The postcranial anatomy of two Middle Devonian lungfishes (Osteichthyes, Dipnoi) from Mt. Howitt, Victoria, Australia

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Abstract

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The postcranial skeletons of two upper Givetian lungfishes from Mt. Howitt, Victoria, Australia, show remarkable similarities, despite the fact that one is a tooth-plated form (*Howidipterus* Long 1992) whilst the other has a denticulate dentition (*Barwickia* Long 1992). Both genera show identical body shape with a short first dorsal fin and greatly elongated second dorsal fin, and small anal fin. The cleithra and clavicles are remarkably similar except for *Barwickia* lacking external ornament on the lateral lamina of the cleithrum and having a smaller branchial lamina on the clavicle. Both have paddle-shaped subdermal anocleithra that meet the posterior process of the I bone, approximately the same numbers of cranial ribs, pleural ribs, supraneural and subhaemal spines, the same expanded dorsal and anal fin basals with similar number of proximal and middle radials supporting the fins, and approximately the same number of radials supporting the hypochordal lobe of the caudal fin. These numerous similarities in the postcranial skeletons of the two genera strongly suggest that their differing feeding mechanisms probably evolved from a shared ancestral form having a similar postcranial skeleton. Implications for hypotheses of dipnoan phylogeny are discussed.

Introduction

Since the time of Dollo (1895) the significance of postcranial features in the large scale evolutionary trends of the Dipnoi has been repeatedly noted (Graham-Smith and Westoll, 1937; Westoll, 1949; Lehman, 1966; Bemis, 1984; Long, 1990; Pridmore and Barwick, 1993). However, despite the recent wealth of new information on the cranial anatomy of early lungfishes, there is a lack of information on their postcranial skeletons. Over seventy Devonian genera of lungfish are now known (Marshall, 1987; Jarvik, 1980; Janvier 1996) yet only four of these, *Fleurantia denticulata* (Graham-Smith and Westoll, 1937), *Dipterus valencienessi* (Ahlberg and Trewin, 1994) and two genera from the Late Devonian Gogo Formation of Western Australia, *Chirodipterus australis* and *Griphognathus whitei* (Pridmore and Barwick, 1993; Campbell and Barwick, 2002), have had the postcranial skeleton described in detail. Other Devonian dipnoans which have had aspects of the postcranial skeleton described include *Uranolophus* (Denison, 1968; Campbell and Barwick, 1988a), *Dipterus* (e.g. Schultze 1970, 1975; Campbell and Barwick, 1988a, Campbell et al. 2006), *Rhinodipterus* (Schultze, 1975),

Pillararhynchus (Barwick and Campbell 1996), *Adololopas* (Campbell and Barwick 1998), *Griphognathus* (Schultze, 1969; Campbell and Barwick, 1988a; Pridmore and Barwick, 1993). Isolated vertebral centra of dipnoans from indeterminate taxa have been figured and described also by several workers (e.g. Jarvik, 1952). Therefore the complete description of the postcranial skeleton in two more Devonian genera, presented in this paper, contributes significant new information to the subject, and allows discussion of phylogenetic problems concerning the monophyly of tooth plated versus denticulated dipnoan lineages.

The Mt. Howitt fauna, of uppermost Givetian age (Young, 1993, 1999), represents one of the best preserved and most diverse late Middle Devonian freshwater fish assemblages from any single site in the Southern Hemisphere, and is also significant in being the keystone for biostratigraphic correlations throughout eastern Victoria (Long, 1983, 2004; Long and Werdelin, 1986; Cas et al 2003). There are two genera of lungfish at Mt. Howitt, regarded by Long (1993) as members of the Family Fleurantiidae (*contra* Long, 1992, in which *Howidipterus* was placed provisionally in the Dipteridae). One has tooth-plates with occasional denticles between the tooth-

ridges *(Howidipterus)*; the other has a denticle-covered dentition, although rows of teeth may be clearly distinguished on the pterygoids *(Barwickia)*. Although Long (1993) suggested that the fleurantiid dentitions probably evolved by heterochronic processes (McKinney and McNamara, 1991), namely paedomorphic retention of tooth-row development in conjuction with peramorphic development of denticle fields ("dissociated heterochony"), it is the nature of the postcranial skeletons in these forms that gives further information on their possible phylogenetic affinities. The phylogenetic analysis of Devonian lungfishes by Ahlberg et al. (2006) supported a close relationship between *Howidipterus* and *Barwickia*.

Materials and methods

The Mt. Howitt lungfishes were studied from latex casts of the natural moulds preserved in black shale. The specimens are generally preserved as flattened, slightly disrupted carcasses, but often fine preservation of cartilage bones, such as elements of the visceral skeleton, are clearly seen from the latex peels. Photographs are of latex casts dusted with ammonium chloride. The description of the postcranial skeleton follows terminology used by Goodrich (1958), Graham-Smith and Westoll (1937), Long (1987, for the cleithrum) and Cloutier (1996). Figure 1 outlines the terminology used for axial skeleton components used in this work.

Outline drawings and descriptions of postcranial features have been made using a camera lucida. Comparative material examined includes three-dimensional lungfish bodies from the Gogo Formation of Western Australia held in the W.A. Museum and in the Geology Department, The Australian National University, Canberra, and collections of North American and European Devonian lungfishes held in the British Museum of Natural History, London, The National Museum of Scotland, Edinburgh and the Australian Museum, Sydney. Specimens referred to in this work are housed in the palaeontological collections of the Museum of Victoria, Melbourne (MV), The Australian Museum, Sydney (AM), and the Western Australian Museum (WAM), Perth.

Descriptions of the postcranial skeletons

The two genera show remarkably similar body form and postcranial skeletal morphology. Both genera are commonly preserved in size ranges of 10–20 cm, the largest individual indicating a maximum length estimated at close to 40 cm *(Howidipterus)*. Although there are many specimens representing both forms which show the overall shape and proportions of the body and fins (e.g. figs. 4, 6), very few specimens show good preservation of the axial skeletal elements, and in most specimens the counts of these elements are based on impressions of ribs and supraneurals that have been overprinted by the squamation.

Pectoral girdle

The exoskeletal pectoral girdle in both genera consists of a large cleithrum and clavicle, and a smaller paddle-shaped subdermal anocleithrum which articulates anterodorsally with
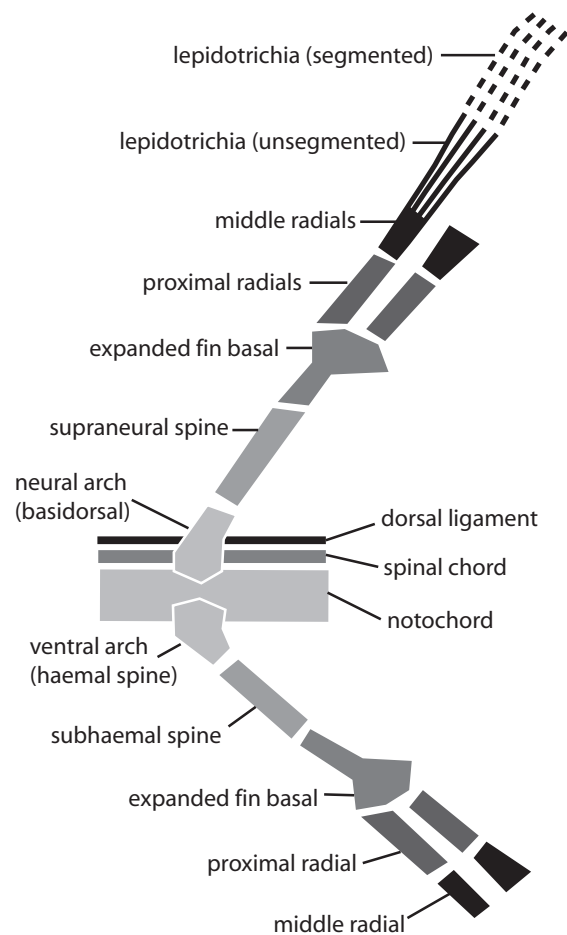

Figure 1. Terminology used for axial skeleton components.

the posterior subdermal process of the I bone. The scapulocoracoid is not commonly preserved, and was probably largely cartilaginous, as were the axial mesomeres that presumably formed the pectoral and pelvic fin skeletons. In one specimen *(Barwickia,* MV P198046) there is an impression of part of the scapulocoracoid showing the exposed portion to have a similar form as that figured for *Chirodipterus* (Campbell and Barwick, 1987). Neither the shape of the glenoid fossa nor the support buttresses for the scapulocoracoid can be determined from the latex peel.

