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Long, John A., 1992. Cranial anatomy of two new Late Devonian lungfishes (Pisces: Dipnoi) from Mount Howitt, Victoria. *Records of the Australian Museum* 44(3): 299–318. [5 December 1992].

doi:10.3853/j.0067-1975.44.1992.37

ISSN 0067-1975

Published by the Australian Museum, Sydney

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Cranial Anatomy of Two New Late Devonian Lungfishes (Pisces: Dipnoi) from Mount Howitt, Victoria

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ABSTRACT. Two new lungfishes are described from the Frasnian lacustrine sediments near Mount Howitt, eastern Victoria. *Howidipterus donnae* n.gen., n.sp. has toothplates with well-developed marginal teeth, and has a skull roof pattern similar to *Scaumenacia* but with a D bone present and large paired rostral bones anterior to the E bones. The cheek has moderately deep infraorbitals. The scales have a coarse ornament with widely spaced ridges. *Barwickia downunda* n.gen., n.sp. has a skull roof pattern characterised by a narrow, small D bone, narrow E bones as long as the C bones, and I bones which are indented well into the rear of the B bone and on occasion may contact each other. The dentition is denticulate as in *Fleurantia*. The cheek has a narrow, bar-like bone 6 + 7. The scales of *Barwickia* are finely ornamented.

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Lungfishes are one of the last groups of fishes to be studied from the diverse Mount Howitt fossil fish fauna which contains the following taxa: the placoderms *Bothriolepis gippslandiensis*, *B. cullodenensis* and *B. fergusonii* (Long, 1983a; Long & Werdelin, 1986), *Austrophyllolepis ritchiei*, *A. youngi* (Long, 1984) and *Groenlandaspis* sp. (Long, 1982); the acanthodians *Culmacanthus stewarti* (Long, 1983b) and *Howittacanthus kentoni* (Long 1986); the actinopterygian *Howqualepis rostridens* (Long, 1988a); the crossopterygians *Marsdenichthys longiocipitus* (Long, 1985) and *Beelarongia patrichae* (Long, 1987a), and the two new dipnoans described in this paper. In addition there are partial bodies of prolepipiforms with *Glyptolepis*-type

scales and a possible actinistian. The fauna represents one of the best preserved and diverse Late Devonian freshwater fish assemblages from a single site in the Southern Hemisphere, and is also significant in being the keystone for biostratigraphic correlations throughout eastern Victoria (Long, 1983a; Long & Werdelin, 1986).

This paper briefly describes the cranial anatomy of two new genera, based on examination of approximately 80 of the best preserved heads. The scales are described, as these are an important feature for distinguishing the two genera when the skulls are poorly preserved. Many additional specimens, now registered in the Museum of Victoria, would require further

preparation before detailed measurement of the postcranial skeleton could be made. Discussion of the phylogenetic relationships of the two new forms has been deferred until the complete anatomy of the fishes has been described.

Material and Methods

The Mount Howitt lungfishes are studied from latex casts of the natural moulds in black shale, so there are no details of toothplate histology available. 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 seen from latex peels. Photographs are of latex casts dusted with ammonium chloride. The description of the material follows terminology used by Miles (1977). Classification follows the new scheme of Campbell & Barwick (1990). Comparative material examined includes 3-dimensional lungfish skulls from the Gogo Formation of Western Australia held in the WA Museum and in the Geology Department, The Australian National University, Canberra.

Specimens are housed in the palaeontological collections of the Museum of Victoria, Melbourne (NMV), and the Western Australian Museum (WAM).

Abbreviations used in the figures are listed in the Appendix.

Systematic Palaeontology

Subclass OSTEICHTHYES

Infraclass DIPNOI

Suborder Speonesyrionina

Dipteridae Owen 1846

Remarks. Although the postcranial skeleton is to be described in a future work, it is suffice to say here that the new genus is placed in this family because of the presence of two dorsal fins, the anterior dorsal fin not being reduced as in *Scaumenacia* and *Phaneropleuron* (Phaneropleuridae). However, the modification of the second dorsal fin (in being larger than the first dorsal fin), and the loss of cosmine, indicates that this new form is more derived than *Dipterus*.

Howidipterus n.gen.

Type species. *Howidipterus donnae* n.sp.

Etymology. After Mount Howitt and the well-known

genus *Dipterus*.

Diagnosis. A lungfish having a maximum body length up to 0.5 m. Skull roof approximately 82% as broad as long, and dermal bone pattern highly variable; general configuration with B bone one third as long as skull; C bones equidimensional with E bones; (both E and C being as long as B). D small, being about half the length of the C bones, and about two thirds as broad as long. Paired rostral ossifications anterior to E bone, rest of snout unossified. Occipital commissure passes through A bone. Cheek with deep 1A+B bone, separate small 1C bone. Pterygoid toothplates elongated, subtriangular in form with up to 17 toothridges. Toothridges terminate in the mesial half of each toothplate which has a concave surface, but isolated cusps may be present in this region. Small, narrow anterior median toothed bone present anterior to upper jaw toothplates. Parasphenoid with a diamond-shaped corpus half total length of bone and lacking a buccohypophysial foramen. Externally exposed regions of scales bearing widely-spaced thin bony ridges.

Remarks. The above diagnosis separates *Howidipterus* from the few other known Devonian dipnoans possessing toothplates and a D bone (e.g., *Dipterus*, *Chirodipterus*, *Scaumenacia*, some specimens of *Rhinodipterus secans*) by the unusual morphology of the toothplates, absence of cosmine, general proportions of the skull roof and, where known, the body and fin shape. Most post-Devonian forms which retain a D bone (e.g., *Scaumenacia*, *Ctenodus*, *Tranodis*, *Conchopoma*) are distinguished from *Howidipterus* by having a shorter broader skull roof, the occipital commissure passing through the much enlarged B bone, and the coalescence of the two dorsal fins and anal fin into a diphyccercal caudal fin. *Delatitia*, which also retains bone D, does not have the commissure in B and is distinguished by skull roof proportions.

Howidipterus donnae n.sp.

Figs 1-11, 20A

Etymology. For Donna Long, who diligently assisted in field work at Mount Howitt.

Material. HOLOTYPE, NMV P181884, a cranium showing little abnormal fusion or space capture between skull roof elements (Fig.1A). PARATYPES, NMV P181877 (showing tooth plates, Fig.1B), and NMV P181806 (showing ventral skull bones and lower jaw, Fig.3D). Other material (all NMV specimens): P172632, P181788-P181810, P181860-P181867, P181869-P181873, P181875, P181878-P181883, P181886-P181889, P186574, P186568, P186570. Many other specimens which have not yet been registered are in the Zoology Department, Monash University.

Locality and age. Mount Howitt spur quarry, lower

mudstone, Avon River Group (Long, 1983a, fig.1). Late Devonian (Frasnian), lacustrine facies.

Diagnosis. As for genus, only species.

Description. *Skull roof.* The skull roof bones of *Howidipterus* show considerable variation (Figs 1-5), resulting from fusion and/or space capture, as in most dipnoans. Because of this the description will be based largely on specimens showing the unfused pattern of skull roof elements (e.g., seen in the holotype Fig.1A). A restoration of the head, based on the best specimens, is shown in Figure 6. Cosmine is not present on the skull roof or any other dermal bone, as seen in specimens with some surficial bone preserved. The posterior skull bones are thicker than

the anterior and lateral elements. Surface ornamentation consists of low radiating ridges and isolated small tubercles on skull roof bones, with extensive pitting on some of the circumorbital series carrying the infraorbital sensory line. On average the breadth of the flattened skull roof is about 82% of its length.

Bone A is short, occupying 8% of the skull roof length. Its width is twice its length (Fig.1A,D). Bone B occupies about 25% of the skull length, is raised in its centre and lacks a median thickening on the visceral surface (Fig.1C). The middle and posterior pit-line grooves may both converge towards the centre of B. The occipital sensory-line canal passes from I through to A as in most other Devonian dipnoans. The length of each C bone is more than

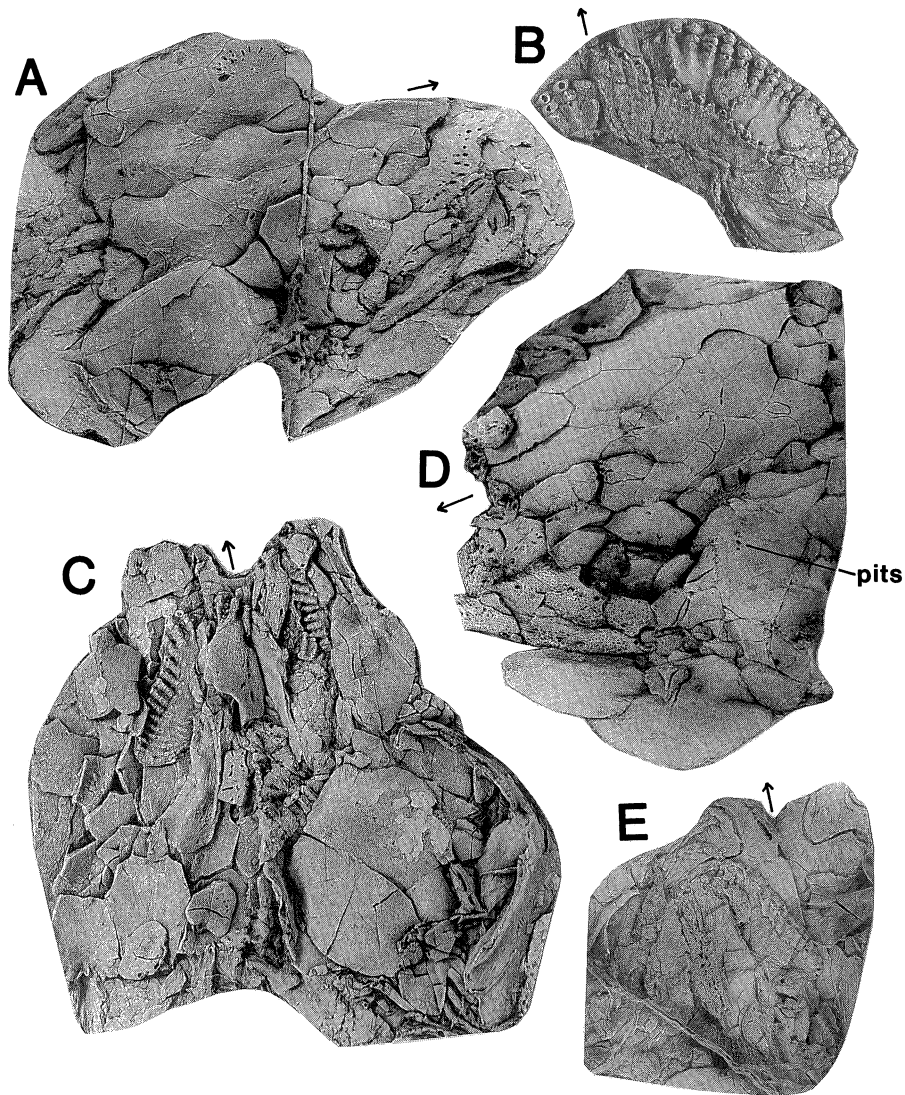


Fig.1. *Howidipterus donnae* n.gen., n.sp. arrow indicates median line and anterior direction. A, holotype NMV P181884, skull and cheek, X1. B, paratype NMV P181877, showing pterygoid toothplates, X1.5. C, NMV P 181799, showing skull roof in visceral view and pterygoid tooth plates, X1.5. D, NMV P 181886, showing skull roof and cheek, X1.5. E, anterior part of skull of NMV P181883 showing rostral bones, X2.

