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A redescription of the lungfish *Eoctenodus* Hills 1929, with reassessment of other Australian records of the genus *Dipterus* Sedgwick & Murchison 1828.

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Abstract

Eoctenodus microsoma Hills 1929 (= *Dipterus microsoma* Hills, 1931) from the Frasnian Blue Range Formation, near Taggerty, Victoria, is found to be a valid genus, differing from *Dipterus*, and other dipnoans, by the shape of the parasphenoid and toothplates. The upper jaw toothplates and entopterygoids, parasphenoid, cleithrum, anocleithrum and scales of *Eoctenodus* are described. *Eoctenodus* may represent the earliest member of the Ctenodontidae. *Dipterus* cf. *D. digitatus*. from the Late Devonian Gneudna Formation, Western Australia (Seddon, 1969), is assigned to *Chirodipterus australis* Miles 1977; and *Dipterus* sp. from the Late Devonian of Gingham Gap, New South Wales (Hills, 1936) is thought to be congeneric with a dipnoan of similar age from the Hunter Siltstone, New South Wales. This form differs from *Dipterus* in the shape of the parasphenoid. The genus *Dipterus* appears to be restricted to the Middle-Upper Devonian of Europe, North America and the USSR (Laurasia).

Introduction

Although Hills (1929) recognised a new dipnoan, *Eoctenodus microsoma,* in the Late Devonian fish remains from the Blue Range Formation, near Taggerty, he later (Hills 1931) altered the generic status of this species after a study trip to Britain in which D.M.S. Watson pointed out similarities between the Australian form and the British genus *Dipterus* Sedgwick and Murchison 1828. Studies of the head of *Dipterus* by Westoll (1949) and White (1965) showed the structure of the palate and, in particular, the shape of the parasphenoid which differs from that in the Taggerty dipnoan. These works, together with new discoveries of Upper Devonian dipnoans from Victoria at Mt Howitt, have prompted a re-examination of Hill's original material of *Eoctenodus*. The aim of this paper is to redescribe *Eoctenodus* and clarify the generic status of the other Australian Devonian dipnoans which have been referred to the genus *Dipterus.*

Australia has a particularly good record of fossil dipnoans from the Devonian, including superb specimens of Early Devonian dipnorhynchids from Taemas, New South Wales (Thomson and Campbell 1971, Campbell and Barwick, 1983, 1984, 1985), and good representation in both marine and terrestrial facies of the Late Devonian. The best preserved fossil lungfish material comes from the Frasnian

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Gogo Formation, Western Australia, where four local species are known (Miles 1977), all belonging to genera known from the Northern Hemisphere (*Griphognathus, Chirodipterus* and *Holodipterus*). *Soederberghia,* also known from the Northern Hemisphere, was recorded from the Cloughnan Shale, New South Wales, by Campbell and Bell (1982). Well preserved dipnoans from Mt Howitt, Victoria, are currently under study by the author. These comprise two new genera which have resemblances to *Scaumenacia* and *Fleurantia* in overall morphology and cranial bone patterns.

The Taggerty fauna was the first Late Devonian fish assemblage described from Australia, and from the nature of its fauna, Hills (1929, 1931) was able to deduce the age of the Cerberean Cauldron complex. The fauna includes *Bothriolepis gippslandiensis* Hills (1929), an indeterminate phyllolepid, scales of the osteolepiform *Marsdenichthys longioccipitus* (personal observation) and the dipnoan *Eoctenodus microsoma.* The placoderm plates are found in an orange silty-sandstone whereas the dipnoan remains and the osteolepiform scales occur in a laminated dark blue-grey shale which outcrops a short distance across strike from the placoderm-bearing sandstone. New collections from this site were made during 1981-1983 by Dr Anne Warren (Latrobe University) and the author, enabling redescription of *Bothriolepis gippslandiensis* (Long 1983; Long and Werdelin, 1986). Williams *et al.* (1982) discussed the age of the Cerberean succession, giving a minimum date of 367+–2 million years for the early Frasnian Blue Range Formation. Long (1982*b*) commented on the depositional environment of the Taggerty fish beds.

Specimens were studied by latex casting of the natural moulds as all traces of the original bone were weathered away. Nearly all of the Taggerty material comprised isolated bones and scales, except for two specimens which contained closely associated skeletal elements (MUGD 772, cleithrum and anocleithrum; MUGD 775, toothplate and suboperculum). The Taggerty material is housed in the Geology Department, Melbourne University (MUGD), although some specimens (prefix NMV) are in the Museum of Victoria. The specimens of *Chirodipterus australis* from the Gneudna Formation are housed in the Geology Museum, University of Western Australia (UWA). Terminology used in this work follows that of Miles (1977) for cranial bones and toothplates, and Jarvik (1980) for the shoulder girdle.

