficial enamel and dentine layers are absent, disclosing the external face of the trabecular layer." Concentric rings have also been reported from the basal layer of the scales from *Gyroptychius* (Jarvik, 1948). Both Westoll (1936) and Jarvik (1948) caution the use of such scale morphology in establishing the phylogenetic relationships of tetrapodomorph fishes. Such assertions should also be considered when regarding the similarities between the scales of *Rhizodopsis* and *Marsdenichthys*.

Records of *Marsdenichthys*-like scales from other Devonian fossil sites within Australia are sparse. Rounded scales bearing a median boss are attributed to *Marsdenichthys* from the Upper Devonian sediments of the Blue Hills, Taggerty Victoria (NMV P186564), but lack the concentric lines on the exposed region on the external surface, and thus should be regarded as Tetrapodomorpha incertae sedis. Scales collected from the Givetian sediments along the Pambula River, NSW, have been listed as cf. *Marsdenichthys* (Young, 1993), although there seems to be some confusion regarding their exact morphology (Young, 2007). We therefore reject all current records of *Marsdenichthys* outside of Mt. Howitt, Victoria, until further study is undertaken.

ACKNOWLEDGMENTS

We would like to thank Lucinda Gibson (Museum Victoria) and Erich Fitzgerald (Museum Victoria, Monash University, Clayton) for their help with photography. For various support, we would also like to thank Martin Brazeau (Uppsala University, Sweden), Anne Warren (La Trobe University, Bundoora), Gavin Young (Australian National University, Canberra), and Patricia Vickers-Rich (Monash University, Clayton). Tim Holland is supported by a Monash University Dean's Postgraduate Scholarship.