twice their breadth and slightly longer than B, occupying 30% of the skull roof length. C bones laterally contact J, K, L and some contact M bones, and

anteriorly contact the D and E bones. The E bones are narrower and shorter than C bones, and occasionally are divided into anterior and posterior

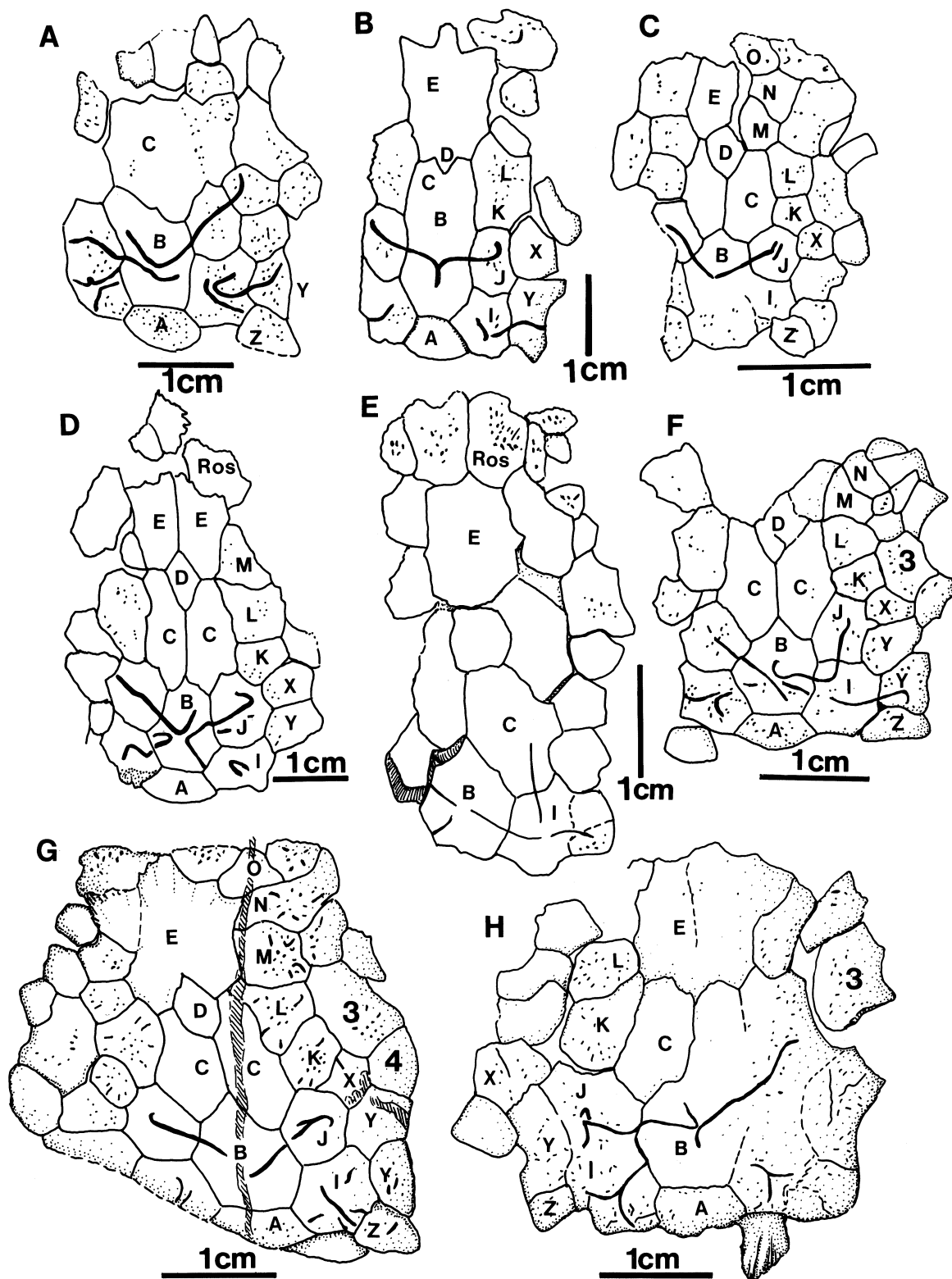


Fig.2. Unusual variations in the skull roof patterns, in dorsal view, of *Howidipterus donnae* n.gen., n.sp. A, NMV P181804. B, NMV P181790. C, NMV P181791. D, NMV P181884. E, NMV P181796. F, NMV P181802. G, NMV P181803. H, NMV P181809.

elements, or fused together (Fig.2B,E) or fused with other lateral bones (Fig.2G,H). Bone D is stable, rarely being subdivided (e.g., P181790). It is quite small, and broad for its length relative to the other roof bones.

The supratemporal series (X, Y1, Y2) occupy about 40 to 45% of the skull roof length. Y2 generally has a strong posterolateral projection which flanks most of Z. There is often a deep notch between Y1 and Y2. Y1 bears a thickening on the visceral surface where it contacted the top of the lateral commissure as in *Chirodipterus*. Y1 has a weak depression in its posterior half so that the visceral thickening

becomes prominent, presumably for contact with the dorsolateral cristae of the neurocranium as in *Chirodipterus* (Miles, 1977).

A maximum of seven elements has been recorded on the supraorbital lateral line canal (P181800) but commonly there are four or five: K, L, M and N, and subdivisions of these. In the extrascapular series there are three bones usually present: Z, A, Z. In some specimens there appears to be a small bone present behind A and Z, possibly the G bone. It is very thin compared to the other extrascapulars. Posterior to Z on some specimens there is an element carrying the lateral line canal which is here

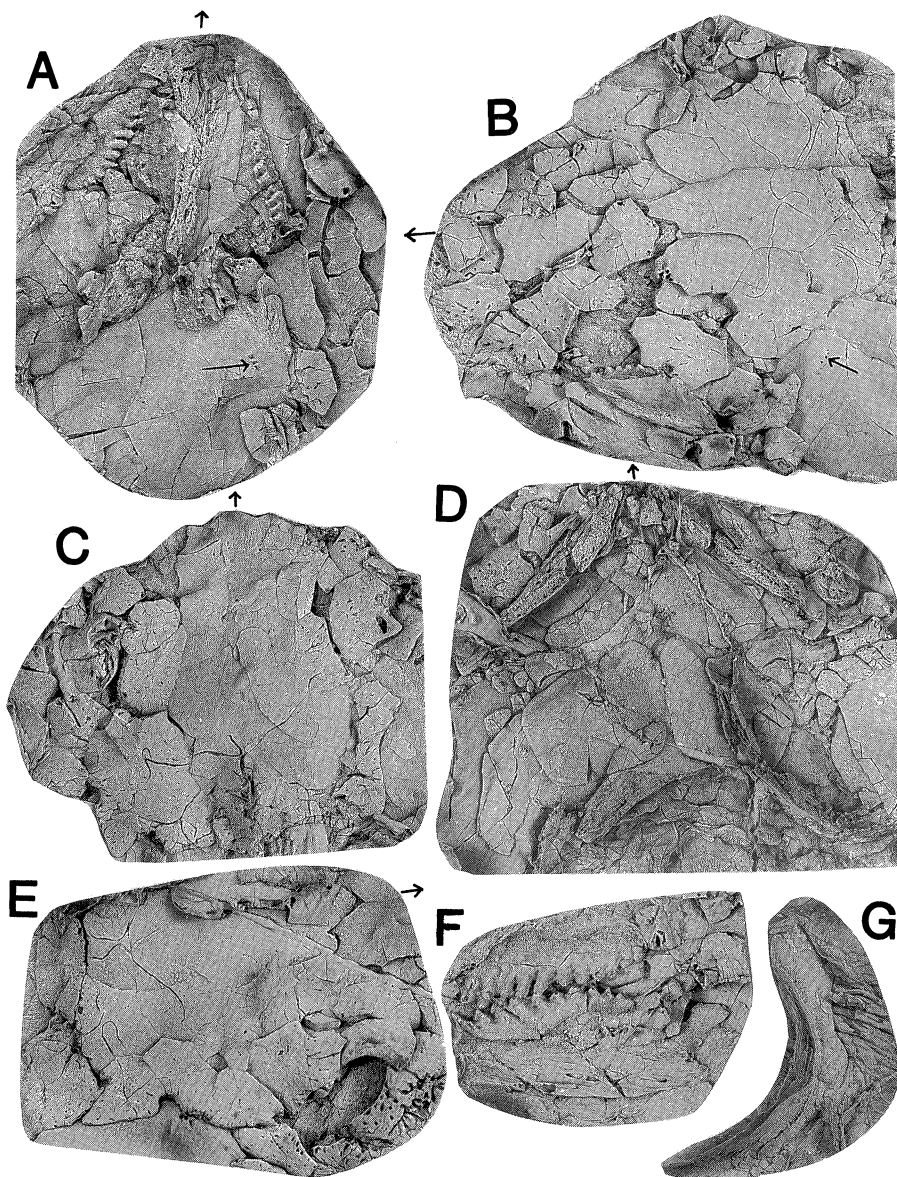


Fig.3. *Howidipterus donnae* n.gen., n.sp., arrow indicates median line and anterior direction. A, NMV P181863, showing pterygoid toothplates and lower jaw, x2. B, NMV P181880, showing skull roof and cheek, x1.5. C, NMV P181809, showing skull roof and cheek, x1.5. D, paratype NMV P181806, showing skull bones in ventral aspect, including both lower jaw rami, x1.3. E, NMV P181805, skull roof in dorsal view, x1.5. F, NMV P181888, showing upper and lower jaw dentition in occlusion, visceral aspect, x2. G, cleithrum and clavicle of NMV P181883, x2.

interpreted as a post-temporal. It is an external bone and lacks forward processes, thus distinguishing it from the subdermal anocleithrum of other Dipnoi (e.g., *Scaumenacia* Jarvik, 1980; *Eoectenodus* Long, 1987b). An anocleithrum has not yet been seen in the material of *Howidipterus*.