Systematics

Subclass Osteichthyes
Infraclass Dipnoi
Family Ctenodontidae Woodward 1891

Remarks

Although the skull roof of *Eoctenodus* is unknown apart from a single imperfect B-bone (Hills 1929, Fig. 2-2) the close resemblance to *Ctenodus* in the shape of the parasphenoid, toothplates and cleithrum (Watson and Gill 1923) are here considered as indicative of close affinity between *Eoctenodus* and the Ctenodontidae. I agree with Miles (1977) in referring *Sagenodus, Straitonia* (Thomson 1965) and closely related forms to a separate family, Sagenodontidae, but accept that this family has close affinity to the Ctenodontidae as exemplified by the similar morphology of the parasphenoid and dentition (Miles 1977, page 157).

Eoctenodus Hills 1929

Type species

Eoctenodus microsoma Hills 1929.

Amended diagnosis

A ctenodontid having a parasphenoid one third as broad as long, and being of almost uniform breadth for the anterior two thirds of its length, and with anterolateral margins forming an angle of approximately 60 degrees. Upper jaw toothplates more ovoid than triangular, with up to 10 subparallel, relatively straight tooth ridges of separated cusps which coalesce towards the centre of radiation of the tooth plate, and separated by relatively deep clefts. Cleithrum with a very narrow waist between the ventral and dorsal division of the external lamina, and having a very large branchial lamina. Scales, thin, subrectangular and cycloid with an ornament of fine wavy ridges which are not closely packed but sparsely distributed.

Remarks

The above diagnosis distinguishes *Eoctenodus* from *Dipterus* and other Devonian dipnoans principally by the shape of the parasphenoid and toothplates (Figure 3-A), and from *Ctenodus* (Figure 3-C) and other ctenodontids by the relative shape of the parasphenoid, apical angle of the parasphenoid, and number of tooth-rows on the toothplates.

Eoctenodus microsoma Hills, 1929, p. 193

Figures 1-7

1931 . . . . *Dipterus microsoma* Hills, p. 222.
1958 . . . . *Dipterus microsoma* Hills, p. 89.
1966 . . . . *Dipterus* Lehman, pp. 249, 289.
1976 . . . . *Dipterus microsoma* Marsden, pp. 87, 122.
1977 . . . . *Dipterus* Kemp, p. 253.
1977 . . . . *Dipterus microsoma* Kemp, p. 256.
1982 . . . . *Dipterus* Long, p. 63, Fig. 5-H.
1983 . . . . *Dipterus (Eoctenodus)*, Long, p. 298.
1984 . . . . *Dipterus microsoma,* Long & Turner, p. 241.

Holotype

MUGD 775 (fig. 1-C), left upper toothplate and entopterygoid (figured Hills, 1929, pl. 18, fig. 7).

Other material

MUGD 773a, b (782), parasphenoid; MUGD 772, (counterpart 781) Cleithrum and part of anocleithrum; MUGD 770, very small toothplate; MUGD 784, moderate sized toothplate. In addition Hills lists other elements (e.g. a B-bone, Hills 1929, fig. 2-2) which were not found with the borrowed MUGD collection in the Bureau of Mineral Resources from which this study was based. Scale number P 186565 is housed in the Museum of Victoria.

Diagnosis

As for genus.

Description

Eoctenodus was a moderate-sized Devonian dipnoan having an estimated skull length around 6 cm, based on proportions of the toothplates compared with those of *Dipterus valenciennesi.*