Cleithrum. The cleithra in *Howidipterus* (fig. 3) and *Barwickia* (figs. 3, 5) are very similar in overall form and shape. Both are generally similar to the cleithra of other Late Devonian dipnoans, especially *Eoctenodus microsoma* (Long, 1987) and *Scaumenacia* (Jarvik, 1980). The cleithrum has an expanded dorsal end, strong dorsoventral lateral thickening and extensive, inwardly directed branchial lamina that meets the branchial lamina of the clavicle along a prominent thickened ridge. They differ from each other in that the externally exposed region of
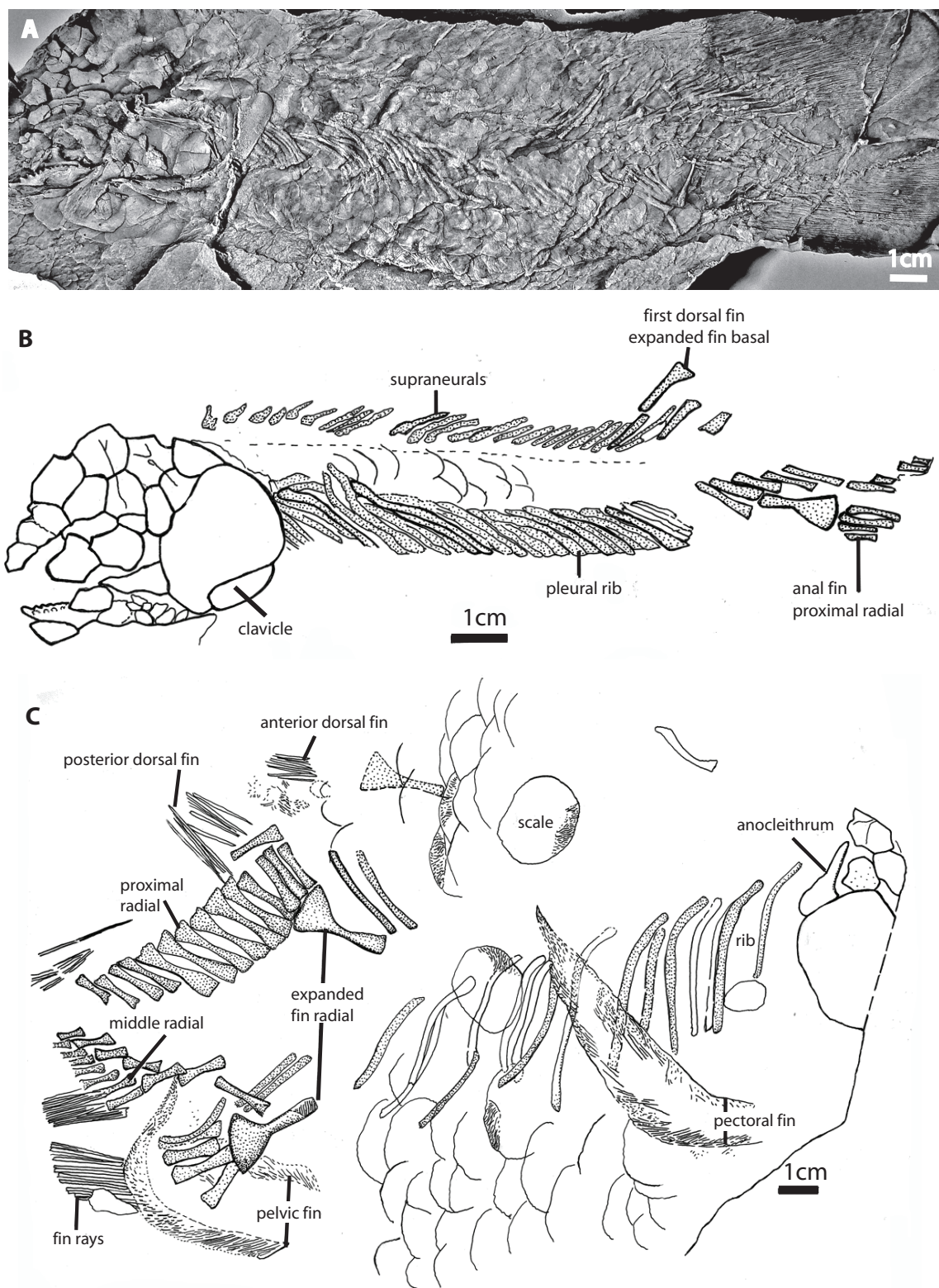
Figure 2. *Howidipterus donnae*: a, photograph of MV P181792; b, interpretive drawing of MV P198045; c, MV P198042, sketch interpretation of large specimen, slightly disarticulated.
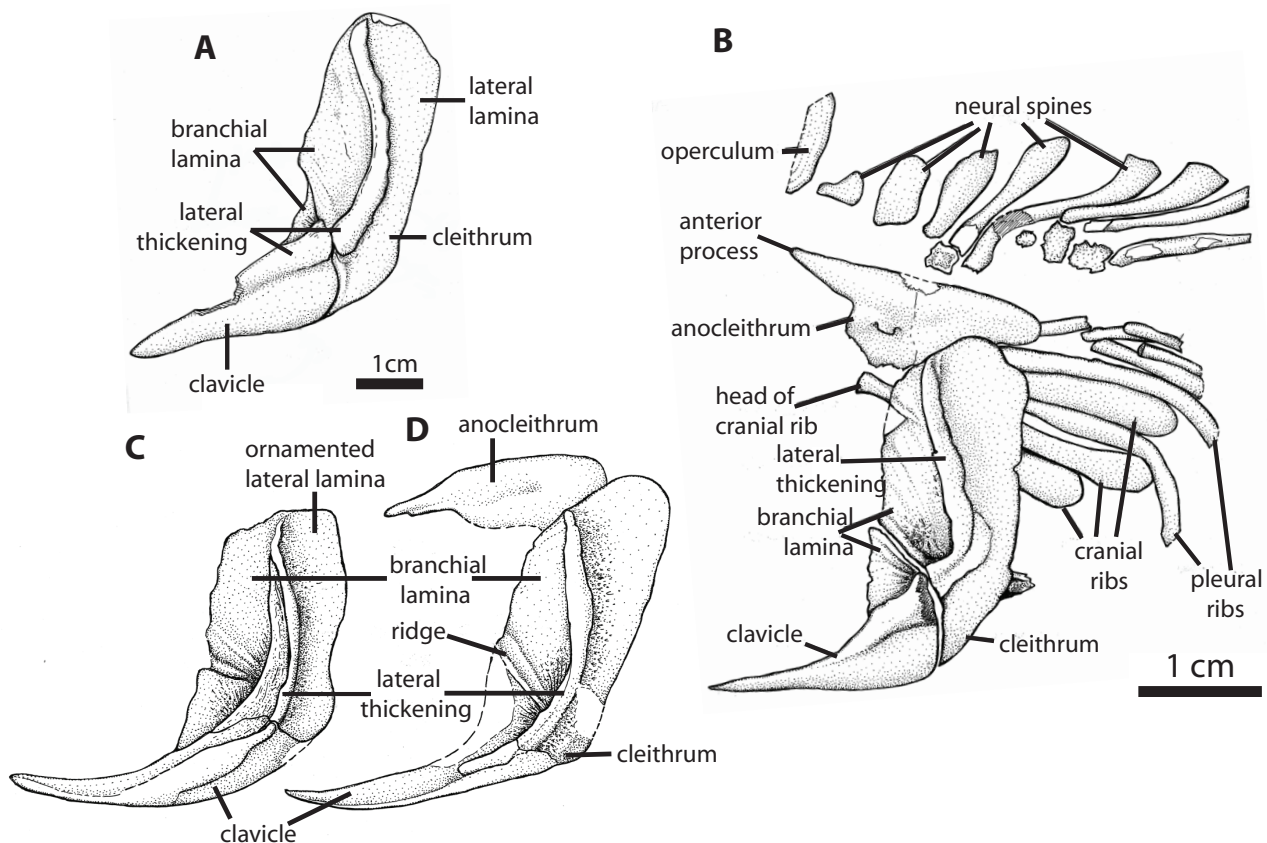
Figure 3. Shoulder girdle: a, *Barwickia downunda* cleithrum and clavicle, MV P181890; b, *Barwickia downunda* with anterior ribs and neural spines, MV P198046; c, *Howidipterus donnae* exoskeletal shoulder girdle, MV P 181883; and d, also showing anocleithrum, MV P181792.

the cleithrum (lateral lamina) in *Howidipterus* has weakly developed surface pitting, indicating it was situated just below the dermis in life. The cleithrum of *Barwickia* shows no external ornament or marking on its lateral lamina, and appears to have a more strongly developed lateral thickening. As in *Eoctenodus* there is a marked anterior angle on the branchial lamina in both forms, and a roughened mesial pit is formed where the branchial lamina meets the lateral lamina. *Eoctenodus* differs in having a notch present at the ventromesial corner of the branchial lamina (Long 1987, Fig. 6) which is not seen in either of the Mt. Howitt forms.

There are some variations seen within the cleithra of *Howidipterus*. P181883 (Fig. 3; figured only in part by Long, 1992, Fig. 3G) shows the presence of a distinct mesial lamina in addition to a branchial lamina. This outer, mesial lamina is part of the lateral thickening of the cleithrum, and may have served to separate the overlap area of the operculum from the gill chamber.

In visceral view there is no indication of the shape or size of the scapulocoracoid attachment area in either form, as seen in some other early lungfishes (e.g. *Uranolophus,* Campbell and Barwick, 1988b; *Chirodipterus,* Campbell and Barwick, 1999).

Clavicle. The clavicles are well-preserved in several specimens from both genera (figs. 2, 3, 5). They are large bones, almost as long as the cleithrum and smoothly curved throughout their extent. Overlap between the cleithrum and clavicle in the Mt. Howitt genera was relatively short and narrow, unlike the primitive form *Uranolophus* in which the clavicle had an elongate, extensive dorsal overlap surface (Campbell Barwick, 1988b). The ventral laminae in both Mt. Howitt forms are of simple triangular shape, lacking a notch for overlap of the principal gular plate as seen in some other Devonian lungfish such as *Chirodipterus* (e.g. WAM 90.10.8) and *Uranolophus* (Campbell and Barwick, 1988b, Figs. 23–25). The clavicles of both *Howidipterus* and *Barwickia* possess a strong lateral thickening along the outermost edge, which increases in thickness towards the junction with the cleithrum. The branchial lamina of the clavicle of *Howidipterus* is notably more extensive than that in *Barwickia* (fig. 3).