Cheek. The circumorbital series normally comprises bones 1 to 7, and these are relatively high as in *Dipterus* or *Scaumenacia*. In some cases bone 7 may be absent as an independent element and bone 4 may be excluded from the orbital margin. Posterior to bone 5, bones 8 and 9 are constantly present and partially overlies the operculum. The region ventral to bone 9 is rarely well preserved but it appears that there are normally 3 to 7 elements of approximately the same size (Figs 10, 9b-9g), these being just a little smaller than bone 9a. Bone 1a+b is rather deep anteriorly and can be readily used to distinguish *Howidipterus* from *Barwickia*, in which this element is very narrow. A small bone 1c is present as in *Chirodipterus* (Miles, 1977; Campbell & Barwick, 1982). Dorsal to bone 2 bone 0 is usually present. The space normally occupied by these elements may, however, be occupied by a single bone (e.g., P1818000) or the 0 space may be captured by supraorbital lateral line elements (e.g., P181794, P181795).

Snout. The tip of the snout and its ventral surface with narial grooves is not seen in any specimen and was probably unossified. There are two separate rostral elements (Ros) that meet in the midline on the dorsal surface of the nasal capsule; these elements carry a loop of the supraorbital sensory line.

Sensory line system. The lateral line system of the skull roof of *Howidipterus* is developed as normal for other Middle and Late Devonian dipnoans (e.g., *Scaumenacia*, *Dipterus*, *Rhinodipterus*; Lehman, 1966; Stensiö, 1947; White, 1965). Bone 3 carries a short anterior extension of sensory line canal from bone 4. Pit lines are well developed on the skull roof, cheek and gulars. They are deeply incised into the

dermal bones, and often show irregularities in their course.

Palate. The palate is not completely preserved on any one specimen, but it can be reconstructed using a number of specimens (Figs 1C,3A). Most specimens show just the pterygoids and upper toothplates. Where the parasphenoid is preserved it is composed of very thin, cancellous bone. It is of normal shape for a Late Devonian dipnoan having a stalk and a rhombic corpus, the latter comprising about half the total parasphenoid length. The buccal surface of the corpus is smooth apart from a median thickening where the stalk meets the corpus, as in *Eoectenodus* (Long, 1987b). The region where the buccohypophysial foramen is expected to be found is not preserved on any specimen, and the anterior end of the corpus is here reconstructed from its adjacent contact with the pterygoids.

The posteromesial margins of the pterygoids are gently concave and the boundary with the parasphenoid well marked. There is a small anterior median bone (Campbell & Barwick, 1984; vomer, Miles, 1977) present in a few specimens (Fig.7), here labelled as the vomer. It is a very narrow, curved element which bears rounded tubercles. It does not appear to be paired, so it is assumed to be a median bone and reconstructed in this position (Fig.8).

Lower jaw. Although the lower jaw is present in many specimens the symphyseal region is usually poorly preserved and the glenoid fossa has not been observed (Fig.9). Specimen P181880 indicates that lower jaw was probably close to 65% of the skull length. The angular is the largest element in the lower jaw, occupying about half its length. It has two distinct regions: a thick section forming most of the ventral and some of the lateral face of the lower jaw, and a thin ascending lamina which occupies most of the lateral and some of the ventral face posteriorly. The surface of the former is pitted and meets the post-splenial at a V-shaped suture. The course of the oral and mandibular sensory-line canals

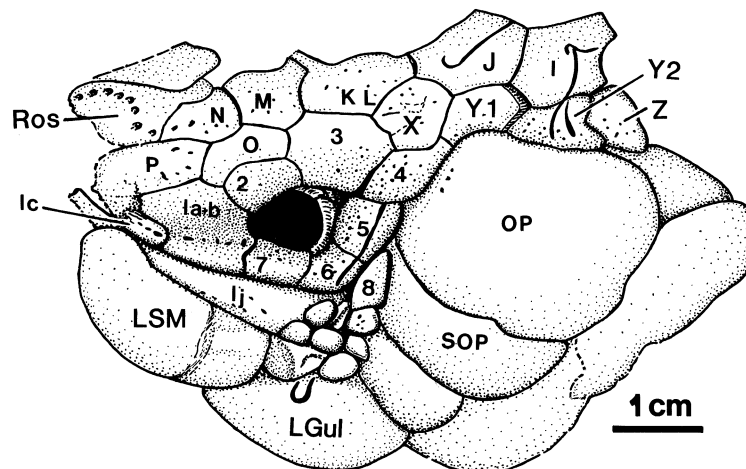


Fig.4. *Howidipterus donnae* n.gen, n.sp. Head of NMV P181799 showing well-preserved cheek bone pattern, lower jaw and ventral bones of the head.

is marked by very large, irregularly-shaped pores. The postsplenial is much shorter than the angular, and has a similar external appearance. An elongate depression on the lateral face indicates a labial pit extended back onto the postsplenial. The postsplenial is gently concave where it joins anteromesially with the splenial. The anastomosis between the mandibular and oral sensory line canals is visible on P181806, represented by two large, elongated pores. The internal face of the postsplenial is hollowed out along its entire length for the Meckelian cartilage. In all specimens showing this there are two foramina with grooves running a short distance posteriorly. These correspond to those identified by Thomson & Campbell (1971) on *Dipnorhynchus* as for the first efferent branchial artery and the anterior ramus

intermandibularis V, and the second foramen for the ramus mentalis internus VII and the ramus alveolus VII. In *Howidipterus* these foramina are of about equal size.

The splenial is a small, 5-sided element, the longest edge forming the mesial suture with its antimere. Only one example of the dentary is seen in the material (P181799). It is clearly a paired element, as in *Uronemus* and possibly *Conchopoma* (Watson & Gill, 1923). The surface of the dentary is quite smooth, like the ascending lamina of the angular.

The prearticular is divided into a thick section bearing the dentition and a thin descending lamina which forms most of the mesial face of the jaw. The descending lamina is smooth, and bears four large foramina and numerous smaller foramina just dorsal to

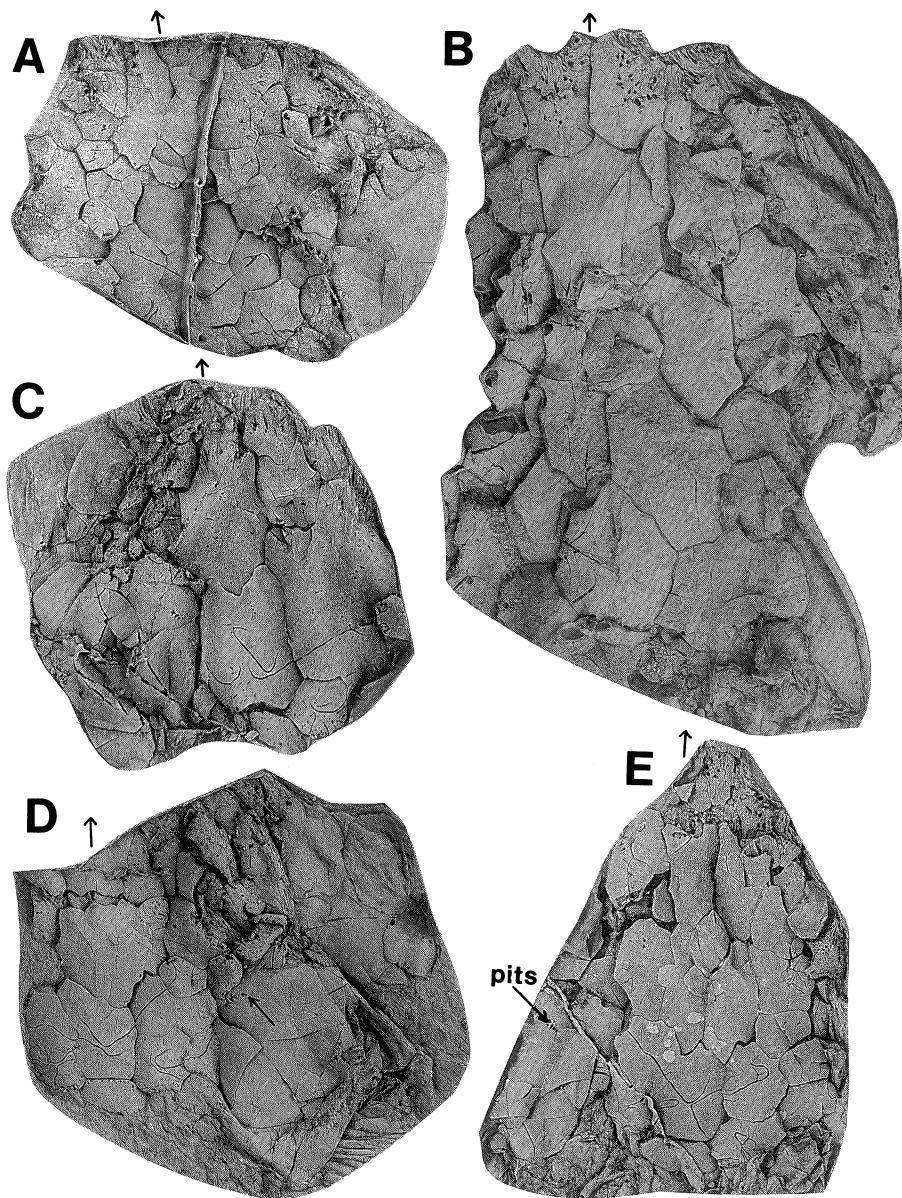


Fig.5. *Howidipterus donnae* n.gen., n.sp., arrow indicates median line and anterior direction. All are skull roofs in dorsal view, some also showing cheek bones. A, NMV P181803, x1.5. B, NMV P181796, x1.5. C, NMV P181882, x1.5. D, NMV P181804, x1.5. E, NMV P181884, x1.5.