The parasphenoid (Figures 1-A, E; 2; 3-B) is almost completely preserved from natural moulds of both dorsal and ventral surfaces, missing only the posterior tip of the stalk. It is a rather thin bone of almost uniform thickness, being slightly thicker at the anterior end. It comprises a large anterior division (corpus, Miles 1977) which occupies two-thirds of the estimated total length of the bone, and a very narrow occipital stalk (st). The anterior angle, contained by the straight anterolateral margins of the corpus (Miles, 1977 page 153), is close to 60 degrees, being quite distinct from both *Dipterus* (70-72 degrees, as measured from figures in White 1965) and *Ctenodus* (ca 105 degrees, Watson and Gill 1923, fig. 25). The dorsal surface (Figure 2-A) has thickened anterolateral margins for the overlap surfaces of the entopterygoids (ov. pt) which anteriorly meet two pairs of parallel grooves which are separated medially by a central ridge. The grooves are presumably for the palatine nerves and arteries (gr. pal). The probable course of arteries in close contact with the parasphenoid is shown in Figure 2-C, showing a pattern not far from that known in *Dipnorhynchus sussmilchi* (Campbell and Barwick 1982) or *Chirodipterus* (Save-Soderbergh 1952). The hypophysial fossa (hyp) is a large keyhole shaped depression which does not appear to penetrate through to the ventral surface of the bone, similar to the condition in *Chirodipterus* (Campbell and Barwick 1982). This condition is a feature of advanced dipnoans in which the palate is well known, as only a few primitive forms retain a bucco-hypophysial opening on the ventral side of the parasphenoid (e.g. *Dipnorhynchus, Speonesydrion and Dipterus).* Inside the hypophysial fossa appear to be irregular tubules, possibly a vascular plexus as occurs in the hypophyseos of *Dipnorhynchus* (Campbell and Barwick 1982, fig. 16) and in most fishes, e.g. *Amia* (Bjerring 1977). The stalk is seen running anteriorly as a raised thickening on the dorsal surface of the bone, terminating just posterior to the hypophysial fossa. The stalk broadens slightly as it leaves the corpus posteriorly, becoming thinner distally.