Anocleithrum. The anocleithrum is well-preserved and of similar paddle-shape in several specimens of both forms *(Barwickia, figs. 3, 5; Howidipterus, Long, 1993: Fig. 5).* In *Barwickia* the anocleithrum is 80% as long as the cleithrum.
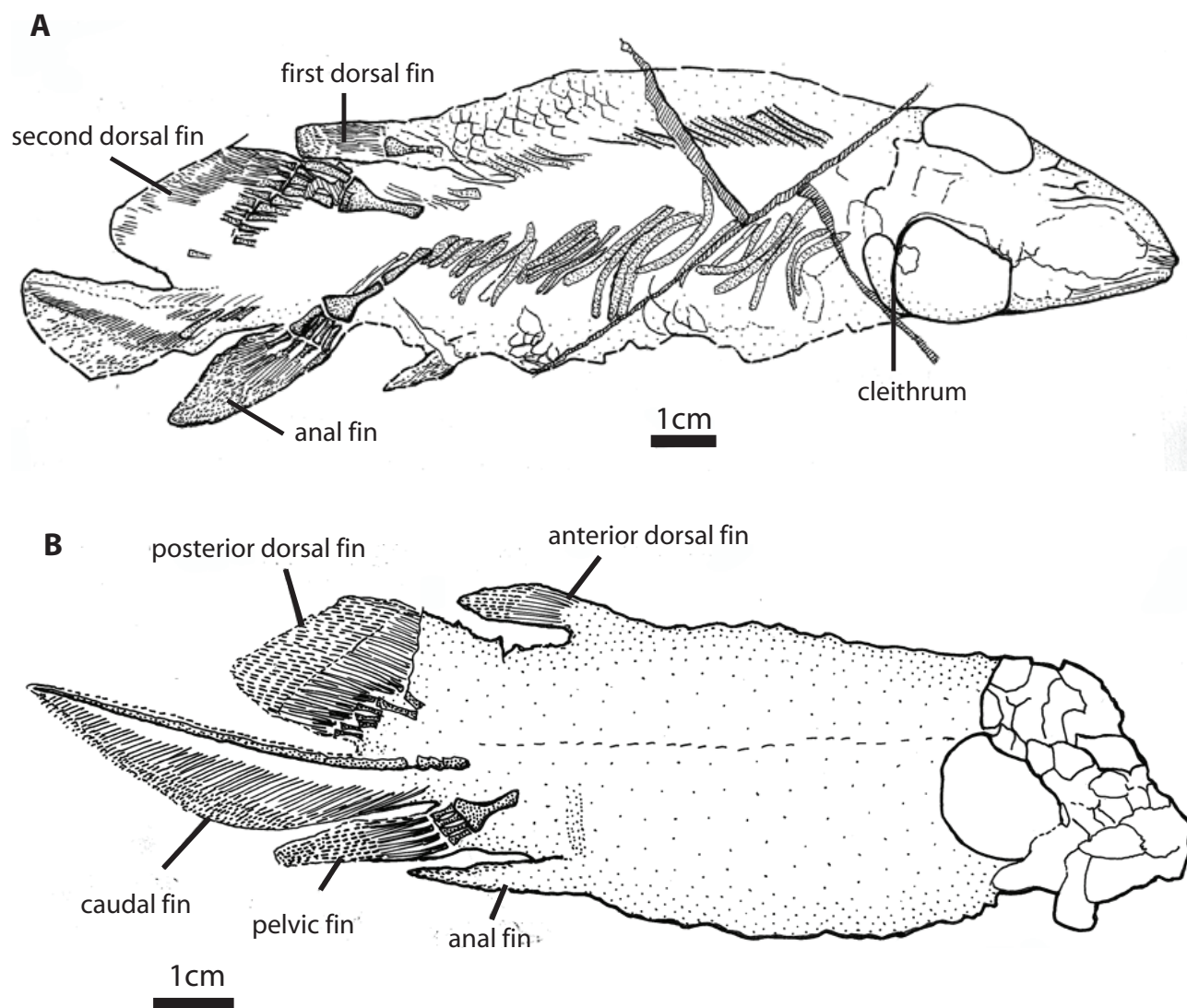
Figure 4. Outline of postcranial body and fins: a, *Barwickia downunda*; b, *Howidipterus donnae*.

In *Howidipterus* the anocleithrum appears to be slightly smaller compared with the cleithrum. The anterior end of the anocleithrum is slender and produced into a strong anterior spine that remains in contact with the posterior process of the I bone of the skull in many specimens, suggesting a strong ligamentous connection in life.

Pectoral and pelvic fins

Pectoral fin. The pectoral fin is well-preserved in many specimens, although it shows only the outline of the fringing fin rays and some small scales covering the fin. There is no preservation of endoskeletal fin bones in either genus. In both genera the pectoral fin approximates to the same length as the skull roof, and is approximately four times as long as its broadest part. The fin rays emerge from the edges of the fin as long, curved, unbroken elements which then subdivide into smaller elements close to the margins of the fin. The fin rays emerge a short distance from the beginning of the fins, and there are approximately 45–50 rows of lepidotrichia present.

Pelvic fin and girdle. Part of the endoskeletal pelvic girdle is seen preserved only in one specimen of *Barwickia* (AM F98074 part and counterpart, fig. 6 A, B). It shows a large articulatory facet for the axial mesomeres of the pelvic fin, and a short process near this facet which might be the homologue of the dorsomesial process described on the pelvic girdle of *Chirodipterus* (Young et al., 1990, Fig. 4). The overall shape and size of the girdle in *Barwickia* closely matches the girdle of *Chirodipterus* being almost a parallelogram in shape, not elongated with a long anterior process as in *Griphognathus*.
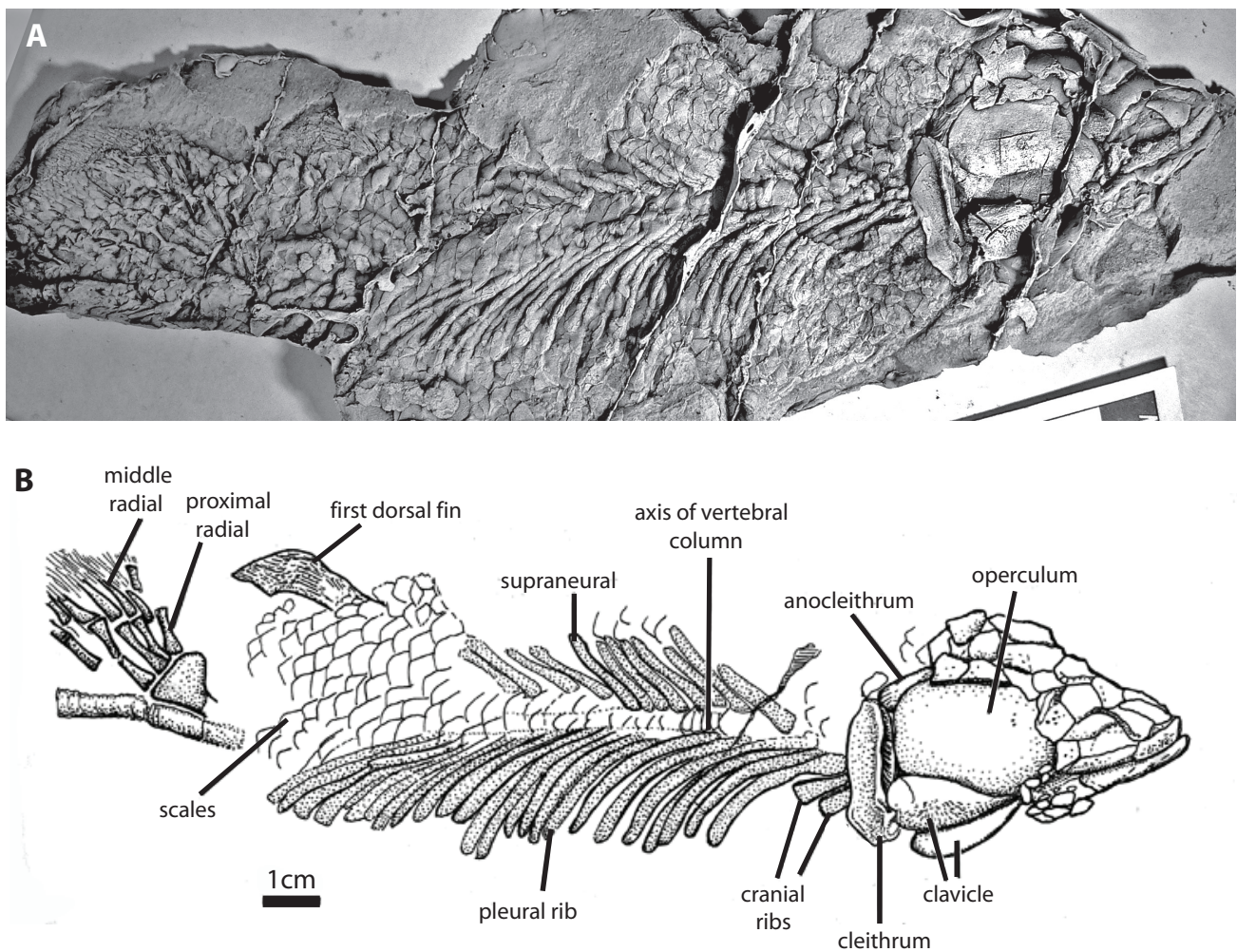
Figure 5. *Barwickia downunda*, features of postcranial skeleton: a, MV P181784; b, interpretive drawing of same.

The pelvic fin is well-preserved in many specimens (e.g. figs. 4, 6) and is of identical shape and proportions to that of the pectoral fin in both genera, exhibiting exactly the same style of fin-ray bifurcation and proportions. The pelvic fin emerges opposite the first dorsal fin, at the point where the paired pleural ribs end. Approximately 40–50 rows of lepidotrichia fringe the dorsal and ventral margins of the fin.