LITERATURE CITED

- Ahlberg, P. E. 1991. A re-examination of sarcopterygian interrelationships, with special reference to the Porolepiformes. *Zoological Journal of the Linnean Society* 103:241–287.
- Ahlberg, P. E., and Z. Johanson. 1997. Second Tristichopterid (Sarcopterygii, Osteolepiformes) from the Upper Devonian of Canowindra, New South Wales, Australia. *Journal of Vertebrate Paleontology* 17:653–673.
- Ahlberg, P. E., and Z. Johanson. 1998. Osteolepiforms and the ancestry of tetrapods. *Nature* 395:792–794.
- Ahlberg, P. E., J. A. Clack, and E. Lukševič. 1996. Rapid braincase evolution between *Panderichthys* and the earliest tetrapods. *Nature* 381:61–64.
- Ahlberg, P. E., Z. Johanson, and E. B. Daeschler. 2001. The Late Devonian lungfish *Soederberghia* (Sarcopterygii, Dipnoi) from Australia and North America, and its biogeographical implications. *Journal of Vertebrate Paleontology* 21:1–12.
- Andrews, S. M. 1985. Rhizodont crossopterygian fish from the Dinantian of Foulden, Berwickshire, Scotland, with a re-evaluation of this group. *Transactions of the Royal Society of Edinburgh, Earth Sciences* 76:67–95.
- Andrews, S. M., and T. S. Westoll. 1970. The postcranial skeleton of rhipidistian fishes excluding *Eusthenopteron*. *Transactions of the Royal Society of Edinburgh* 68:391–489.
- Berg, L. S. 1940. A Classification of Fishes, both living and fossil. *Trudy Zoologicheskogo Instituta* 5:85–517.
- Cas, R. A. F., G. J. O'Halloran, J. A. Long, and A. H. M. Vandenberg. 2003. Middle Devonian to Carboniferous; pp. 157–194 in W. D. Birch (ed.), *Geology of Victoria*. Special Publication of the Geological Society of Australia.
- Chabakov, A. W. 1927. On the remains of the crossopterygians of the Carboniferous of Russia. *Izvestiya Geologicheskogo Komiteta* 46:299–309.
- Clack, J. A. 2002. Patterns and processes in the early evolution of the tetrapod ear. *Journal of Neurobiology* 53:251–264.
- Clément, G. 2002. Large Tristichopteridae (Sarcopterygii, Tetrapodomorpha) from the Late Famennian Evieux Formation of Belgium. *Palaeontology* 45:577–593.
- Cloutier, R., and P. E. Ahlberg. 1995. Sarcopterygian interrelationships: How far are we from a phylogenetic consensus. *Geobios* 19:241–248.
- Cloutier, R., and A.-M. Candilier. 1995. Palaeozoic vertebrates of northern France and Belgium: part III—Sarcopterygii (Devonian to Carboniferous). *Geobios* 19:335–341.
- Coates, M. I., and M. Friedman. In press. *Litoptychus bryanti* and the characteristics of stem tetrapod neurocrania. In *Fossil Fishes and Related Biota: Morphology, Phylogeny and Palaeobiogeography—in honor of Meemann Chang*.
- Cope, E. D. 1889. Synopsis of the families of Vertebrata. *American Naturalist* 23:849–877.
- Fox, R. C., K. S. W. Campbell, R. E. Barwick, and J. A. Long. 1995. A new osteolepiform fish from the Lower Carboniferous Raymond Formation, Drummond Basin, Queensland. *Memoirs of the Queensland Museum* 38:97–221.
- Friedman, M., M. I. Coates, and P. Anderson. 2007. First discovery of a primitive coelacanth fin fills a major gap in the evolution of paired fins and limbs. *Evolution and Development* 9:329–337.
- Holland, T., and J. A. Long. 2009. On the phylogenetic position of *Gogonasus andrewsae* Long 1985, within the Tetrapodomorpha. *Acta Zoologica* 90 (Supplement 1):285–296.
- Iwaniw, E. 1984. Lower Cantabrian basin margin deposits in NE León, Spain—a model for valley-fill sedimentation in a tectonically active, humid climatic setting. *Sedimentology* 31:91–110.
- Jarvik, E. 1948. On the morphology and taxonomy of the Middle Devonian osteolepid fishes of Scotland. *Kungliga svenska Vetenskapsakademiens Handlingar* 25:1–301.
- Jarvik, E. 1950a. On some osteolepiform crossopterygians from the Upper Old Red Sandstone of Scotland. *Kungliga svenska Vetenskapsakademiens Handlingar* 2:1–35.
- Jarvik, E. 1950b. Middle Devonian vertebrates from Canning Land and Wegeners Halvö (East Greenland), Part II. Crossopterygii. *Meddelelser om Grønland* 96:1–132.
- Jarvik, E. 1952. On the fish-like tail in the ichthyostegid stegocephalians with descriptions of a new stegocephalian and a new crossopterygian from the Upper Devonian of East Greenland. *Meddelelser om Grønland* 114:1–90.
- Jarvik, E. 1954. On the visceral skeleton in *Eusthenopteron* with a discussion of the parapophoid and palatoquadrate in fishes. *Kungliga Svenska Vetenskapsakademiens Handlingar* 9:1–74.
- Jarvik, E. 1980. *Basic Structure and Evolution of Vertebrates*, Volumes 1, 2. Academic Press, London, New York, 575 pp.
- Jessen, H. 1973. Weitere Fischreste aus dem Oberen Plattenkalk der Bergisch-Gladbach-Paffrather Mulde (Oberdevon, Rheinisches Schiefergebirge). [Further Devonian Fishes of the Oberer