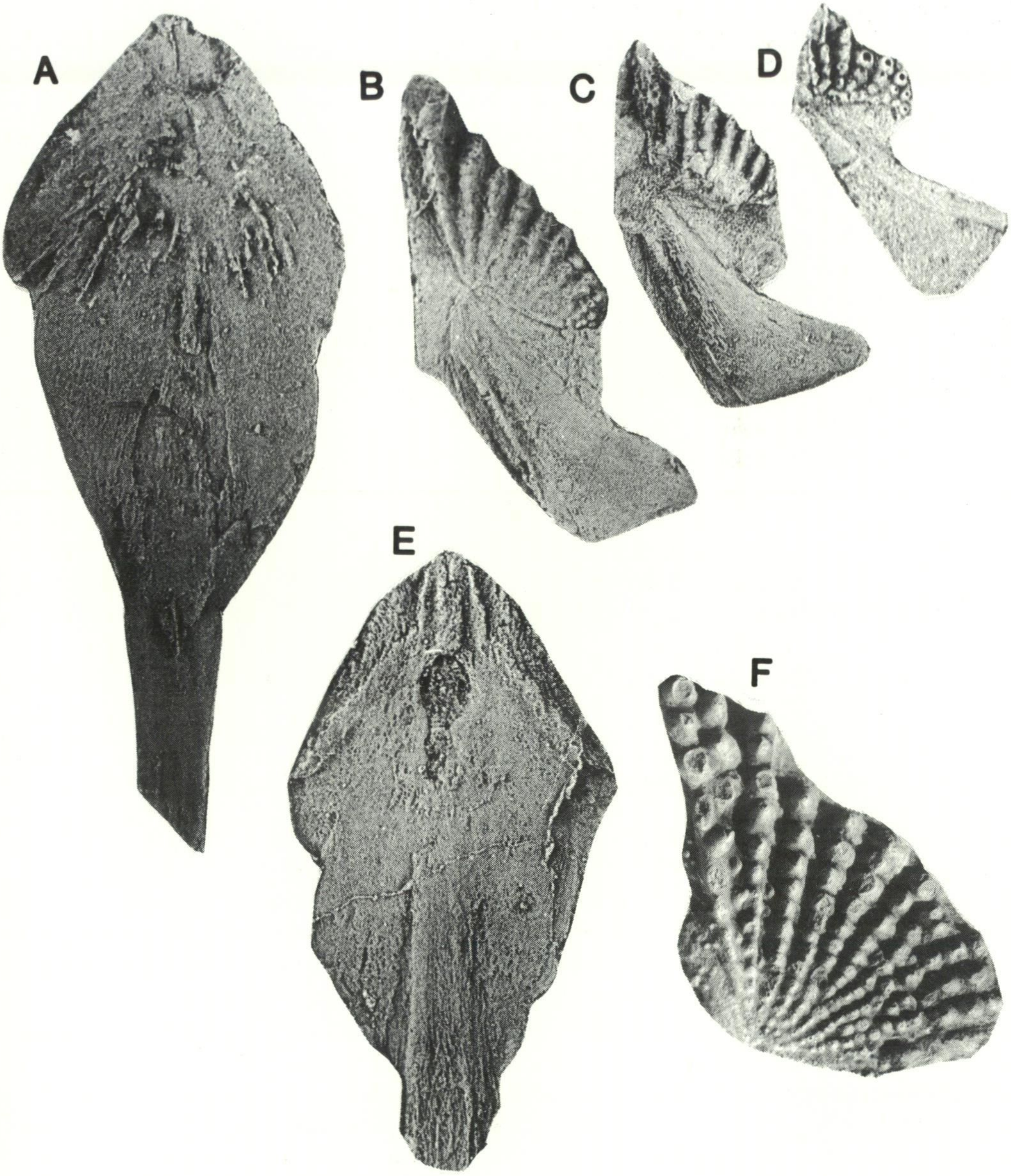

Figure 1 A-E, *Eoctenodus microsoma* Hills. A, E, parasphenoid in ventral (A) and dorsal (E) views, MUGD 773, X3.5. B-D, left pterygoids and entopterygoids in various stages of growth, youngest to the right. B, MUGD 775, X2.5. C, MUGD 784, X2. D, MUGD 770, X4. F, left pterygoid toothplate of *Dipterus valencienessi* Sedgewick and Murchison, British Museum (Nat. Hist.) P 34549, X3.5, photograph courtesy Dr Moya Smith.

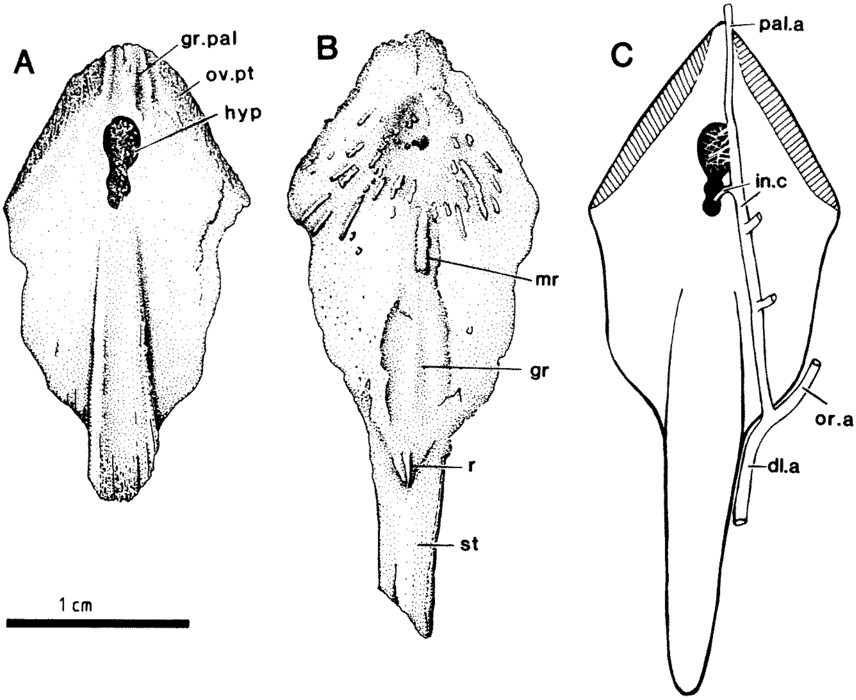

Figure 2 *Eoctenodus microsoma* Hills. Parasphenoid in (A) dorsal view and (B) ventral view. C, attempted restoration of complete parasphenoid shape, dorsal view, showing possible course of arteries. dla, dorsolateral aorta; gr, median groove; gr.pal, groove for palatine artery and nerve; hyp, hypophysial fossa; in. c, internal carotid artery; mr, median ridge; or.a, orbital artery; ov.pt, overlap surface for pterygoid; pal.a, palatine artery; r, posterior ridge on parasphenoid; st, stalk of parasphenoid.

The ventral surface of the parasphenoid is rather flat and featureless. The anterior region of the corpus has some irregularly disposed thin ridges of bone running radially out from the depressed area adjacent to the hypophysial fossa. In the midline there is a short median ridge (mr) which separates paired shallow grooves which broaden posteriorly (gr). At the posterior end of the corpus there is another short median ridge where the corpus is slightly elevated above the stalk. Figure 2-C shows an attempted restoration of the shape of the parasphenoid and possible vascular supply to the region.