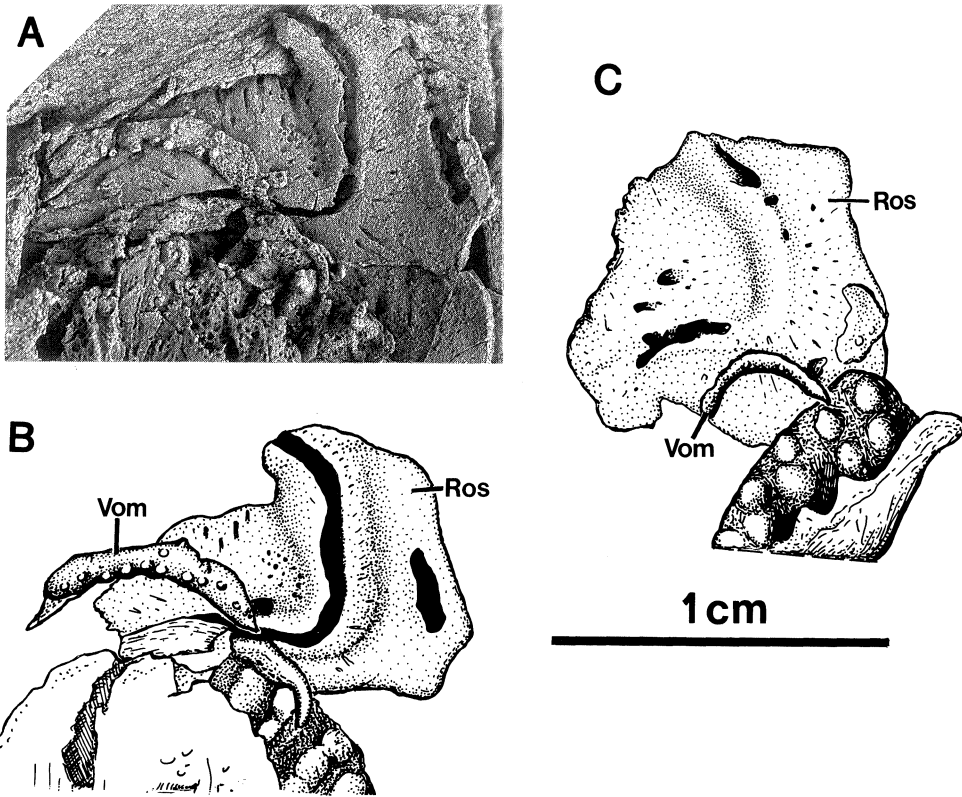


Fig.7. *Howidipterus donnae* n.gen., n.sp. A, B, NMV P181883 showing anterior toothed bone (vomer, Vom). C, NMV P181880, also showing vomer.

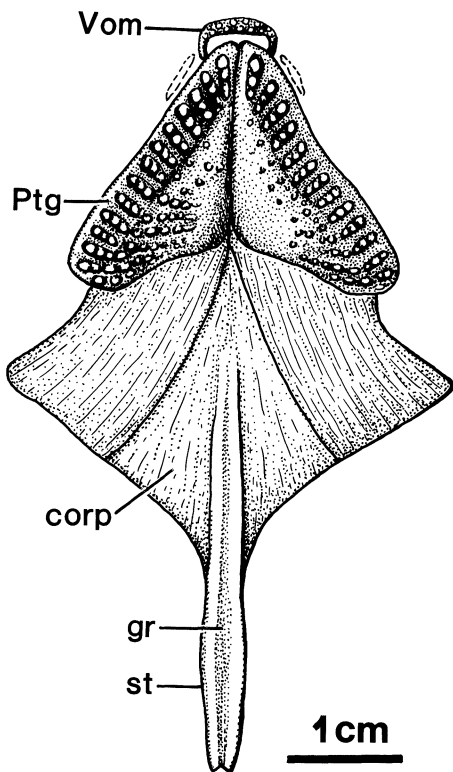


Fig.8. *Howidipterus donnae* n.gen., n.sp. reconstruction of palate showing pterygoid toothplates and parasphenoid.

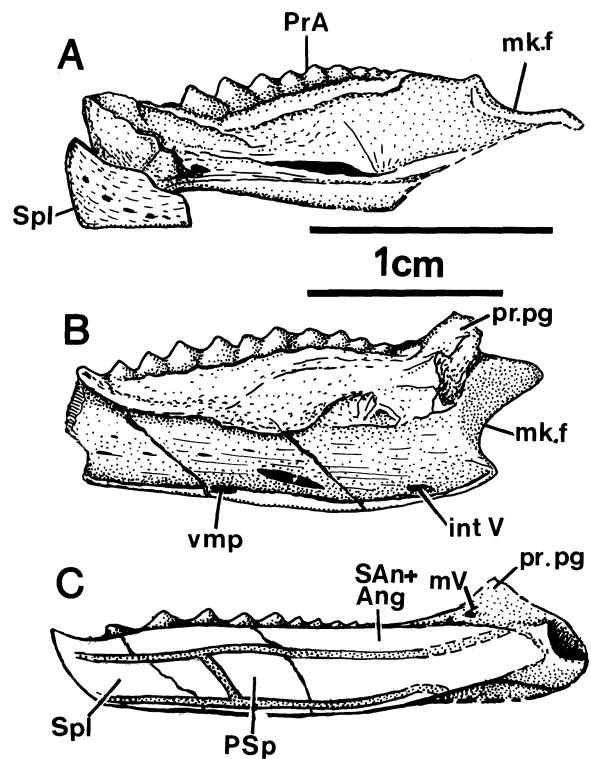


Fig.9. *Howidipterus donnae* n.gen., n.sp. Lower jaw bones. A, B, internal views. A, NMV P181792. B, NMV P181888. C, reconstruction of left ramus of lower jaw in lateral view.

of the area mesial to these functional cusps is worn down to a level much lower than the margins of the toothplate. Some secondary cusps may be present on this wear surface, which do not fit in with the radiating pattern of the cusp rows. The functional teeth are close together in each row. The teeth terminate mesially very abruptly, with worn teeth mesial to the functional teeth not usually preserved at all. Wear pits between teeth are generally not deep. The dentition of the anterior median bone, or vomer, comprises small peg-like teeth arranged in across the bone (Figs 6,7). The prearticular dentition is essentially the same as that of the pterygoids.

Operculogular bones. The operculogular series of *Howidipterus* is well represented. The operculum is a large, thick, more or less rounded bone, being clearly longer than high. There is a slight anterodorsal process which fits into a notch between the Y elements as in *Delatitia* (Long & Campbell, 1985). Some specimens show quite large foramina or surficial pits in the bone on the external surface of the operculum, numbering between 3 and 8 (Figs 1A,C,D; 3A,B; 5E). These can also be seen on the visceral surface, but their function is unknown. The subopercular 1 is shorter than the operculum, slightly thinner and about one third as high as that bone. About 40% of this bone was overlain by the operculum. There is a raised area with large pits on the visceral surface of P181806, possibly correlating with the "...distinct pit with roughened surface..." and the "...well defined knot of bone..." reported for *Griphognathus* and *Holodipterus* by Miles (1977: 253, 256). This feature is more

posteriorly placed than in the two Gogo forms. Miles considered this area as possibly for attachment of the hyosuspensory eminence of the neurocranium. Subopercular 2 is poorly represented in the material, being mostly covered by the principal gular. It is somewhat triangular in form, not as long as subopercular 1 but with approximately similar exposed surface area (Fig.4).

The lateral gular is the second largest bone of the skull apart from the operculum. It is of trapezoidal shape with rounded corners, and there are overlap areas along the anterolateral edge for the two submandibulars. There is no evidence that the gulars overlapped each other very extensively, as in other dipnoans (*Speonesydrion*, *Dipterus*, *Scaumenacia*; Campbell & Barwick, 1984b; Westoll, 1949). The median gular is small, rounded anteriorly and drawn out posteriorly. When overlapped by the submandibulars and gulars only a small diamond-shaped area of the median gular is exposed. The lateral submandibular plate is suboval in shape, somewhere between the shapes of the bone in *Dipterus valenciennesi* and *Scaumenacia*. The posterolateral submandibular is triangular with rounded edges as in *Scaumenacia* and *Chirodipterus australis*. Anterolaterally it bears a large overlap area for the lateral submandibular plate. The median submandibular is a small diamond-shaped bone with two cusped pitlines (Fig.10).

Scales and surface ornament of bones. The surface of the skull roof bones has a fine pustular ornament with radiating grooves present near bone margins (Fig.11). The scales have a surface ornamentation of

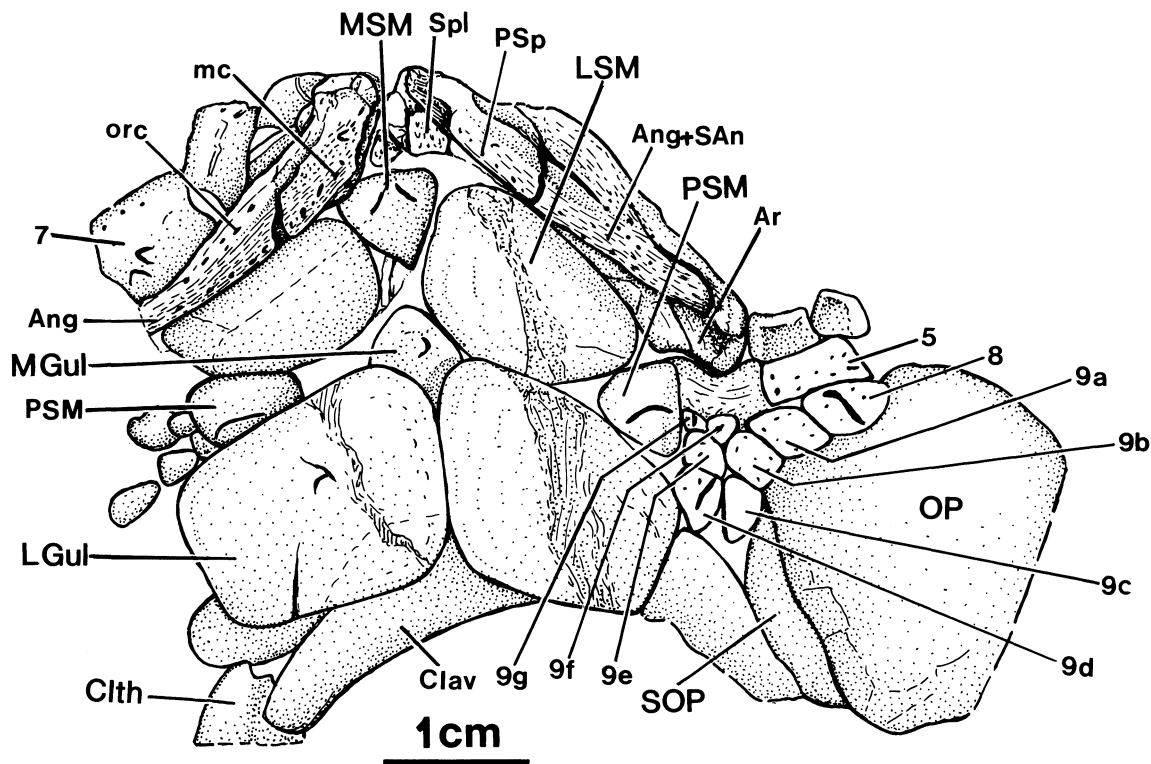


Fig.10. *Howidipterus donnae* n.gen., n.sp. NMV P181806, showing ventral bones of the head.

gently curved thin ridges of bone which are widely spaced, with smaller curved ridges occurring between them (Fig.20A). In this respect they are not 'packed' with radiating ridges as in *Scaumenacia* nor are they considered sparsely ornamented as described in *Eoetenodus* (Long, 1987b). In general the coarser ornamentation of the scales of *Howidipterus* make it easy to distinguish from the finer ornamentation of the scales on *Barwickia*.