Median fins

Anterior dorsal fin. The anterior, or first dorsal fin, is the smallest of the median fins, being about one fifth the length of the second dorsal fin at its base, and slightly smaller than the anal fin, being approximately 3% of the total length of the fish in both forms. It originates from approximately the 20th to 22nd myotomal segment, and is supported by a dorsally expanded racquet-shaped fin basal (radial), which itself is supported by a shortened supraneural relative to the lengths of

the supraneurals anterior and posterior to it. In some specimens of *Barwickia* there is a short median anteriorly directed process developed on the expanded fin support (fig. 6E), a feature not seen in any specimen of *Howidipterus*. The expanded fin basal is approximately half as broad as the expanded anterior support bone for the second dorsal fin.

Groups of three or four stiff lepidotrichia attach to approximately three proximal radials that articulate ventrally with the anterior dorsal fin support bone. These bunches of four or more unsegmented lepidotrichia continue for about half the extent of the fin before giving way to smaller segmented and bifurcating fin rays for the distal extent of the fin. About 16–18 lepidotrichial rows are present at the insertion of the anterior dorsal fin of both genera. The area of the fin supported by unsegmented lepidotrichia was covered by small scales.

Posterior dorsal fin. The posterior, or second dorsal fin, is the largest median fin and extends for approximately 15% the total
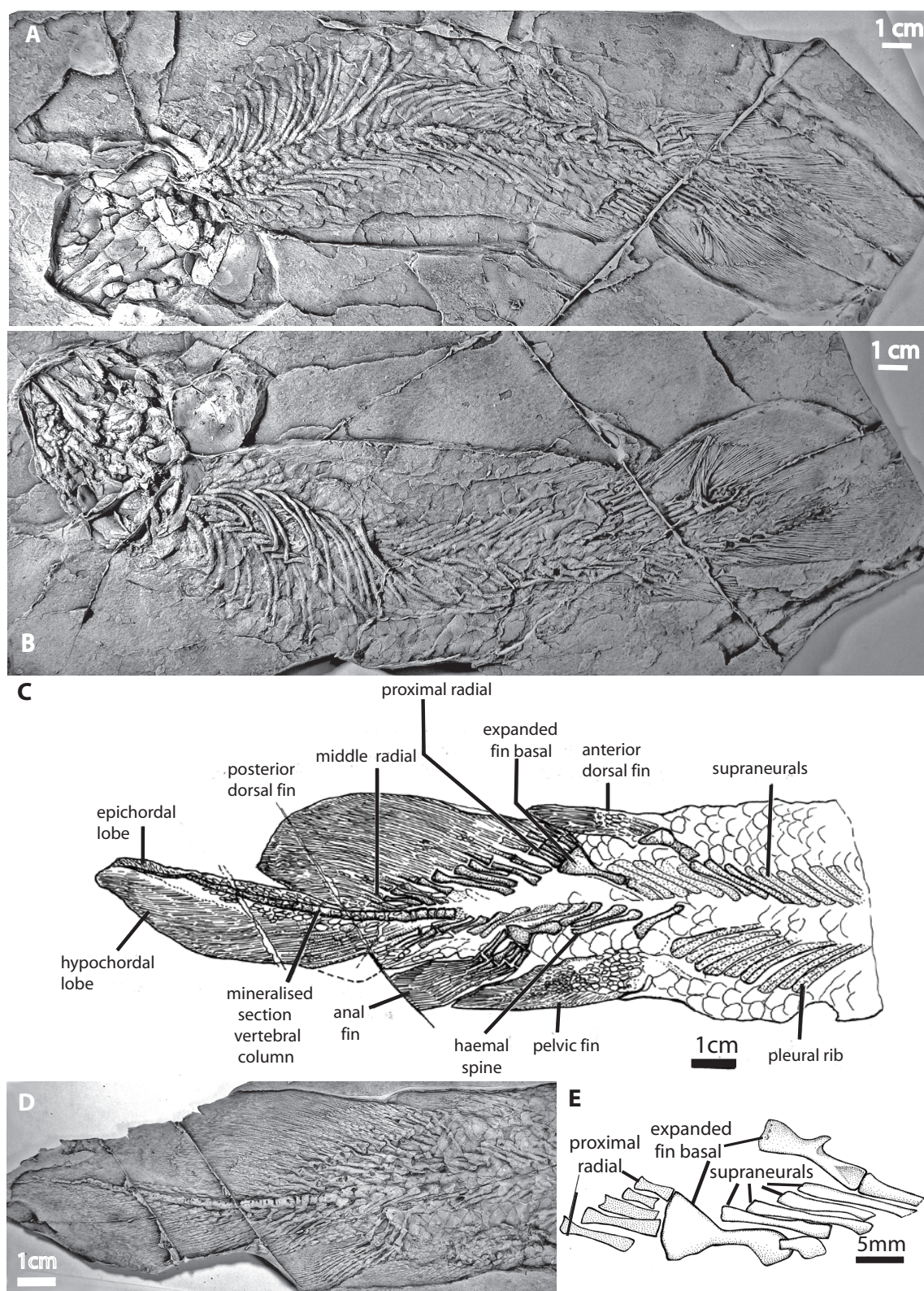
Figure 6. *Barwickia downunda* a and b, AM F98074 body flattened showing postcranial skeleton and head: a, dorsal view; b, ventral view; c, MV P181784, showing details of tail and fins; d, MV P181784, photograph of tail and fins; e, MV P198044, internal support bones for first and second dorsal fins.

length of the fish in both genera (figs. 4, 6). It begins at a point slightly anterior to the anterior margin of the anal fin, although the supraneural leading to the fin-support bones of this fin meets the notochordal axis at the same myotomal segment as the infrahaemal supporting the expanded anal fin bone. In both genera the posterior dorsal fin has a gently lobate shape, and is supported anteriorly by a large expanded radial that articulates distally with five proximal radials that support four middle radials (fig. 6 C, D) that each carry the bunches of 3–4 unsegmented lepidotrichia. This expanded radial has a waisted, stout shaft that expands ventrally to articulate with a thick supraneural. The five proximal radials that support the anterior end of the fin increase evenly in size posteriorly. There are 10–11 other proximal radials that follow posteriorly from the five, articulating with the anterior expanded bone thus totalling 15 or 16 elements. Each of the anterior proximal radials and the anterior expanded bone are supported by supraneurals articulating to the vertebral column, although the posteriormost three or four may articulate directly to the mineralised section of the vertebral column. Their exact position is not clear from the preservation of the material. About 60 rows of unsegmented lepidotrichia support the ventral half of the fin. The expanded anterior fin basal is approximately as large and of identical shape to that of the anal fin support bone.

Anal fin. The anal fin in both genera is only slightly broader in shape than the first dorsal fin and inserts into the same myotomal segment (c. 24th) as the anterior margin of the second dorsal fin. It is supported by a stout racquet-shaped fin basal bone (*Howidipterus*, fig. 2; *Barwickia*, fig. 6C) which articulates dorsally with a short but thick infrahaemal spine. Four proximal radials articulate posteroventrally with the expanded fin basal and these each articulate with a middle radial that supports bunches of 3–5 stiff lepidotrichia. Approximately 15–20 lepidotrichial rows support the dorsal half of the fin.

Caudal fin. The caudal fin is well-preserved in several specimens of both genera and appears to have exactly the same outline and development of fin-ray support bones. The tail is heterocercal with a triangular shape, the axis of the vertebral column being deflected about 20° from the main axis of the body (figs. 4, 6, 8). The ventral edge of the hypochordal lobe begins almost immediately posterior to the anal fin, and equivalent in position to half-way along the posterior dorsal fin. The anterior edge of the hypochordal lobe is supported by three rows of fin support bones: the dorsal series (subhaemals) articulate with the vertebral axis, and distally these articulate with a row of proximal radials which articulate with a 1:1 ratio with middle radials. The middle radials have bunches of unsegmented lepidotrichia attached to them. There appears to be only 8–9 rows of middle radials before the tail narrows, and the proximal radials or subhaemals support the fin directly on the vertebral axis. At this point the rest of the fin structure is unclear, and appears to consist largely of bunches of lepidotrichia inserting directly into the axis of the vertebral column. A small epichordal lobe of segmented lepidotrichia is present in both genera (e.g. *Barwickia*, fig. 6C).

Axial skeleton

The axial skeleton consists of the vertebral column and its articulating spines and ribs. Paired pleural ribs are present throughout the anterior half of the fish, articulating with the first 19–21 vertebral elements within each myoseptum in *Howidipterus*, and between the 20–22 myosepta in *Barwickia*, thereby being almost identical (exact counts are difficult to make due to the overprinting of paired ribs in the crushed state of preservation).