The parasphenoid of certain primitive dipnoans *(Chirodipterus* and dipnorhynchids, Campbell and Barwick 1982) is small, being about 30% of the length and breadth of the braincase, with a weakly developed anterior division. In *Dipterus* the parasphenoid is much larger, being approximately half the length and breadth of the braincase, with a well developed anterior end and a posterior stalk which extends almost as far posteriorly as the braincase (White 1965). In other freshwater dipnoans from the Late Devonian onwards this trend has continued (e.g. *Gnathorhiza*, Carlson 1968; *Megapleuron*, Schultze 1977) and the parasphenoid in living dipnoans is typically very large relative to the braincase (e.g. *Neoceratodus* Figure 3-G). Although the relative size of the parasphenoid to braincase is not known for *Eoctenodus*, the relative sizes of the corpus to upper jaw toothplates is similar for *Dipterus*, *Eoctenodus* and *Ctenodus* (Figure 3 A-C), indicating that the parasphenoid of *Eoctenodus* can be assumed to have been relatively large, with a much longer posterior stalk in relation to braincase length compared to *Dipterus*. The development of the long occipital stalk on the parasphenoid of

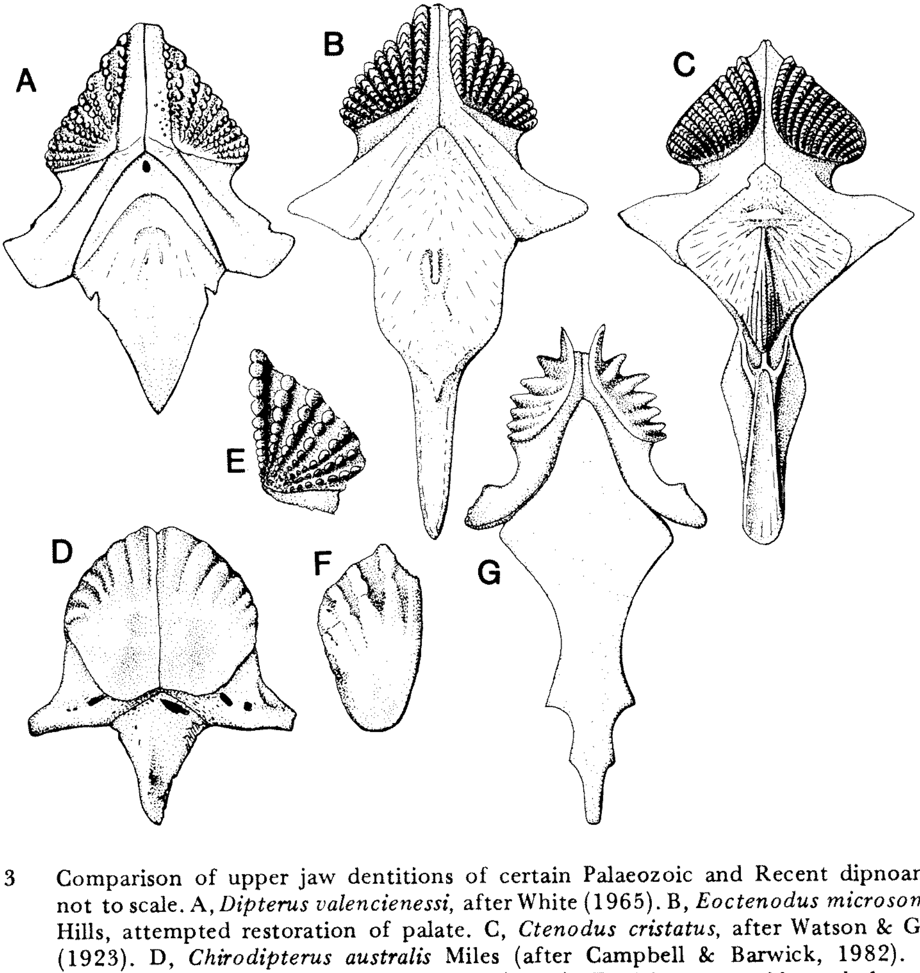

Figure 3 Comparison of upper jaw dentitions of certain Palaeozoic and Recent dipnoans, not to scale. A, *Dipterus valencienessi*, after White (1965). B, *Eoctenodus microsoma* Hills, attempted restoration of palate. C, *Ctenodus cristatus*, after Watson & Gill (1923). D, *Chirodipterus australis* Miles (after Campbell & Barwick, 1982). E, '*Dipterus*' sp., Hervey Range, after Hills (1936). F, right pterygoid toothplate of *Chirodipterus australis* from the Gneudna Fm, Western Australia (U.W.A. 62148). G, *Neoceratodus forsteri*, palate after Jarvik (1980).