- Plattenkalk of the Bergisch-Gladbach-Paffrath Trough (Upper Devonian Rhineland)]. *Palaeontographica Abteilung A* 143:159–187.
- Johanson, Z. 2004. Late Devonian sarcopterygian fishes from eastern Gondwana (Australia and Antarctica) and their importance in phylogeny and biogeography; pp. 287–308 in G. Arratia, M. V. H. Wilson, and R. Cloutier (eds.), *Recent Advances in the Origin and Early Radiation of Vertebrates*. Verlag, Munich, Germany.
- Johanson, Z., and P. E. Ahlberg. 1997. New tristichopterid (*Osteolepiformes; Sarcopterygii*) from the Mandagery Sandstone (Famennian) near Canowindra, N.S.W., Australia. *Transactions of the Royal Society of Edinburgh* 88:39–53.
- Johanson, Z., and A. Ritchie. 2000. Rhipidistians (*Sarcopterygii*) from the Hunter Siltstone (Late Famennian) near Grenfell, NSW, Australia. *Geowissenschaftliche Reihe* 3:111–136.
- Lebedev, O. A. 1995. Morphology of a new osteolepidid fish from Russia. *Bulletin du Muséum national d'Histoire naturelle, Paris*. 4e Série. Section C. Sciences de la Terre. *Paléontologie, Géologie, Minéralogie* 17:287–341.
- Lebedev, O. A. 1996. Fish assemblages in the Tournaisian-Viséan environments of the East European Platform; pp. 387–415 in P. Strogen, I. D. Somerville, and G. L. L. Jones (eds.), *Recent Advances in Lower Carboniferous Geology*. Geological Society Special Publication No. 107.
- Leriche, M. 1908. Sur les poissons carbonifères du Nord de la France. *Extrait des Annales de la Société géologique du Nord*. 37: 266–281.
- Long, J. 1985a. The structure and relationships of a new osteolepiform fish from the Late Devonian of Victoria, Australia. *Alcheringa* 9:1–22.
- Long, J. A. 1985b. New information on the head and shoulder girdle of *Canowindra grossi* Thomson from the Upper Devonian Mandagery Sandstone, New South Wales. *Records of the Australian Museum* 37:91–99.
- Long, J. A. 1987. An unusual osteolepiform fish from the Late Devonian of Victoria, Australia. *Paleontology* 30:839–852.
- Long, J. A. 1989. A new rhizodontiform fish from the Early Carboniferous of Victoria, Australia, with remarks on the phylogenetic position of the group. *Journal of Vertebrate Paleontology* 9:1–17.
- Long, J. A. 1999. A new genus of fossil coelacanth (*Osteichthyes: Coelacanthiformes*) from the Middle Devonian of southeastern Australia. *Records of the Western Australian Museum Supplement* 57:37–53.
- Long, J. A., R. E. Barwick, and K. S. W. Campbell. 1997. Osteology and functional morphology of the osteolepiform fish *Gogoniasus andrewsae* Long 1985, from the Upper Devonian Gogo Formation, Western Australia. *Records of the Western Australian Museum Supplement* 53:1–89.
- Long, J. A., and Holland, T. 2008. A possible elpistostegalid from the Devonian of Gondwana. *Proceedings of the Royal Society of Victoria* 120:182–192.
- Long, J. A., G. C. Young, T. Holland, T. J. Senden, and E. M. G. Fitzgerald. 2006. An exceptional Devonian fish from Australia sheds light on tetrapod origins. *Nature* 444:199–202.
- Miall, L. C. 1885. Description of the remains of *Megalichthys* in the Leeds Museum. McCorquodale, London.
- Obruchev, D. V. 1955. Devonskie ryby minusinskoi kotloviny; pp. 45–47 in M. A. Rzhonsnitskaya and V. S. Meleshchenko (eds.), *Field Atlas of Characteristic Faunal and Flora Complexes of the Devonian Beds of the Minusinsk Valley (Central Asia)*. All-Union Scientific Research Institute of Geology (VSEGEI). Ministry of Geology and Conservation Mineral Resources, Moscow.
- Roemer, F. 1865. Ueber das Vorkommen von *Rhizodus hibberti*, Owen, *Megalichthys hibberti*, Agassiz and Hibbert, in den schieferterrassen des Steinkohlengebirges von Volpersdorf in der Grafschaft Glatz. *Zeitschrift der Deutschen Geologischen Gesellschaft* 17: 272–276.