Suborder Uranolophina

Fleurantiidae

Remarks. The family Fleurantiidae includes *Fleurantia* and *Jarvikia*, both of which share a skull with an elongate snout, a large single snout bone anterior to the C bones, and one large bone lateral to C incorporating K, L and M bones. The body is well known in *Fleurantia*, but not at all for *Jarvikia*. The new genus is provisionally assigned to this family because it shares a similar body plan to *Fleurantia* with

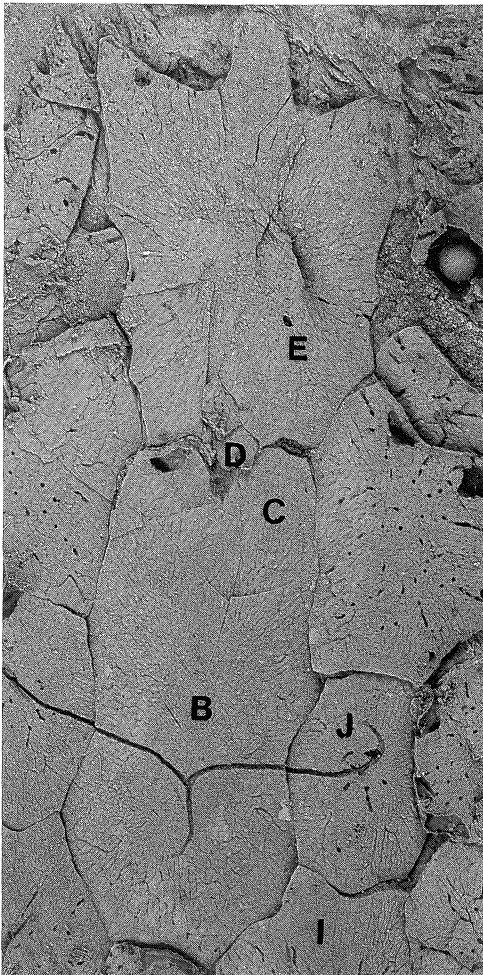


Fig.11. *Howidipterus donnae* n.gen., n.sp. Detail of surface bone ornamentation, NMV P1181790.

one enlarged dorsal fin (the posterior one), and has a similar cheek bone pattern to *Fleurantia* with bone 10 lost from the cheek unit (unlike the rhynchodipterids *Griphognathus* and *Soederberghia*, Miles, 1977; Lehman, 1959).

Barwickia n.gen.

Type species. *Barwickia downunda* n.sp.

Etymology. In honour of Dr Richard Barwick, Zoology Department, The Australian National University, for his contributions to the study of fossil lungfish.

Diagnosis. A dipnoan having a denticulate dentition and a skull roof which is about 60% as broad as long with a large B bone, indented posteriorly for the I bones: D small, sliver-like; C bones as long as B but considerably narrower; E bones elongated, often shorter and narrower than C bones. K absent. Infraorbital bone 6 very elongated, incorporating bone 7. Rostral bones anterior to E bones are absent. Body shape and fin disposition as for *Fleurantia*.

Remarks. *Barwickia* is readily distinguished from the only other Devonian dipnoans having a denticulate (i.e., denticle-shedding) dentition by its body shape, short snout and skull roof pattern. It differs from *Fleurantia* in the skull roof retaining a D-bone, by the shorter snout, and several details of the postcranial skeleton (not yet described, author's observation). It is readily distinguished from *Howidipterus*, not only by the presence of tooth-plates in the latter form, but also particularly by the skull roof having narrow E bones and lacking rostral ossification, by the very slender 6+7 bone below the orbit, and by having scales with finer ornamentation.

Barwickia downunda n.sp.

Figs 12-19, 20B

Etymology. A fortuitous collocation of letters.

Material. HOLOTYPE, NMV P181782, a good skull and cheek, with counterpart showing the palate and dentition (Fig.14). Other NMV specimens: P181780-P181787, P181868, P181874, P181876, P181885, P181890, P186566, P186567, P186573, P186575-77, P181579. WAM material: 90.7.1-90.7.7.

Locality and age. From Mount Howitt, in the lower mudstone, Avon River Group. This genus is more prevalent in the upper sections of the Mount Howitt fish beds exposure (snig track-"J" localities, about 50 m due east of main quarry, as marked in Long, 1983a, fig.1, "locality 8"). Upper Devonian (Frasnian).

Diagnosis. As for genus, only species.

Description. As in *Howidipterus* there is no evidence of cosmine in the dermal skeleton of *Barwickia*. The bones, particularly the anterior elements, are rather thinner than for the previous genus, and the ornamentation is much finer, consisting of pits and fine radial striae.

Skull roof. The skull of *Barwickia* is about 60% as broad as long (Fig.13), and the pattern of skull roof bones is notably less variable than for *Howidipterus*. In

one example (WAM 90.7.7, Figs 12D, 13C) there is an unusual abnormality in which the I bones meet mesially behind the B bone, a condition otherwise seen only in primitive Early Devonian lungfishes (*Uranolophus*, *Dipnorhynchus* and *Speonesydrion*; Schultze & Campbell, 1987; Campbell & Barwick, 1987).

Bone B is about 30% of the skull roof length, and is indented posteriorly for the I bones. It bears a well-developed occipital flange, also found on the I bones, for overlap of the A bone, and anteriorly is a well-

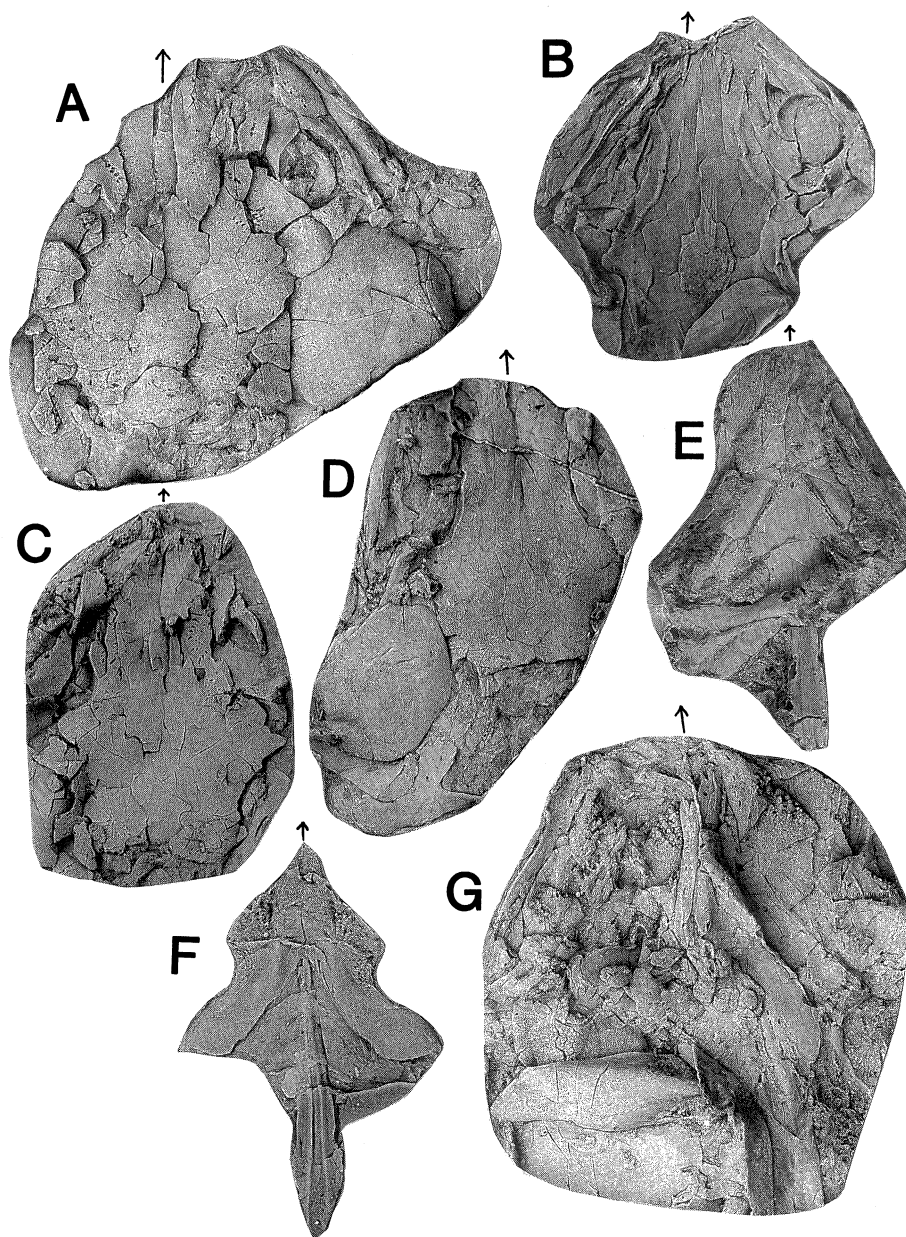


Fig.12. *Barwickia downunda* n.gen., n.sp., arrow indicates median line and anterior direction. A, G, WAM 90.7.1, showing (A) skull roof, cheek and lower jaw in external view, x1.5; and (G) aspects of the visceral skeleton and upper jaw dentition, x2. B, NMV P181780, showing skull roof and cheek in visceral view, x1. C, NMV P186566, showing skull roof, x1.3. D, WAM 90.7.1, showing abnormal skull roof pattern with I bones in mesial contact behind B bone, x1.5. E, NMV P181868, showing parasphenoid and pterygoids in ventral view, x1. F, NMV P181780 showing parasphenoid and pterygoids in dorsal view, x1.

developed point inserted between the C bones. Although B lacks a median thickening on the visceral surface, the Y1 and Y2 elements have thickenings for the quadrate and dorsolateral cristae of the braincase. The C bones are long but much narrower than the B bone. They are thin, as many specimens show postmortem cracking of these bones. Occasionally the C bones may be extended to occupy the E space (P181780, WAM 90.7.7, Fig.13C). The E bones are elongate and narrower than the C bones, and may terminate at an irregular anterior margin. In some cases, the C and E bones have fused

(Fig.13B,C). There is no evidence of separate rostral bones anterior to E bones, nor any evidence that the snout was ossified. The D bone is very narrow, and is absent in one specimen (P181786). The supratemporal series is slightly longer than for *Howidipterus* due to longer Y bones. There is no notch between the Y bones, and the posterolateral projection of Y2 is weakly developed. The supraorbital lateral line series generally contains 3 or 4 bones: K, L, M, N or fused variants of these bones. M is particularly long and in some specimens fits into a V-shaped notch between L and C (Fig.13D). N is small and has an irregular