Eoctenodus seems to represent an intermediate condition between that of *Dipterus* and *Ctenodus,* and is here taken to represent an incipient stage towards the ctenodontid line of evolution. The enlargement of the parasphenoid in dipnoans is a specialised condition which may relate to the invasion of freshwater habitats and the development of air gulping (Prof. K. Campbell, pers comm.).

The upper jaw toothplates are known from three examples in different stages of growth, showing only the oral surfaces. The largest (holotype, Figure 1-B) has a toothplate 16 mm long whereas the smallest (Figure 1-D) is almost complete yet the toothplate is only 4 mm in length. The major changes observable with this growth sequence are, firstly, in the ratio of toothplate (pterygoid) size compared with pterygoid size (Table 1), showing a significant increase in the growth of the pterygoid toothplate relative to the pterygoid. Secondly there is an increase in number of tooth rows and cusps in each row, although this is well known for dipnoans (e.g. Schultze 1977, *Megapleuron).* The angles between the first tooth row and all other tooth rows (as measured according to Kemp and Molnar, 1981 fig. 1) also differs considerably with growth (Table 2), a feature noted for *Neoceratodus* by Kemp (1977).

Table 1 Changes in upper jaw toothplate: entopterygoid relative sizes with growth.

	A.	B.	C.
MUGD 770	app. 4 mm	app. 9 mm	44
MUGD 784	13 mm	24 mm	54
MUGD 775	17 mm	29 mm	59

A, maximum linear dimension of the upper jaw toothplate.
B, maximum linear dimension of the entopterygoid bone.
C, index A/B x 100.

Table 2 Changes in angle between tooth ridges relative to growth.

	MUGD 775	MUGD 784	MUGD 770
Angle between tooth			
ridge 1-2	14°	8°	6°
1-3	25°	10°	12°
1-4	31°	15°	17°
1-5	40°	17°	25°
1-6	50°	21°	39°
1-7	57°	26°	-
1-8	62°	-	
1-9	66°		
1-10	69°		

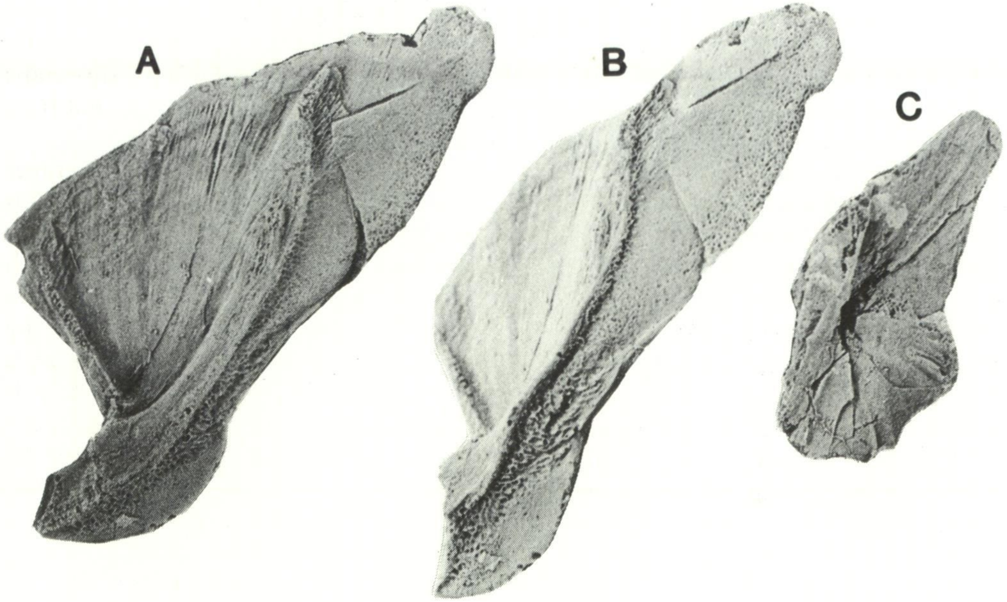

Figure 4 *Eoctenodus microsoma* Hills. Shoulder girdle bones. A, B, cleithrum in (A) anterolateral and (B) lateral veiws. MUGD 781, X3. C, anocleithrum associated with MUGD 781, in mesial view, X3.