The vertebral column is well-ossified in the tail region of both species, although individual centra are not clearly differentiated, instead there is a continuous ossified or mineralised column. This may represent mineralisation of the notochord in this region as suggested by Schultze (1970) and Arratia *et al.* (2001), or they could be individual ring centra that are only well-ossified in the caudal part of the vertebral column. Anteriorly there are poorly preserved remains of vertebral arches in some specimens (fig. 7). These closely resemble the dorsal arch elements (basidorsals) described in *Griphognathus* by Campbell and Barwick (1988a, Figs. 34, 35). Ventral elements, possibly representing ossified basiventrals are sometimes seen, and impressions of whole body specimens suggest that they were present throughout the vertebral column in younger individuals. The largest specimens
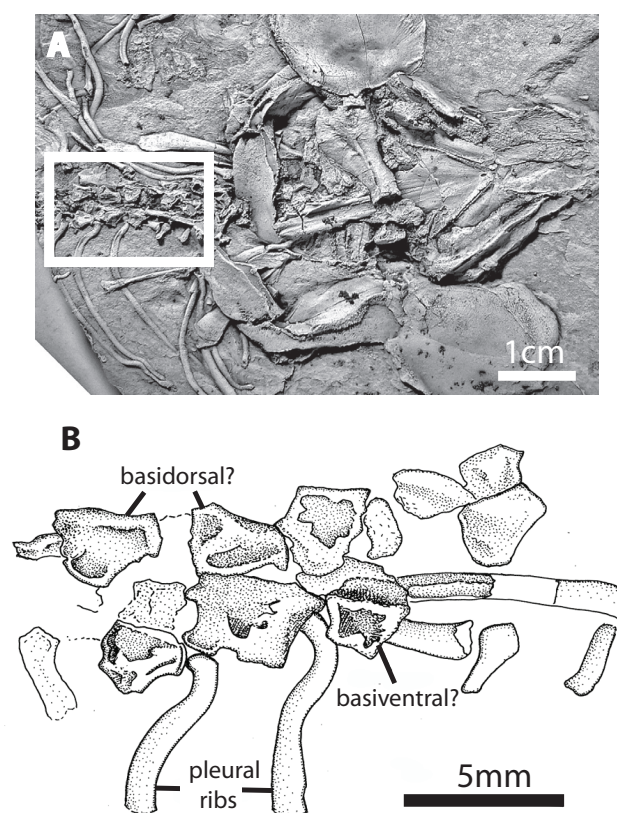

Figure 7. *Barwickia downunda*: a, photograph and b, interpretive drawing of MV P181868, details of anterior vertebral elements.

show no vertebral ossification at all (e.g. large *Howidipterus*, fig. 2). Supraneurals articulate to the vertebral column throughout its length, but no secondary supraneurals are present as exists near the first dorsal fin as in *Fleurantia* (Graham-Smith and Westoll, 1937).

Howidipterus and *Barwickia* have approximately 20–22 vertebrae and supraneurals anterior to the first dorsal fin, then 4–5 or so supraneurals before the second dorsal fin support in *Barwickia*, and 5–7 supraneurals before the second dorsal fin support in *Howidipterus* (these are accurate counts and reflect individual variations). Both forms then show identical development of the second dorsal fin shape and the numbers of supraneurals supporting this fin and subhaemal spines, as described above.

Cranial ribs. Cranial ribs are present in both forms, and appear identical in shape (figs. 3, 5). Long (1993) gave a preliminary description of the cranial ribs in both the Mt. Howitt lungfishes. The expanded rectangular distal ends of the cranial ribs can be often recognised in specimens where the squamation has overprinted the axial skeleton. Each cranial rib has a slightly expanded flat head, narrow neck, and a flat shaft that broadens

gradually throughout its distal length. Two pairs of cranial ribs are present in each genus. They are easily identified as being present in the head region of weakly disarticulated specimens of *Barwickia*, being followed by the first pair of pleural ribs. In no specimens can we see the neurocranium preserved, so we can only deduce from the anterior extent of the cranial ribs, moreso than for the pleural ribs (e.g. Long 1993, Fig. 3) that they did articulate to the ventral suture of the brainacase and posterior stalk of the parsphenoidid as in other lungfishes. In AM F89074 (fig. 6) the flat articulatory heads of the cranial ribs are seen lying adjacent to the posterior end of the ossified neurocranium. In *Neoceratodus forsteri* the cranial ribs are oriented almost horizontally (Goodrich, 1958), and it appears that in the fossilised forms from Mt. Howitt the orientation of the cranial ribs was similar as they are commonly observed lying in a different orientation to the paired pleural ribs.

Pleural ribs. Paired pleural ribs (figs. 2, 3, 5–8) are gently curved, almost sigmoid shaped elongate rounded elements which run for most of the length of the trunk, terminating at the level of origin of the pelvic fin. Anterior pleural ribs are longer than the posterior elements, and have a more distinct curvature.
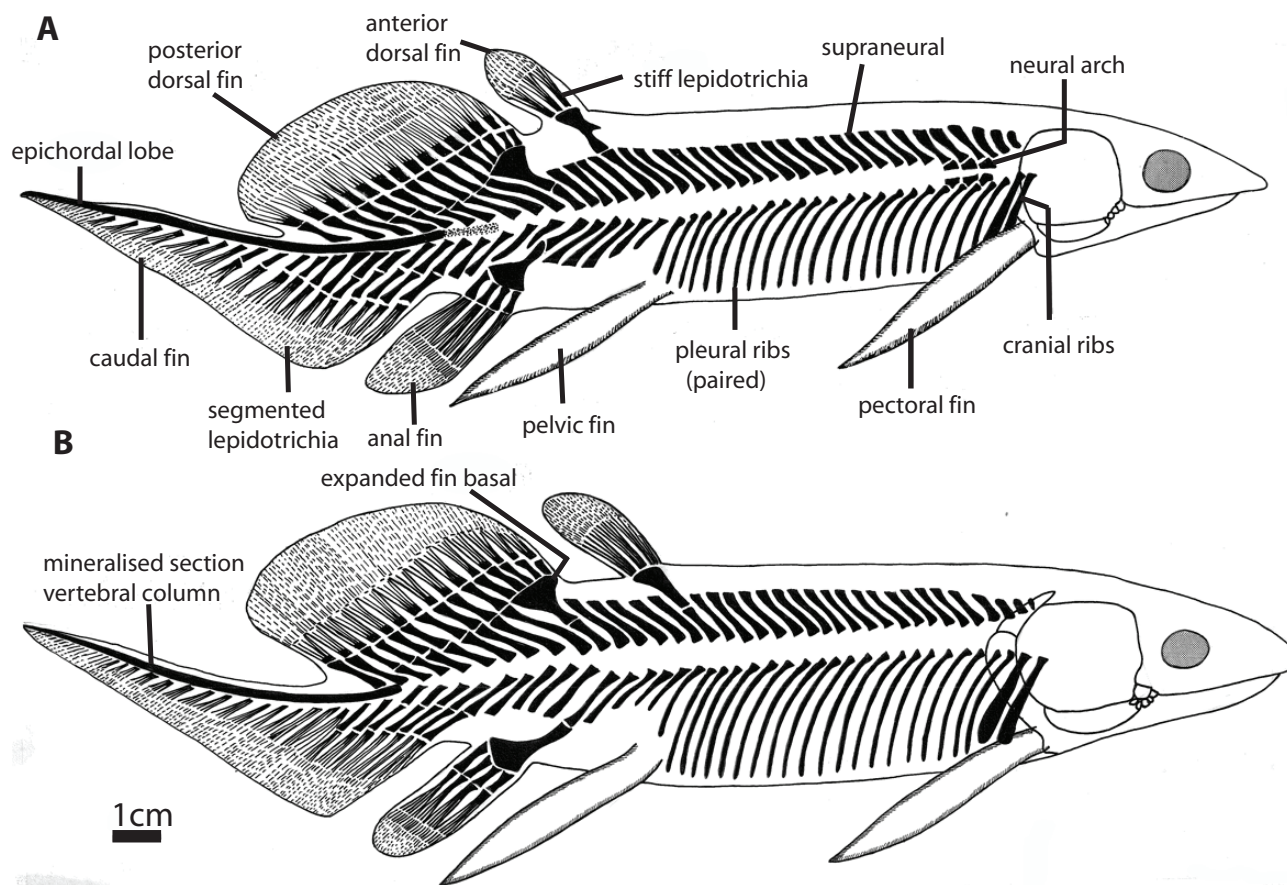

Figure 8. Reconstructions of postcranial skeletons: a, *Barwickia* and b, *Howidipterus*. Paired elements such as pleural and cranial ribs are drawn in full.

Approximately 18–20 pairs of these ribs are present in both forms. They articulate dorsally with the basiventral element of the vertebral column at a slightly expanded head having a flat articulatory surface meeting the basiventral (fig. 7).

Phylogenetic significance of dipnoan postcranial features

During the Devonian Period lungfishes underwent major changes in both their cranial and postcranial skeletons, leading directly to the lineage of tooth-plated forms including the modern genera. By the Early Carboniferous, forms like *Uronemus (Ganopristodus)* had acquired essentially the same body and fin shape seen in all subsequent lungfishes, including extant forms: a single continuous dorsal fin that is merged with the caudal and anal fins to give a diphycercal fin shape. A transformation series of intermediate morphological stages in acquiring this pattern can be seen in various Devonian dipnoans, represented by the few known from complete or near complete body fossils (e.g. Long 1993, Fig 7).

The series begins with the only Early Devonian genus in which the approximate form of the body and fins is known, *Uranolophus*. It shows the presence of two dorsal fins and a large, separate anal fin, and a heterocercal caudal fin with high angle axis of tail to body (although it is incompletely preserved, Denison, 1968; Campbell and Barwick, 1988b). Even in the earliest known dipnoan the anterior dorsal fin is slightly smaller than the posterior fin. Some Late Devonian forms, like *Rhynchodipterus* retain this primitive pattern in having two almost equidimensional dorsal fins, a similarly sized anal fin and large upturned heterocercal tail (Save-Soderbergh, 1937). In *Griphognathus* there are also two widely separated dorsal fins, with the anterior fin is seen to be slightly smaller than the posterior dorsal fin (Schultze 1969; Campbell and Barwick 2002).

Dipterus shows a slightly more derived condition than these forms in that the second dorsal fin is enlarged much more than the first dorsal fin (Forster-Cooper, 1937 plate 3; Ahlberg and Trewin, 1994). In *Dipterus* the first dorsal fin has about 18 unsegmented lepidotrichia as in *Howidipterus* and *Barwickia*, while the second dorsal fin has about 40 or so unsegmented lepidotrichia, as compared with approximately 60 or so in the Mt. Howitt forms. Whilst these Australian genera closely resemble *Pentlandia* in this respect, the latter, from the Middle Devonian of Scotland, has several distinguishing differences in the skull morphology. However *Pentlandia* requires a detailed study to determine its exact affinities and is here regarded as having similar level of organisation in its postcranial skeleton as the two Mt. Howitt genera. *Pinnalongus* from the Eifelian of Scotland shows a similar condition to the Mt Howitt forms in having a very small anterior dorsal fin and extensive posterior dorsal fin (Newman and Den Blaawen 2007).