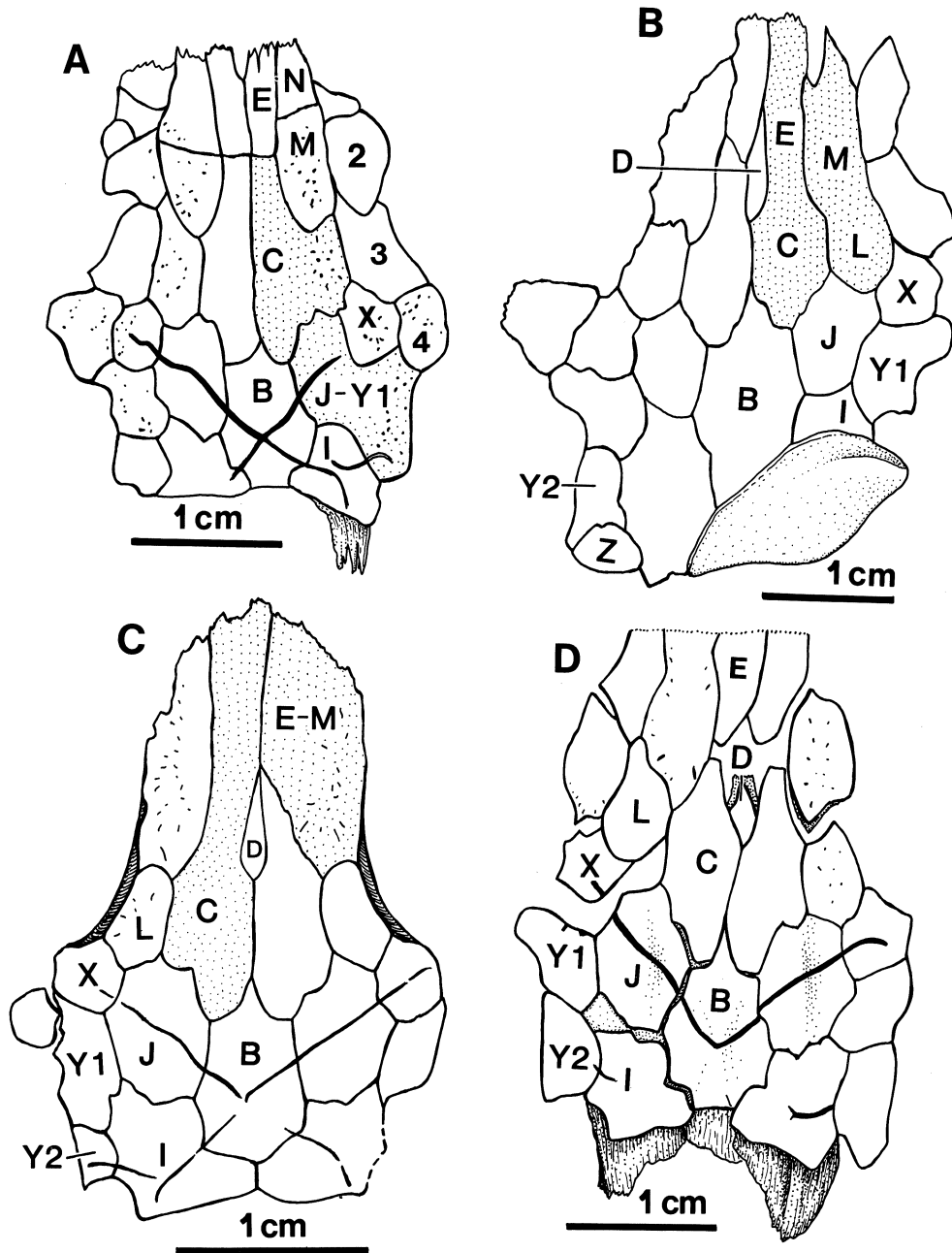


Fig.13. *Barwickia downunda* n.gen., n.sp., showing variations in skull roof patterns, with bone fusions shown as stippled areas. A, NMV P181786, dorsal view. B, NMV P181780, ventral view. C, WAM 90.7.1, dorsal view. D, NMV P181885, dorsal view.

anterior margin as in the E bones. The extrascapular bones comprise only Z-A-Z elements, with no evidence for G being present. Bone A is preserved *in situ* in a few specimens, suggesting it was loosely attached to the rest of the skull. In WAM 90.7.1 (Figs 12A, 15) it is shown as a robust quadrilateral bone deeply inserted into the skull roof, but in other specimens it is absent (WAM 90.7.7., Fig.13C).

Cheek. The pattern of cheek bones is quite variable and two variations are reconstructed in Figures 19B and C. The circumorbital bones are fewer in number than for *Howidipterus*. Bone 4 is larger and participates in more of the orbital margin than in the

previous species. Bone O is always separately developed and large, with sometimes a smaller element anterior to it. As in *Fleurantia* (Graham-Smith & Westoll, 1937) the posteroventral, ventral and anteroventral margins of the orbit are bounded by only two bones, here designated 4 and 5 (Fig.19B), or combinations with 4+5 and 5+6 (Figs 14, 19C). Anterior to the very long and relatively thin 6+7 bone is a small but elongated 1a bone. The narrowness of these elements suggests that the skull of *Barwickia* was flatter anteriorly than in *Howidipterus*. Ventral to bone 4+5 in P181782 (Fig.14) there are five small elements, three of which are presumably bones 8, 9a, 9b and 9c, indicating extreme

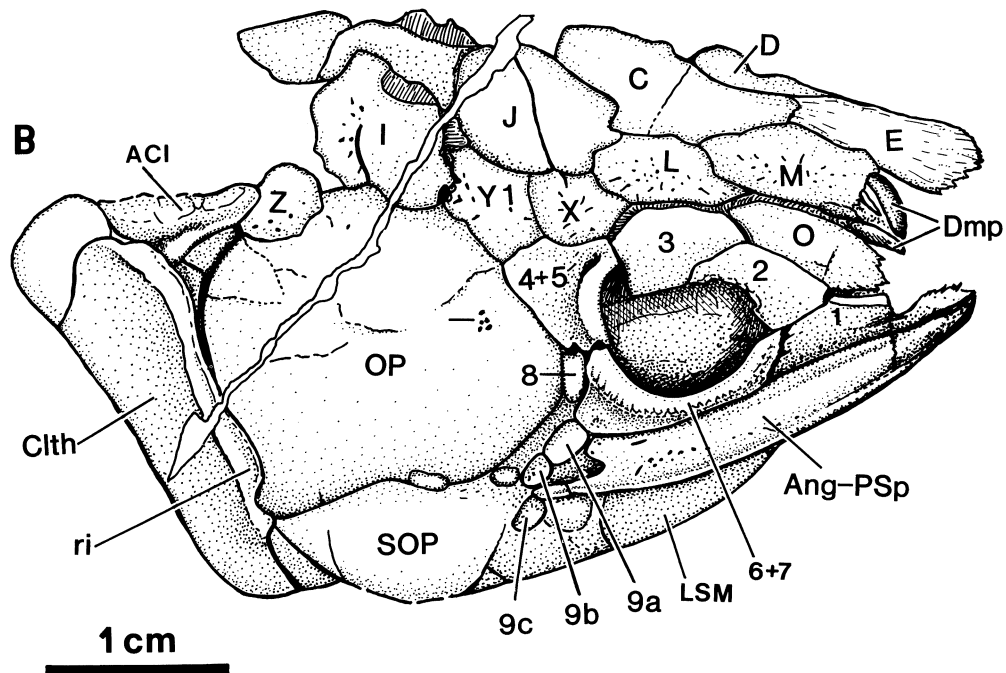


Fig.14. *Barwickia downunda* n.gen., n.sp., holotype specimen, NMV P181782, showing head in right lateral view.

reduction of these elements in *Barwickia*.

Sensory line system. The courses of the lateral line system in *Barwickia* are directly comparable with *Howidipterus*. Bone 3 sometimes has a short section of lateral line canal entering from bone 4, shown clearly by the visceral surface of P181780 (Fig.12B). The surface pit lines are not as deeply incised into the bones as those of *Howidipterus*. No pit lines are visible on bones 5, 6 or 8 in *Barwickia*.

Palate and dentition. The palate of *Barwickia* is well preserved in several specimens. Both P181780 and the holotype show the palate and part of the dentition (Figs 12E,F,G; 17). The parasphenoid (Fig.12E,F; restored in Fig.17) has a smooth buccal surface to the corpus with a well-defined buccohypophysial foramen. The stalk is slightly shorter, but much broader than for the previous species, terminating in an expanding region with a well-defined notch. It is grooved on the buccal surface. The pterygoids are composed of compact bone with radiating rows of large denticles with interspersed smaller denticles. The denticles are only found close to the lateral margins of the buccal surface of the pterygoids and prearticulars, not forming an extensive cover of denticles as occurs in *Griphognathus*, but similar to the condition in *Fleurantia*. There is no evidence of these tooth rows being formed on well-defined tooth-plate bases that attach to the pterygoid as in dipterids, and it is evident that *Barwickia* was a denticulate lungfish (*sensu* Campbell & Barwick 1986, 1990). This is seen

not only from the morphology of the pterygoid and prearticular biting surfaces, but also in the fact that the hyoid arch is more strongly ossified than in *Howidipterus*, a condition better developed in the rasping feeders (e.g., *Uranolophus*, *Griphognathus*, Campbell & Barwick, 1983 1987, 1988).

Lower jaw. The lower jaw is poorly known from the material, and the course of the sensory line canals is only estimated from observation of pores in these few specimens. It is estimated to have been about 70% of the length of the skull roof. The combined angular plus postsplenial bone occupies most of the lower jaw length, forming most of the dorsolateral face of the lower jaw. Anterior to this long bone is a short, rather featureless splenial bone. In mesial view the angular + surangular bone bears a well-developed high pregenoid process (Fig.18C,D,E) as in other denticulate forms (e.g., Campbell & Barwick, 1986), with a well-rounded, narrow glenoid fossa. A small opening for the mandibularis V nerve is present just anterior to the pregenoid process (Fig.18B). Only small fragments on the prearticular are seen, and therefore the overall shape of this bone cannot be described. A small area of denticles is seen on the prearticular of P181890 (Fig.18A).