- Romer, A. S. 1942. Notes on certain American Paleozoic fish. *American Journal of Science* 240:216–228.
- Romer, A. S. 1955. Herpetichthyes, Amphibioidei, Choanichthyes, or Sarcopterygii? *Nature* 176:126.
- Säve-Söderbergh, G. 1936. On the morphology of the Triassic stegoccephalians from Spitsbergen, and the interpretation of the endocranum in the Labyrinthodontia. *Kungliga Svenska Vetenskapsakademien Handlingar*, 3 serien 16:1–181.
- Schultze, H.-P. 1974. *Osteolepide Rhipidistia* (Pisces) aus dem Pennsylvanian von Illinois/USA. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 146:29–50.
- Schultze, H.-P., and U. Heidtke. 1986. *Rhizodopsidae Rhipidistia* (Pisces) aus dem Perm der Pfalz (W-Deutschland). *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 3:165–170.
- Schultze, H.-P., and U. Heidtke. 1993. *Rhizodopsis hanbuchi* nov. sp., a new rhizodopsid rhipidistian (*Sarcopterygii, Osteichthyes*) from the Lower Rotliegend (Lower Permian) of the Palatinate, SW-Germany. In Heidtke U. (ed.), *New Research on Permo-Carboniferous Faunas*. Pollicchia 29:133–142.
- Thomson, K. S. 1964. Revised generic diagnosis of the fossil fishes *Megalichthys* and *Ectosteorhachis* (family Osteolepidae). *Bulletin of the Museum of Comparative Zoology* 131:283–311.
- Thomson, K. S. 1973. Observations on a new rhipidistian fish from the Upper Devonian of Australia. *Palaeontographica* 143A:209–220.
- Thomson, K. S., and K. V. Hahn. 1968. Growth and form in fossil rhipidistian fishes (Crossopterygii). *Journal of Zoology (London)* 156:199–223.
- Traquair, R. H. 1881. On the cranial osteology of *Rhizodopsis*. *Transactions of the Royal Society of Edinburgh* 30:167–179.
- Vorobyeva, E. I. 1977. Morphology and nature of evolution of crossopterygian fishes. *Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR* 163:1–239. [Russian]
- Vorobyeva, E. I. 1992. The problem of the origin of terrestrial vertebrates. *Nauka*, Moscow. [Russian]
- Vorobyeva, E. I., and D. V. Obruchev. 1964. Subclass Sarcopterygii; pp. 268–322 in D. V. Obruchev (ed.), *Osnovy Paleontologii*, Volume XI, Agnatha, Pisces. Izdatel'stvo NAUKA SSR, Moscow.
- Westoll, T. S. 1936. On the structures of the dermal ethmoid shield of *Osteolepis*. *Geological Magazine*. 73:157–171.
- Williamson, W. C. 1837. On the affinity of fossils scales of fish from the Lancashire coal measures with those of the recent Salmonidae. *The London and Edinburgh Philosophical Magazine* 2:300–301.
- Woodward, A. S. 1891. Catalogue of the Fossil Fishes in the British Museum of Natural History, Part 3.
- Wyse Jackson, P. N., and N. T. Monaghan. 1995. Transfer of the Huxley and Wright (1867) Carboniferous amphibian and fish material to Trinity College Dublin from the National Museum of Ireland. *Journal of Paleontology* 69:602–603.
- Young, G. C. 1993. Middle Palaeozoic macrovertebrate biostratigraphy of eastern Gondwana; pp. 208–251 in J. A. Long (ed.), *Palaeozoic Vertebrate Biostratigraphy and Biogeography*. Belhaven Press, London.
- Young, G. C. 2007. Devonian formations, vertebrate faunas and age control on the far south coast of New South Wales and adjacent Victoria. *Australian Journal of Earth Sciences* 54:991–1008.
- Young, G. C., J. A. Long, and A. Ritchie. 1992. Crossopterygian fishes from the Devonian of Antarctica: systematic, relationships and biogeographic significance. *Records of the Australian Museum* 14:1–77.
- Young, J. 1866. On the affinities of *Chondrosteus*, Ag. *Proceedings of the Geological Society* 22:596–608.
- Zhu, M., and Ahlberg, P. E. 2004. The origin of the internal nostril of tetrapods. *Nature* 432:94–97.

Submitted May 20, 2008; accepted April 18, 2009.