Fleurantia represents the next stage in the transformation series from the Mt. Howitt forms (and possibly *Pentlandia*). *Fleurantia* has a much larger second dorsal fin, with many more proximal radials (16–21 elements, approximately 100 rows of unsegmented lepidotrichia; Cloutier, 1996). The first dorsal fin is approximately the same size and has a similar number of unsegmented lepidotrichia as in the Mt. Howitt forms, but the anal fin in *Fleurantia* is further reduced in only having 3 proximal radials articulating with the expanded fin basal. Unlike the Mt. Howitt forms, *Fleurantia* lacks an expanded fin basal supporting the anterior region of the second dorsal fin and has a few secondary supraneurals present near the first dorsal fin.

Scaumenacia represents the next stage in the series in having a greatly expanded, but low first dorsal fin, and a larger second dorsal fin (supporting approximately 180 long lepidotrichia; Cloutier, 1996). It is also more derived than *Fleurantia* and the Mt. Howitt forms in having lost the ossified radials supporting the first dorsal fin, and in having the tail terminate in a long, thin caudal filament.

Phaneropleuron, from the Famennian Rosebrae Beds of Scotland, shows similar level of organisation to *Scaumenacia* but incorporates both dorsal fins with the enlarged epichordal lobe of the tail, which has now achieved a diphycercal shape, although the anal fin is still separate. This genus also requires further study of its postcranial skeleton before it can be compared in detail with the previous forms.

Finally, merging the anal fin with the diphycercal tail arrives at the condition seen in all later lungfishes, as typified in the Lower Carboniferous genus *Uronemus* (= *Ganopristodus*, Schultze, 1992).

From the above descriptions and discussion the following observations and hypotheses can be suggested regarding the phylogenetic significance of each character.

Cleithrum. In primitive dipnoans the cleithrum has a weakly developed branchial lamina (*Uranolophus*, Campbell and Barwick, 1988b), although the feature is subsequently well-developed in many Devonian forms (e.g. *Scaumenacia*, *Chirodipterus*, *Eoctenodus*, *Barwickia*, *Howidipterus*). Campbell and Barwick (1988a) pointed out several differences between the cleithrum of denticulate lungfishes and that of the presumed monophyletic 'tooth-plated forms'. Their comparisons used *Griphognathus* and *Uranolophus* as denticulated forms, and *Chirodipterus*, *Scaumenacia* and *Eoctenodus* as tooth-plated forms. The new material from Mt. Howitt shows that unlike the condition described for *Griphognathus* and *Uranolophus, Barwickia* possessed a cleithrum (and clavicle) that was essentially the same as in *Howidipterus* in possessing a large, medially extensive branchial lamina. The same type of extensive branchial lamina is also present in *Holodipterus*, regarded as one of the members of the denticle-shedding lineage by Campbell and Barwick (1991) but by Smith (in Campbell and Smith 1987, p.165) as a form that could have been derived from earlier tooth-plated forms such as *Dipterus* or *Speonesydrion*.

Fin support bones. The development of expanded racquet-shaped median fin support bones is seen only in the Mt. Howitt forms and in the anal fin of *Fleurantia*. In *Griphognathus whitei* there are large expanded basal bones, but these do not taper into thin rods as occurs in *Fleurantia*, *Barwickia* and *Howidipterus*. Furthermore, *Griphognathus whitei* has a unique type of dorsal and anal fin-support bone with enlarged secondary fin basals supporting several proximal radials, and can be regarded as specialised in this respect (e.g. WAM 86.9.

645, Pridmore and Barwick, 1993, Fig. 8 shows the fin basal for the posterior dorsal fin). Thus the expanded racquet-shaped fin basals could either represent a synapomorphy of *Fleurantia* and the Mt. Howitt lungfishes or a homoplasy. As *Fleurantia* and the Mt. Howitt forms otherwise show very similar levels of development and dentition (Long, 1993), and the similar shaped second dorsal fin of *Scaumenacia* does not have a similar enlarged basal, we here consider it to be a derived feature of the Family Fleurantiidae (defined nodally as the clade *Fleurantia, Howidipterus* and *Barwickia* in Ahlberg et al. 2006), and possibly also including *Jarvikia*, based only on cranial features shared with *Fleurantia* (Campbell and Barwick, 1990, Cloutier, 1996); and *Andreyevichthys*, based on similar dentition (Smith et al., 1993). The presence of a few secondary supraneurals near the first dorsal fin of *Fleurantia* is here considered an autapomorphy of that genus as such bones have not been recorded in any other fossil lungfish.

Fin shapes. The stages leading to the acquisition of the modern dipnoan body and fin shape have been summarised in the discussion above. The primitive condition is having two equidimensional or nearly equally sized dorsal fins, separate anal and heterocercal caudal fins without epichordal lobes as seen in other sarcopterygians (e.g. *Osteolepis, Glyptolepis*). The following characters are therefore seen as derived with respect to this condition, as outlined in Ahlberg and Trewin (1994): (a) reduction of first dorsal fin, slight enlargement of second dorsal fin (e.g. *Dipterus);* (b) enlargement of second dorsal fin *(Howidipterus, Barwickia, Pentlandia);* (c) greater enlargement of second dorsal fin *(Fleurantia)*; (d) first dorsal fin elongated but low, greater expansion of second dorsal fin, long caudal filament developed on main axis of caudal fin *(Scaumenacia); (e),* continuous long dorsal fin axis of tail horizontal, not inclined *(Phaneropleuron); (f)* anal fin merged with continuous dorsal fin *(Conchopoma, Uronemus,* all Late Palaeozoic to Recent lungfishes).

Vertebrae. The vertebrae are weakly ossified in primitive forms, consisting of ossified neural arches that straddle an unconstricted notochord *(Uranolophus,* Campbell and Barwick, 1988b; *Dipterus,* Ahlberg and Trewin, 1994; Schultze, 1975). Through the arches passes the spinal chord and dorsal ligament.

Ossified spool-shaped centra are found only in a few forms (e.g. *Griphognathus),* and are considered to be a derived condition by outgroup comparison with other primitive sarcopterygians (e.g. separate intercentra and pleurocentra are primitive for other sarcopterygians; Andrews and Westoll, 1970; Ahlberg, 1989). The presence of vertebrae, as separate basidorsal and/or basiventral ossifications is observed in *Scaumenacia* (Cloutier, 1996) and at various growth stages in the Mt. Howitt forms. Modern lungfishes have basidorsals and basiventrals present as cartilaginous units (Goodrich, 1958; Shute, 1972), possibly a derived condition due to loss of bone from primitive forms.

Ribs. These have been found in all dipnoans where whole body features are preserved, and are often referred to as 'pleural ribs' in the thoracic region of the body. It is unknown whether paired pleural ribs were extensively present in *Uranolophus* or other primitive marine dipnoans like *Dipnorhynchus, Speonesydrion, Ichnomylax* or *Melanognathus*. If so, then this feature would have no special significance for evolution within the Dipnoi, but otherwise could be a derived condition within later dipnoans that co-evolved with the development of larger lungs. The well-developed ribs present in all the marine dipnoans from the Middle-Late Devonian Gogo (Campbell and Barwick 2002) and Bergisch-Gladbach faunas (Schultze 1975) do not appear to be strongly curved as in the Mt Howitt forms, so we assume this kind of 'pleural' rib found in the Mt Howitt species evolved for accommodation of a larger lung for air-breathing. The pleural ribs in *Dipterus* appear to be primitively short compared with the longer elements seen in *Barwickia* and *Howidipterus*.

Cranial ribs. Early reports of cranial ribs in one specimen of *Fleurantia* (Graham-Smith and Westoll: 255) and in *Scaumenacia* (Goodrich, 1909) have been confirmed by observation of casts of these species held in the collections of the Geology Department at the Australian National University, and of original specimens of *Scaumenacia* held in the Museum of Victoria. Aside from *Barwickia* and *Howidipterus*, the only other Devonian dipnoans to have cranial ribs are *Rhinodipterus ulrichi* (Schultze, 1975), a marine form, and possibly incipient cranial ribs in *Dipterus* (Ahlberg and Trewin, 1994), known from both freshwater and marine environments. Observation of the marine Gogo specimens of *Chirodipterus, Gogodipterus* and *Griphognathus* also show that cranial ribs were absent in these forms (Campbell and Barwick 2002). The presence of cranial ribs in lungfishes, being absent in plesiomorphic fully marine forms), would appear to be a good synapomorphy uniting air-gulping forms (Long, 1993). The actual morphology of the cranial ribs has not been previously considered, although some new information is now at hand. In *Dipterus* (Ahlberg and Trewin, 1994, Fig. 6) the enlarged ribs identified as possible cranial ribs are not ventrally expanded, showing the condition of being enlarged pleural ribs that probably articulated with the posterior end of the braincase. The cranial ribs in *Barwickia* and *Howidipterus* are here considered to be more specialised than those of *Dipterus* in having distally expanded, flat shapes, allowing for more surface area on the lateral and mesial surfaces of the ribs for attachment of ligaments to anchor the pectoral girdle.We note the occipital ribs, that articulate to the posterodorsal surface of the neurocranium, have not been observed in the Mt.Howitt forms.