Operculogular bones. The operculogular series is poorly known apart from the operculum, as there is only one specimen showing part of the ventral surface of the head. The operculum is not as deep relative to its length as in *Howidipterus*. It is strongly

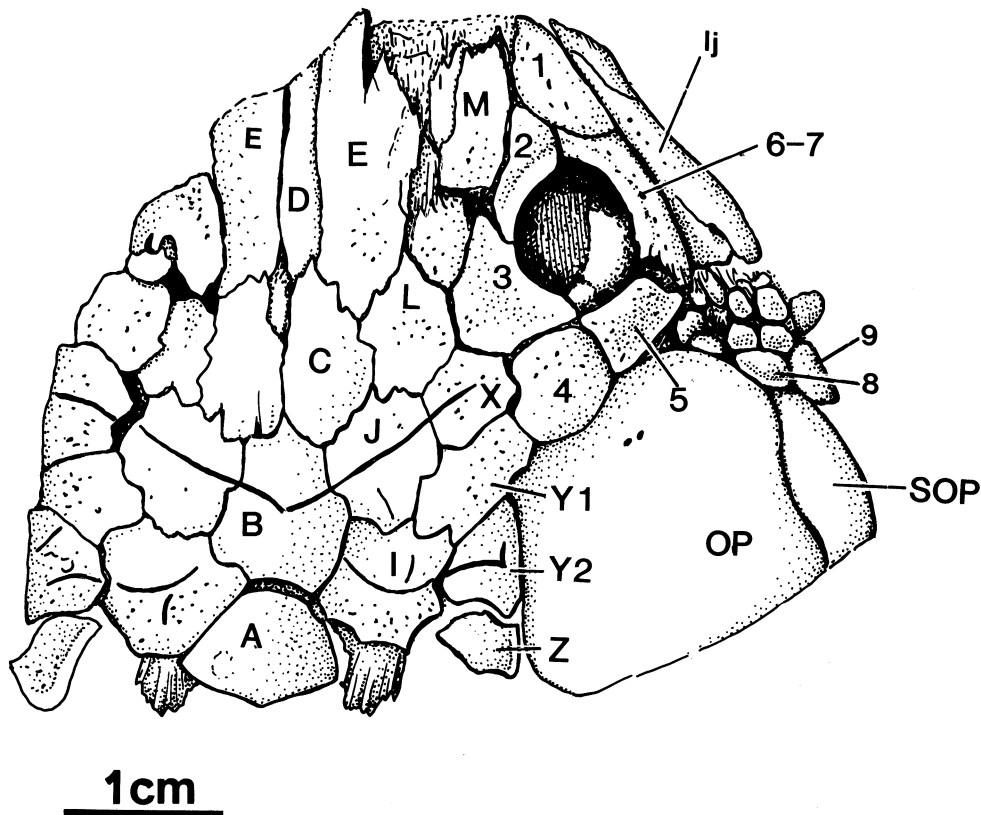


Fig.15. *Barwickia downunda* n.gen., n.sp., WAM 90.7.1., showing bones of the head in external view.

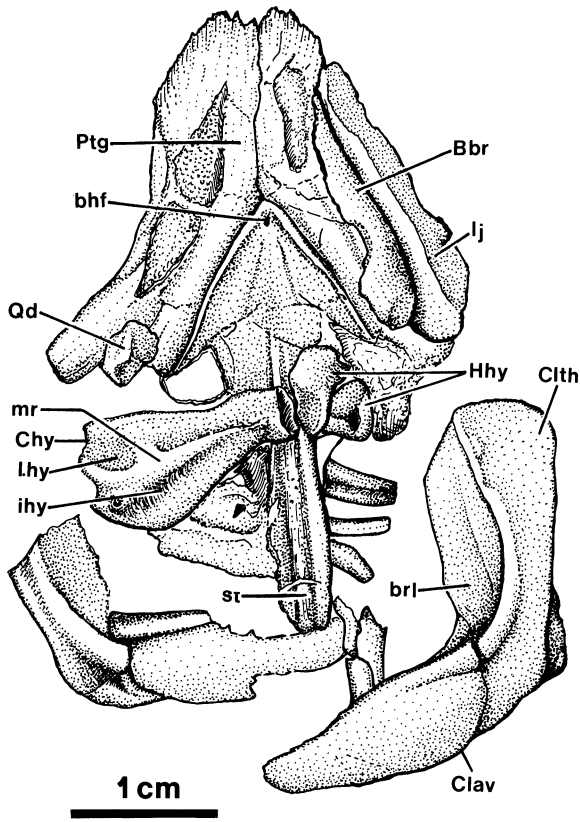


Fig.16. *Barwickia downnunda* n.gen., n.sp., NMV P181868, showing parasphenoid and pterygoids in dorsal view, with elements of the visceral skeleton and shoulder girdle.

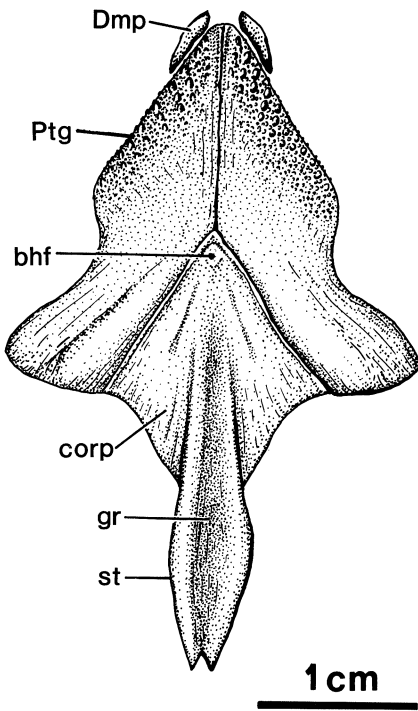


Fig.17. *Barwickia downnunda* n.gen., n.sp., reconstruction of parasphenoid, pterygoid toothplates and vomers in ventral view, based on NMV P181780.

arched anterodorsally with an anteroventral projection reaching into the cheek to occupy the equivalent area that bones 8 and 9 occupy in *Howidipterus*. There is no scarred area on the visceral surface but there may be pits present on the external surface. Suboperculum 1 has not been positively identified, although in P181782 a bone below the operculum is probably this element. It is obscured dorsally by the operculum and ventrally by matrix, but indicates at least that it was greatly overlain by the operculum. Ventral to this bone and partially obscured by it is an element with a visceral surface exposed. It is oval and too large to be a posterior submandibular so it is probably a subopercular 2. P181890 shows a principal gular plate which is shaped similarly, and of comparable size to that bone in *Howidipterus*. The ventral operculogular bones of *Barwickia* need further investigation.

Visceral skeleton. The right ceratohyal is preserved in P181868 (Fig.16), and both ceratohyals, although poorly preserved, are seen in P181579. They are large bones, well ossified and about equal in size to the clavicle. It is of similar shape as the ceratohyal in other dipnoans (*Griphognathus*, *Chirodipterus*, *Uranolophus*, Miles, 1977; Campbell & Barwick, 1988). The lateral face bears a prominent crest running the full length of the bone and terminating posteriorly in a Y-shape.

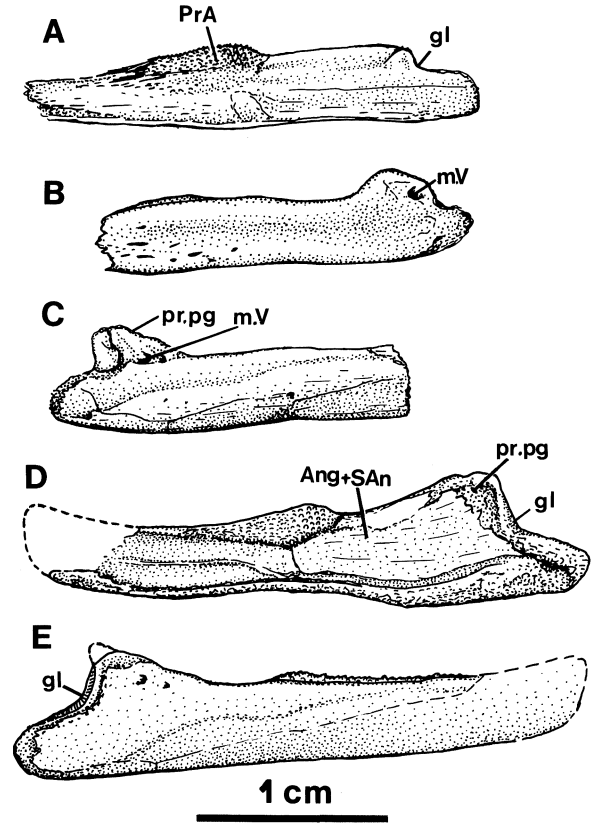


Fig.18. *Barwickia downnunda* n.gen., n.sp., lower jaw bones. A, NMV P181890. B, WAM 90.7.1. C, NMV P181874. D, E composite restorations of the right ramus of the lower jaw in mesial (D) and lateral (E) views.

Anteriorly there is a pitted depression for the insertion of the levator hyoideus muscle, although it is smaller than for *Griphognathus*, being more similar in size to that in *Chirodipterus*. Ventral to the median crest about midway between the dorsal and ventral margins is a deep, slightly pitted groove for the insertion of the interhyoideus muscle. The mesial face of the ceratohyal is depressed along the centre and thin dorsally. Small foramina and grooves are evident close to the ventral margin near the weakly concave articulation surface for the hypohyal. There is no sign of a ventral notch as figured by Miles (1977, fig.136c) for *Griphognathus*.

Overall the ceratohyal of *Barwickia* is more like that of *Griphognathus* than that of *Chirodipterus* in its flatter cross-sectional shape.

The hypohyal is also preserved in both specimens, associated with the ceratohyal. The ceratohyal and basibranchial articulation surfaces are tentatively identified, the latter being depressed, suggesting the bone was not completely ossified. P181869 shows traces of the left epibranchial elements, each being smaller than the element anterior to it. Little information can be obtained from these except that they were weakly ossified.