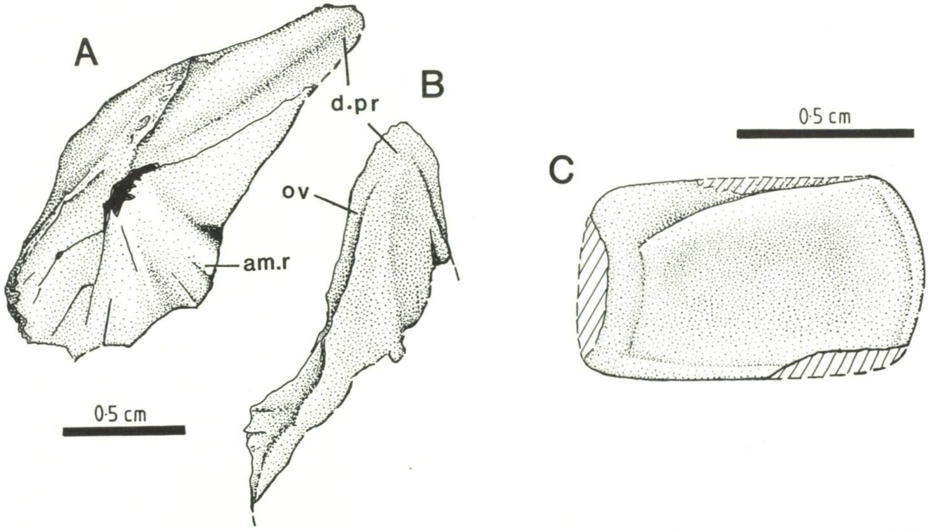

Figure 5 *Eoctenodus microsoma* Hills. A, B, anocleithrum, MUGD 781, in mesial (A) and lateral (B) views. C, possible subopercular bone in mesial view, associated with MUGD 775. am. r, anterior median ridge; d. pr, dorsal process; ov, overlap or ligamentous attachment area.

The following description of the upper jaw toothplate and entopterygoid is based on the presumed adult condition exemplified by the holotype. The toothplate is more ovoid in form than triangular, but is rather narrow relative to the longest (anterolateral) axis. The first tooth row ridge is the longest, extending noticeably further than the second ridge, and diverging from this ridge slightly more than do the remaining ridges. Cusps closer to the centre of radiation of the tooth ridges coalesce to form tooth ridges with an almost continual edge, although the lateral edges of the toothplate show distinctly separate higher cusps with apices directed laterally, similar to the figured condition in *Delatitia* (Long and Campbell 1985, fig. 4-E). The posterior half of each tooth ridge is weakly depressed relative to the rest of the tooth ridges, possibly due to wear. There are 10 distinct tooth ridges, numbering up to about 10 cusps on the first two ridges, although there is some damage to the anterior of the first tooth ridge on the holotype. On the smaller toothplates the cusps are more conical with deeper clefts between the tooth ridges (Figure 1-C, D). The oral face of the entopterygoid has a smooth surface which is gently concave, becoming thicker as a ridge develops along the posteromesial edge that has a roughened margin for contact with parasphenoid. The posterior wing of the entopterygoid splays out into a rounded lateral process, as seen on MUGD 775 (Figure 1-C). The anterior region of the entopterygoid narrows towards the base of the toothplate where an anteromesial ridge develops, ending just posterior to the posterior limit of the first tooth row. The shape of the entopterygoid indicates that the quadrates were widely spaced from the parasphenoid as in *Ctenodus* (Watson and Gill 1923).

The cleithrum in general is poorly known for Devonian dipnoans (e.g. Denison 1968, Schultze 1969), and although recent restorations have been given of this bone for *Scaumenacia* (Jarvik 1980, vol. 1, fig. 335) and for *Chirodipterus* in mesial view (Janvier 1980, fig. 12, Long 1985*a*, fig. 11), there is not a good description of this bone available for any Devonian lungfish. The cleithrum of *Eoctenodus* (Figures 4-A, B; 5) is well preserved in lateral view with partial preservation of the internal or mesial surface. Overall the cleithrum was mostly subdermal with only a narrow lateral lamina being exposed externally (Figure 4-B). It is characterised by having a narrow external lateral lamina (lat. 1) which is strongly waisted ventrally, and by the extensive flat branchial lamina (br. 1). The lateral lamina in *Eoctenodus* is quite narrow, being broadest at the dorsal margin which is relatively straight. The ventral division of the lateral lamina is well rounded, separated from the dorsally broadening upper half by a constricted waist. The anterior edge of this external lateral lamina bears a strong thickening (th) which is broadest anterior to the rounded ventral region of the cleithrum, where it forms a short anteriorly directed mesial process (m.pr) for interlocking with the clavicle. Immediately medial to this process is a concave smooth area for overlap with the clavicle (ov. Clav). The branchial lamina extends forward from the lateral lamina at an acute angle, meeting this lamina along a smooth contact ridge which develops into a deep pit (p) at the ventral edge. The anterior margin of the branchial lamina is also thickened into an anterior ridge (an. r) which bears a small notch (n). The lateral surface of the branchial lamina is smooth with a thickened low ridge running almost vertically back towards the ventral pit. The dorsal (or anterodorsal) margin of the branchial lamina shows a slight angle (a) where it meets this ridge. The mesial surface of the cleithrum is not well preserved as it is obscured by superimposition of the anocleithrum and lacks the anterior and ventral edges. All that is shown by the cast is a smooth surface with a weak thickening parallel to the posterior margin.