Dipnoan evolution: evidence from the Mt. Howitt dipnoans

The two genera of lungfishes from the Mt. Howitt deposit exhibit identical postcranial skeletons, and cranial morphologies that differ slightly but are still at a similar grade of evolution with respect to approximate numbers of skull roof bones and cheek bone patterns (Long, 1992). *Barwickia* shows a dentition that was at first thought to be typical of the denticulate feeding mechanism (Long, 1992) but later shown to be a form of tooth plate with large denticle fields present (Long, 1993). It should be pointed out though that the histology of these tooth plates is not known as the material can only be studied from latex peels.

Howidipterus shows more typical dipnoan tooth plates that closely resemble those of *Scaumenacia* in overall morphology but can also be demonstrated to be closely related to those of *Barwickia*. Dissociated heterochrony was invoked as a possible mechanism for the development of the *Barwickia* type tooth plate based on the known growth changes that occur during the ontogeny of *Andreyevichthys* toothplates (Long, 1993). This means that different rates of growth apply to the developmental stages, such as peramorphic development of the denticle field whilst there is restrained growth of the tooth rows (paedomorphosis). From these observations, and the overall nature of the Mt. Howitt fauna, with a high proportion of endemic fauna, and palaeogeographically representing a highland intermontane sedimentary basin deposit (Cas et al. 2004), and the recent phylogenetic analysis supporting the two lungfishes *Barwickia* and *Howidipterus* as very closely related (Ahlberg et al. 2006), we suggest that they may have had a comparatively recent divergence from a common ancestor. In overall body form they are identical, so must have had identical functional morphologies with respect to their mode and speed of swimming. As they inhabited the same lake system, each must have occupied a different niche primarily based on differing food preference in the lacustrine food chain. To date there are no invertebrate fossils known from the Mt. Howitt deposit, despite delicate, articulated preservation of both the fish (in all stages of growth) and plants, thus sources of food for the lungfish are possibly to be found in the known fossil record of the site, or alternatively as soft-bodied invertebrates not preserved in the fossil deposit. The teeth of *Barwickia* suggest it fed by a mechanism similar to those of denticulate forms, like *Fleurantia* or holodipterids that have predominantly denticle-covered plates with a few larger cusps set in rows (Pridmore et al., 1994), possibly being a predator on either smaller fishes or soft bodied invertebrates. *Howidipterus*, on the other hand, had more typical dipnoan crushing tooth plates suited to triturating food, potentially lycophytous and psilophytous plant material that grew or fell into in the lake.

Lakes are often highly endemic, closed systems (Day et al., 2009) and are analogous to islands in their isolated nature (Danley and Kocher, 2001). Local speciations and adaptive radiations are often influenced by past environmental factors such as climate change (Day et al., 2009) and sea level changes (Beheregaray et al., 2002, Bohlen et al., 2006). Another driving factor is that of resource availability (Liem, 1974), the evolution of variation has been demonstrated particularly for fish in low-resource environments (Schluter, 1995; Roy et al., 2004). There are many examples of sympatric lacustrine speciations of fish (Humphries and Miller, 1981; Day et al., 2009) and invertebrates such as gastropods (Glaubrecht and Kohler, 2004) and shrimp (von Rintelen et al., 2007). The best-known example is that of the cichlids in the great lakes of East Africa (Liem, 1974; Schliewen et al., 1994; Danley and Kocher, 2001; Streelman et al., 2007). These cichlids underwent three major bursts of cladogenesis; driven by habitat choice, competition for food resources, and the third burst has been attributed to sexual selection for male colouration. The secondary radiation (trophic morphology) was most pronounced in the rock-dwelling genera (Danley and Kocher, 2001).

This pattern of diversification of body form and trophic structure is also seen in many other freshwater fishes including the threespine stickleback *Gasterosteus aculeatus* (Cresko and Baker, 1996), the Arctic charr *Salvelinus alpinus* (Snorrason et al., 1989) and the Brook charr *Salvelinus fontinalis* (Dynes et al., 1999). However the condition exhibited by the Mt. Howitt fauna of divergent trophic morphologies with limited postcranial differentiation is much less common. Fish with similar postcranial morphologies are likely to have comparable locomotive ability and occupy a common habitat. Trophic specializations can diverge extremely rapidly (in "contemporary time") in response to different resource availability as seen in the Arctic charr (Adams et al., 2003; Knudsen et al., 2007; Michaud et al., 2008) and some cichlids (Liem, 1974; Streelman et al., 2007). This indicates that the two Mt. Howitt species may have only relatively recently diverged from a common ancestor into two morphs with radically differing dentition, most likely as a result of competition in a low-resource environment.

Acknowledgements

References

Adams, C. E., Woltering, C., and Alexander, G. 2003. Epigenetic regulation of trophic morphology through feeding behaviour in Arctic charr, *Salvelinus alpinus Biological Journal of the Linnean Society* 78: 43–49.

Ahlberg, P.E. 1989. Paired fin skeletons and relationships of the fossil group Porolepiformes (Osteichthyes: Sarcopterygii). *Zoological Journal of the Linnean Society* 96: 119–166.

Andrews, S. M.H. and Westoll, T.S. 1970. The postcranial skeleton of rhipidistian fishes excluding *Eusthenopteron foordi. Transactions of the Royal Society of Edinburgh* 68: 391–489.

Ahlberg, P.E. and Trewin, N.H. 1994. The postcranial skeleton of the Middle devonian lungfish *Dipterus valenciennesi. Transactions of the Royal Society of Edinburgh, Earth Sciences,* 85: 159–175.

Arratia, G., Schultze, H.-P. and Casciotta, J. 2001. Vertebral column and asscoiated elements in dipnoans and comparisons with other fishes: development and homology. *Journal of Morphology* 250: 101–172.

Barwick, R.E. and Campbell, K.S.W. 1996. A Devonian Dipnoan, *Pillararhynchus*, from Gogo, Western Australia and its relationships. *Palaeontographica* Abt. A, 239: 1–42.

Bemis, W.E. 1984. Paedomorphosis and the evolution of the Dipnoi. *Palaeobiology* 10: 293–307.

Beheregaray, L. B., Sunnucks, P., and Briscoe, D. A. 2002. A rapid fish radiation associated with the last sea-level changes in southern Brazil: the silverside *Odontesthes perugiae* complex. *Proceedings of the Royal Society of London Series B-Biological Sciences* 269: 65–73.

Bohlen, J. A., Perdices, A., Doadrio, I., and Economidis, P. S. 2006. Vicariance, colonisation, and fast local speciation in Asia Minor and the Balkans as revealed from the phylogeny of spined loaches (Osteichthyes; Cobitidae). *Molecular Phylogenetics and Evolution* 39: 552–561.

Campbell, K.S.W. and Barwick, R.E. 1987. Palaeozoic lungfishes-a review. *Journal of Morphology, Supplement* 1, 93–131.

Campbell, K.S.W. and Barwick, R.E. 1988a. Geological and palaeontological information and phylogenetic hypotheses. *Geological Magazine* 125: 207–227.

Campbell, K.S.W. and Barwick R.E. 1988b. *Uranolophus:* a reappraisal of a primitive dipnoan. *Memoirs of the Association of Australasian Palaeontologists* 7: 87–144.

Campbell, K.S.W. and Barwick, R.E. 1990. Palaeozoic dipnoan phylogeny: functional complexes and evolution without parsimony. *Paleobiology* 16: 143–169.

Campbell, K.S.W. and Barwick, R.E. 1991. Teeth and tooth plates in primitive lungfish and a new species of *Holodipterus*. In *Early vertebrates and related problems of evolutionary biology,* Chang M.M., Liu Y.H. and Zhang, G.R., eds, Science Press, Beijing, 429–440.

Campbell, K.S.W. and Barwick, R.E. 1999. Dipnoan fishes from the Late Devonian Gogo Formation of Western Australia. *Records of the Western Australian Museum, Supplement* 57: 107–138.

Campbell, K.S.W. and Barwick, R.E. 1998. A new tooth-plated dipnoan from the Upper devonian Gogo Formation and its relationships. *Memoirs of the. Queensland Museum* 42: 403–437.

Campbell, K.S.W. and Barwick, R.E. 2002. The axial postcranial structure of *Griphognathus whitei* from Gogo; comparisons with other Devonian dipnoans. *Records of the Western Australian Museum* 21: 167–201.

Campbell, K.S.W. and Smith, M.M. 1987. The Devonian dipnoan *Holodipterus*: dental form, variation and remodelling growth mechanisms. *Records of the Australian Museum* 39: 131–167.

Campbell, K.S.W., Barwick, R.E. and Den Blaauwen, J.L. 2006. Structure and function of the shoulder girdle in dipnoans: new material from *Dipterus valenciennesi. Senckenbergiana lethaea* 86: 77–91.

Cas, R., O'Halloran, G.J., Long, J.A. and Vandenberg, A.H.M. 2003. Middle Devonian to Carboniferous. *In* W.D. Birch (ed.), '*Geology of Victoria'*, *Geological Society of Australia Special Publications* 23: 157–193.

Cloutier, R. 1996. Dipnoi (Akinetia: Sarcopterygii). *In* H. P. Schultze and R. Cloutier (eds), *Devonian Fishes and Plants of Miguasha, Quebec, Canada*. Munich, Verlag Dr Friedrich Pfeil**:** 198–226.

Cresko, W. A. and Baker, J. A. 1996. Two morphotypes of lacustrine threespine stickleback, *Gasterosteus aculeatus*, in Benka Lake, Alaska. *Environmental Biology of Fishes* 45: 343–350.

Danley, P. D. and Kocher, T. D. 2001. Speciation in rapidly diverging systems: lessons from Lake Malawi. *Molecular Ecology* 10: 1075–1086.

Day, J. J., Bills, R., Friel, J. P. 2009. Lacustrine radiations in African *Synodontis* catfish. *Journal of Evolutionary Biology* 22: 805–817.