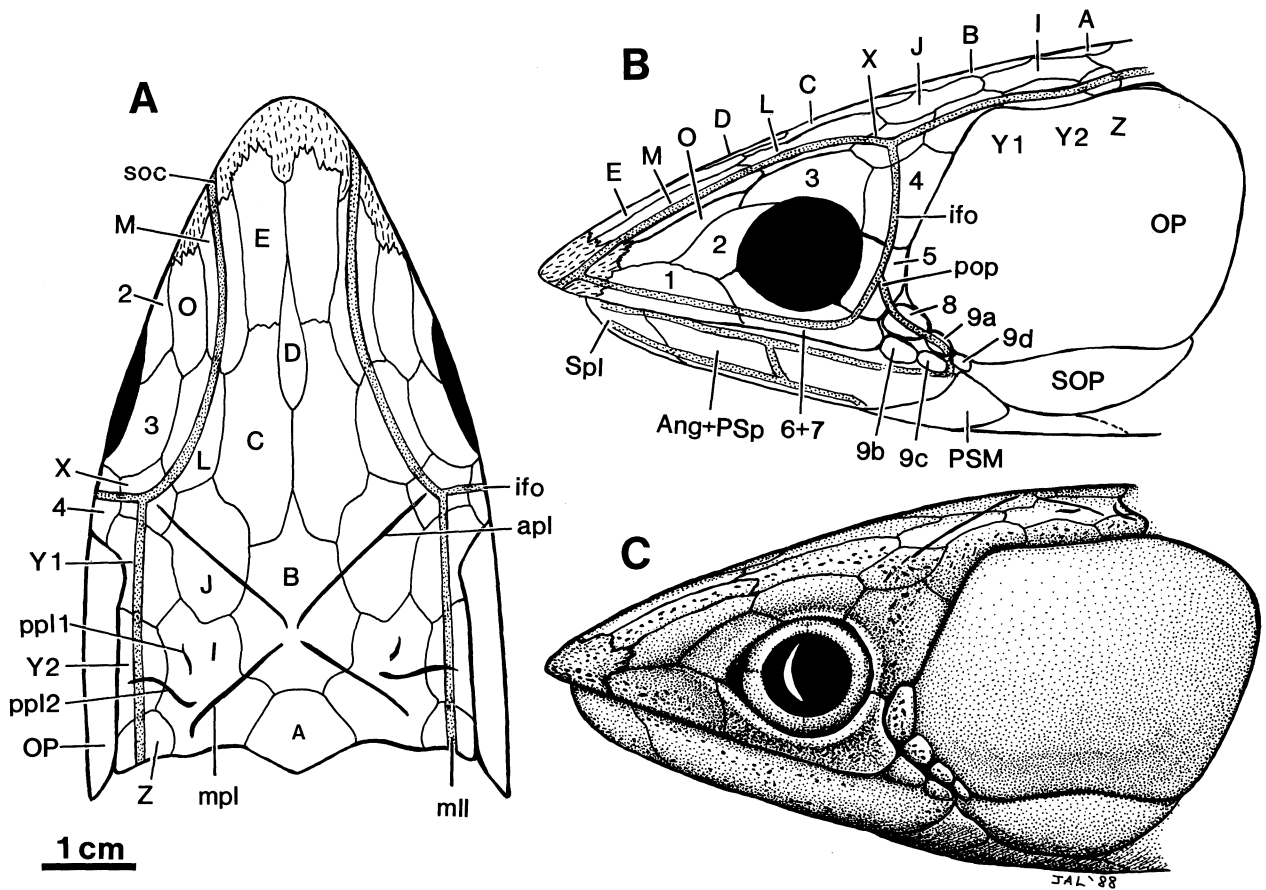


Fig.19. *Barwickia downnunda* n.gen., n.sp., showing restoration of the head in dorsal (A) and lateral views (B, C). The two lateral views show variations in the infraorbital bones.

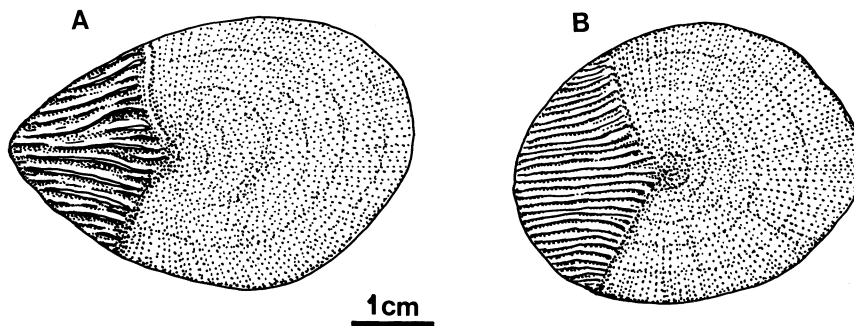


Fig.20. Composite reconstructions of the scales in external views of A, *Howidipterus donnae* n.gen., n.sp., and B, *Barwickia downnunda* n.gen., n.sp. Bar scale = 1 mm.

Comparisons with Other East Gondwana Late Devonian Lungfishes

Few fossil lungfishes have been described from the East Gondwana region (incorporating Australia and Antarctica, Young, 1981) and the new genera can be easily distinguished from other contemporaneous forms, both described and undescribed material. The known forms include the marine Gogo fauna from Western Australia (Miles, 1977; Long, 1988b; Campbell & Barwick, 1990), *Eoectenodus* from Victoria (Long, 1987b), and various undescribed fragmentary remains from New South Wales and central Australia (e.g., Long & Turner, 1984). The Gogo Formation contains the chirodipterids *Chirodipterus* and *Pilliarhynchus* (Miles, 1977; Campbell & Barwick 1990); the rhynchodipterid *Griphognathus* and the holodontid *Holodipterus*. These genera, because of their exquisite preservation, are readily distinguished from the new genera by their overall cranial shape and dentition. The *Soederberghia* skull described from the Cloghnan Shale of New South Wales (Campbell & Bell 1982) differs in its long snout and skull roof pattern.

Eoectenodus microsoma (Hills 1929) was originally described from fragmentary material from the Late Devonian Blue Hills Formation, near Taggerty, Victoria, by Hills (1929) but later referred to the European genus *Dipterus* (Hills, 1931). Long (1987b) redescribed the material and demonstrated that it differs from *Dipterus* by the shape of the parasphenoid and scales, thereby supporting Hills' original designation as a separate genus. *Eoectenodus* is known from well-preserved parasphenoid, pterygoid tooth plates, the cleithrum and isolated scales. In having true tooth plates it clearly differs from *Barwickia*. It differs from *Howidipterus* in the shape of the parasphenoid, which has a posteriorly broad corpus in *Eoectenodus*, and in the nature of the tooth plates, which have fewer tooth ridges in *Eoectenodus*, and even gradation of teeth along the ridges. In *Howidipterus* the tooth plates have well developed teeth near the margins, with mesially smooth and sparsely toothed areas. The scales of *Eoectenodus* and *Howidipterus* differ in that *Eoectenodus* scales have a more regular disposition of thin ridges over the external surface. The cleithrum is similar in its externally-exposed regions in both genera, but has a more extensive branchial lamina in *Eoectenodus*.

Young (1985, fig.8J) figured the skull of a lungfish (CPC 24697) from the Middle - Late Devonian Harajica Sandstone member of the Parkes Siltstone, central Australia. This specimen represents a short-headed fish which presumably lacks an ossified snout, has a large D bone, and retains a K bone in the skull roof. It resembles *Howidipterus* in the shape of the B bone, relative size of the C, D, I, and J bones, but differs in the larger number of bones laterally contacting C, and the smaller E bones (if complete in CPC 24697). It differs clearly from *Barwickia* n.gen. in the overall proportions, *Barwickia* having a longer, more slender roof pattern, and in particular the D bone is always thin

and sliver-like, unlike that of CPC 24697.

The isolated dipnoan tooth plate from the Aztec Siltstone, Antarctica, figured by Campbell & Barwick (1987, fig.2), differs from the tooth plates of *Howidipterus* in having many teeth along each tooth ridge, and the mesial part of the plate has numerous cusps.

Isolated remains of Late Devonian lungfishes from the Hunter Siltstone, near Grenfell, New South Wales have been discussed by Long (1987b: 310-311). The parasphenoid of this undescribed dipnoan (Australian Museum F56323, F56155) clearly differs from both *Barwickia* and *Howidipterus* in having a very long stalk relative to the size of the corpus (30-37% total length). The associated tooth plates from the same locality differ from *Howidipterus* in having teeth along the entire tooth-ridge and in the fewer numbers of tooth ridges.

Comparisons with *Scaumenacia* and *Fleurantia*

The two new genera from Mount Howitt show close similarities to two genera from the contemporaneous Escuminac Formation of Quebec, Canada. To avoid further confusions some clear differences are listed here, but this list will require additional features of the postcranial skeleton when it has been described.

Howidipterus has cranial resemblances to *Scaumenacia*, but differs in the shape of the body and fins as it has a well-developed anterior dorsal fin, unlike the low, elongate anterior dorsal fin of *Scaumenacia*. The skull roof and cheek of *Scaumenacia* were described by Stensiö (1947) and Westoll (1949), and recent studies by Richard Cloutier, when published, will show further details of the cranial anatomy. The skull of *Howidipterus* can be distinguished from *Scaumenacia* by, *inter alia*, (i) having a D-bone always present, except when incorporated by fusion into the E bones, (generally, but not always, absent in *Scaumenacia*), (ii) the narrower B bone which has a well-defined anterior point (iii) the presence of paired rostral bones anterior to the E bones, (iv) the C bones are longer than the E bones, (v) the cheek has several small bones anterior to the orbit rather than a single large fused bone (this may not always be the case in *Scaumenacia* but is shown in Stensiö's reconstruction). The dentition is superficially similar in both genera but *Howidipterus* may have up to 17 tooth rows.

Barwickia has close resemblances to *Fleurantia* in its body and fin shape, but preliminary observation of its postcranial skeleton shows that the number of body ribs (vis. myotomal segments) is different, as is the number of fin basals in the anal fin (3 in *Fleurantia*, 4 in *Barwickia*). The skull of *Barwickia* differs in (i) its shorter snout shape, (ii) fewer supraorbital sensory line bones anterior to X, (iii) large A bone present, (iv) lack of a large single fused bone covering the dorsal surface of the snout. The differing shapes of the head in dorsal view also reflect the width of the pterygoids and parasphenoids –

much longer and narrower in *Fleurantia* than for *Barwickia*.

ACKNOWLEDGMENTS. Thanks to Professor Jim Warren (Zoology Department, Monash University) for suggesting the project and much helpful discussion of the work, and to Mr Gordon Cameron for use of his BSc. honours thesis (1985) as a starting point for my investigations of the material. Professor Ken Campbell and Dr Dick Barwick are thanked for many discussions on fossil lungfish and the Mount Howitt forms in particular. Professor Campbell commented on an earlier draft of the MS. I thank the two referees for drawing my attention to some errors that crept into in the first draft. Mr Ian Stewart (Monash Zoology) is thanked for his help with the casting and photography of specimens.

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Accepted 27 June, 1992

APPENDIX

Abbreviations used in the figures

ACI	anocleithrum	mk.f	fossa for adductor mandibularis muscles
Ang-SAn	combined angular + surangular bone	MSM	median submandibular
Ar	articular bone	occ	occipital sensory line canal
Bbr	basibranchial	OP	operculum
bhf	buccohypophysial foramen	orc	oral sensory line canal
brl	branchial lamina of shoulder girdle	pits	surficial pits in operculum
Chy	ceratohyal	pILG	lateral gular pit line
Clav	clavicle	plMG	median gular pit line groove
Clth	cleithrum	pop	preopercular sensory line canal
corp	corpus of parasphenoid	ppl1,2	posterior pit line grooves
Dmp	dermopalatine bones	PrA	prearticular bone
gr	groove of parasphenoid	pr.pg	preglenoid process on lower jaw
Hhy	hypohyal bones	PSM	posterolateral submandibular bone
ihy	attachment site for interhyoideus muscle	PSp	postsplenial bone
int V	foramen for mandibularis internis V nerve	PT	post-temporal bone
LGul	lateral gular plate	Ptg	pterygoid tooth plate
l.hy	attachment site for levator hyoideus muscle	Qd	quadrate
lj	lower jaw	ri	ridge on cleithrum
LSM	lateral submandibular bone	Ros	rostral bone
mc	mandibular sensory line canal	SAn	surangular bone
MGul	median gular plate	soc	supratemporal sensory line canal
mll	main lateral line canal	SOP	suboperculum
mpl	middle pit line groove	Spl	splenial bone
mr	median ridge on ceratohyal	st	stalk of parasphenoid
m.V	foramen for mandibularis V nerve	Vom	vomer
LSM	lateral submandibular	vmp	foramen for efferent epibranchial artery