Denison, R.H. 1968. Early Devonian lungfishes from Wyoming, Utah and Idaho. *Fieldiana Geology* 17: 353–413.

Dollo, L., 1895. Sur la phylogénie des Dipneustes. *Bulletin Sociéte belgique Geologie et Paléontologie et Hydrologie* 9: 79–128.

Dynes, J., Magnan, P., Bernatchez, L. and Rodriguez, M. A. 1999. Genetic and morphological variation between two forms of lacustrine brook charr. *Journal of Fish Biology* 54**:** 955–972.

Friedman, M. 2007. The interrelationships of Devonian lungfishes (Sarcopterygii: Dipnoi) as inferred from neurocranial evidence and new data from the genus *Soederberghia* Lehman, 1959. *Zoological Journal of the Linnean Society* 151: 115–171.

Forster-Cooper, C., 1937. The Middle Devonian fish fauna of Achanarras. *Transactions of the Royal Society of Edinburgh* 59: 223–239.

Glaubrecht, M. and Kohler, F. 2004. Radiating in a river: systematics, molecular genetics and morphological differentiation of viviparous freshwater gastropods endemic to Kaek River, central Thailand (Cerithioidea, Pachychilidae). *Biological Journal of the Linnean Society* 82: 275–311

Goodrich, E.S. 1909. *A Treatise on Zoology*. Vol. 9., R. Lankaster (ed.), Black and Co, London.

Goodrich, E.S. 1958. *Studies on the structure and development of vertebrates*. Dover, New York.

Graham-Smith, W. and Westoll, T.S. 1937. On a new long-headed dipnoan fish from the Upper Devonian of Scaumenac Bay, P.Q., Canada. *Transactions of the Royal Society of Edinburgh* 59: 241–256.

Humphries, J.M. and Miller., R.R. 1981. A remarkable species flock of pup fishes, genus Cyprinodon, from Yucatan, Mexico. *Copeia* 1: 52–64

Janvier, P. 1996. *Early vertebrates*. Oxford University Press, New York.

Jarvik, E. 1952. On the fish-like tail in the icthyostegid stegocephalians. *Meddeleser om Grønland* 114: 1–90.

Jarvik, E. 1980. *Basic Structure and Evolution of Vertebrates*. Vol. 1., Academic Press, London and New York.

Knudsen, R., Amundsen, P. A., Primicerio, R., Klemetsen, A., and Sorenson, P. 2007. Contrasting niche-based variation in trophic morphology with Arctic charr populations. *Evolutionary Ecology Research* 9: 1005–1021.

Lehman, J.-P., 1966. Dipneustes. *In* Piveteau, J. (ed.), *Traité de Paléontologie,* Vol. 4., part 3, pp. 245–300. Masson, Paris.

Liem, K. F. 1974. Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. *Systematic Zoology* 22: 425–441.

Long, J.A. 1983. New bothriolepid fishes from the Late Devonian of Victoria, Australia. *Palaeontology* 25: 295–320.

Long, J.A. 1987. A redescription of the lungfish *Eoctenodus microsoma* Hills 1929, with reassessment of other Australian records of the genus *Dipterus* Sedgewick and Murchison 1828. *Records of the Western Australian Museum* 13, 297–314.

Long, J.A. 1990. Chapter 11. Fishes. In *Evolutionary trends,* K.J. McNamara, (ed.), Belhaven Press, London, 255–278.

Long, J.A. 1992. Cranial anatomy of two new Late Devonian lungfishes (Pisces: Dipnoi) from Mt. Howitt, Victoria. *Records of the Australian Museum* 44: 299–318.

Long, J.A. 1993. Cranial ribs in Devonian lungfish and the origin of dipnoan air-breathing. *Memoirs of the Australian Association of Palaeontologists* 15: 1991–209.

Long, J.A. 2004. Middle-Devonian Carboniferous, Palaeontology. Pp. 190–193 in *Geology of Victoria*, (ed.) W. Birch. Geological Society of Australia,

Long, J. A. and Werdelin, L. 1986. A new bothriolepid fish from near Tatong, Victoria, with descriptions of other species from the state. *Alcheringa* 10: 355–399.

Marshall, C.R. 1987. Lungfish: phylogeny and parsimony. *Journal of Morphology Supplement* 1: 151–162.

Michaud, W. K., Power, M., and Kinnison, M.T. 2008. Trophically mediated divergence of Arctic charr (*Salvelinus alpinus* L.) populations in contemporary time. *Evolutionary Ecology Research* 10: 1051–1066.

Miles, R.S. 1977. Dipnoan (lungfish) skulls and the relationships of the group: a study based on new species from the Devonian of Australia. *Zoological Journal of the Linnean Society of London* 61: 1–328.

McKinney, M.L. and McNamara, K.J. 1991. *Heterochrony-the evolution of ontogeny.* Plenum Press. New York.

Newman, M.J. and Den Blaawen, J.L. 2007. A new dipnoan fish from the Middle devonian (Eifelian) of Scotland. *Palaeontology* 50: 1403–1419.

Pridmore, P. A. and Barwick, R.E. 1993. Post-cranial morphologies of the Late Devonian dipnoans *Griphognathus* and *Chirodipterus* and locomotor implications. *Memoirs of the Australasian Association of Palaeontologists* 15: 161–182.

Pridmore, P. A., Campbell., K. S. W. and Barwick, R. E. 1994. Morphology and phylogenetic position of the holodipteran dipnoans of the Upper Devonian Gogo Formation of northwestern Australia. *Philosophical Transactions of the Royal Society of London (Biol.)* 344: 105–164.

Roy, D., Docker, M. F., Hehanussa, P., Heath, D.D., and Haffner, G.D. 2004. Genetic and morphological data supporting the hypothesis of adaptive radiation in the endemic fish of Lake Matano. *Journal of Evolutionary Biology* 17: 1268–1276.

Save-Soderbergh, G. 1937. On *Rhynchodipterus elginensis* n.g., n.sp., representing a new group of dipnoan-like Choanata from the Upper Devonian of East Greenland and Scotland. *Arkiv för Zoologi* 29: 1–8.

Schluter, D. 1995. Adaptive radiation in sticklebacks: trade-offs in feeding performance and growth. *Ecology* 76: 82–90.

Schultze, H.-P. 1969. *Griphognathus* Gross, ein langschnauziger Dipnoer aus dem Overdevon von Bergisch-Gladbach (Rheinisches Schiefergebirge) und von Lettland. *Geologica Palaeontologica* 3: 21–79.

Schultze, H.-P. 1970. Die Histologie der Wirbelkörper der Dipnoer. *Neues Jarhbuch Geologie und Paläontologie Abhandlangan* 135: 311–336.

Schultze, H.-P. 1975. Das axialskelett der Dipnoer aus dem Overdevon von Bergisch-Gladbach (westdeutschland). *Colloques international du C.N.R.S.*, 218, Paris, pp.149–159.

Schultze, H.-P. 1992. A new long-headed dipnoan (Osteichthyes) from the Middle Devonian of Iowa, USA. *Journal of Vertebrate Paleontology* 12: 42–58.

Schultze, H.-P. and Campbell, K.S. W. 1987. Characterisation of the Dipnoi, a monophyletic group. *Journal of Morphology Supplement* 1: 25–37.

Shute,C.C.D. 1972. The composition of vertebrae and the occipital region of the skull. Pp. 21–34 *in* Joysey, K. and Kemp, T. (eds). *Problems in Vertebrate Evolution,* Cambridge University Press.

Schliewen., U.K., Tautz, D. and Paabo, S. 1994. Sympatric speciation suggested by monophyly of crater lake cichlids. *Nature* 368: 629–632.

Smith, M.M., Krupina, N. and Cloutier, R., 1993. Form, growth and histogenesis of tooth plates in the Upper Devonian dipnoan, *Andreyevichthys epitomus* from Russia. *Absts AAP Meeting,* Canberra, February 1993, 24.

Snorrason, S. S., Skulason, S., Sandlund, O.T., Malmquist, H.J., Jonsson, B.J., and Jonasson, P.M. 1989. Shape polymorphism in arctic charr, *Salvelinus alpinus*, in Thingvallavatn, Iceland. *Physiology and Ecology Japan* 1: 393–404.

Streelman, J. T., Albertson, R. C., and Kocher, T.D. 2007. Variation in body size and trophic morphology within and among genetically differentiated populations of the cichlid fish, *Metriaclima zebra*, from Lake Malawi. *Freshwater Biology* 52: 525–538.

von Rintelen, K., von Rintelen, T., and Glaubrecht, M. 2007. Molecular phylogeny and diversification of freshwater shrimps (Decapoda, Atyidae, Caridina) from ancient Lake Poso (Sulawesi, Indonesia)— The importance of being colourful. *Molecular Phylogenetics and Evolution* 45: 1033–1041.

Westoll, T.S. 1949. On the evolution of the Dipnoi. In *Genetics, Palaeontology and Evolution*, G.L. Jepsen, G.G. Simpson and E. Mayr, (eds.), Princeton University Press, Princeton.

Young, G.C. 1993. Middle Palaeozoic macrovertebrate biostratigraphy of eastern Gondwana. In *Palaeozoic Vertebrate Biostratigraphy and Biogeography*, J.A. Long (ed.), Belhaven Press, London, pp. 208–251.

Young, G.C. 1999. Preliminary report on the biostratigraphy of new placoderm discoveries in the Hervey Group (Upper Devonian) of central New South Wales. *Records of the Western Australian Museum, Supplement* 57, 139–150.

Young, G.C., Barwick, R.E. and Campbell, K.S.W. 1990. Pelvic girdles of lungfishes (Dipnoi). In *Pathways in Geology,* R.W. LeMaitre (ed.), Blackwell Press, Melbourne, 59–75.