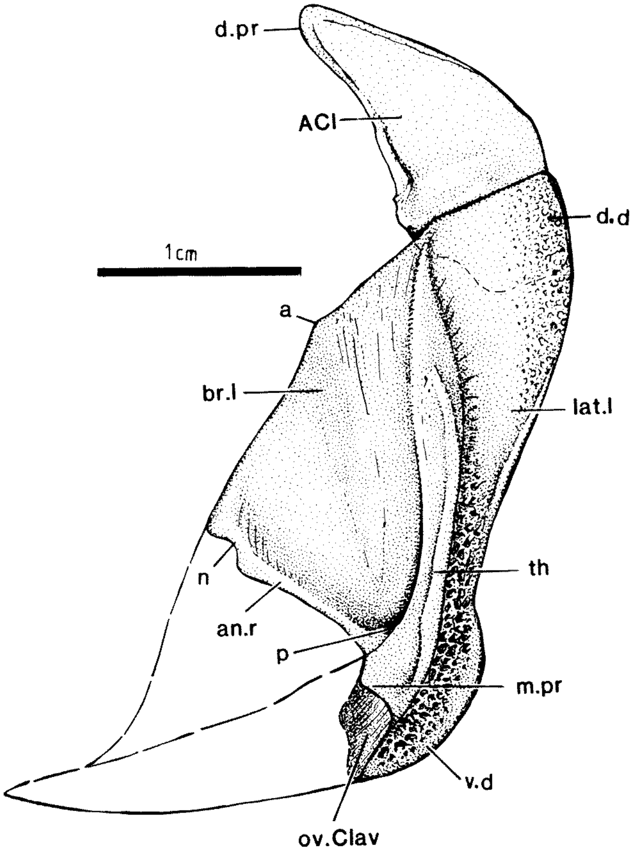

Figure 6 *Eoctenodus microsoma* Hills. Attempted reconstruction of the shoulder girdle. a, anterior angle of branchial lamina; ACl, anocleithrum; an. r, anterior ridge of branchial lamina; br. l, branchial lamina of cleithrum; d.d, dorsal division of cleithrum; d. pr, dorsal process of anocleithrum; lat. l, lateral lamina of cleithrum; m. pr, median process of ventromesial surface of cleithrum; n, notch on the anterior apex of the branchial lamina; ov. Clav, overlap surface for clavicle; p, mesial pit where branchial lamina meets lateral lamina; th, lateral thickening of cleithrum; v.d, ventral division of external (lateral) lamina of cleithrum.

Figure 7 *Eoctenodus microsoma* Hills. Scale, NMV P 186565 in A, external and B, basal view. X2.

The mesial surface of the anocleithrum (Figures 4-C; restored in Figure 5) is found resting inside the cleithrum. The close association of these two bones indicates that in life they were probably held together by ligaments, as most of the material from Taggerty consists of detached, isolated bones. It is identified as an anocleithrum by its large size relative to the cleithrum, close association with the cleithrum, and by having a well developed anterior median ridge (am. r) and long tapering dorsal process (d. pr). In these respects it corresponds with that of other Devonian Dipnoi (*Scaumenacia,* Jarvik 1980, vol. 1, fig. 335; *Chirodipterus australis, Griphognathus whitei* – A.N.U. specimens). It is a rather flat, irregularly-shaped bone, approximately twice as long as broad, and was situated mesial to the cleithrum, probably buried in the dermis (subdermal) as appears to be the case in all the known dipnoans. A small part of the lateral surface of the anocleithrum is preserved, showing some fine pitting close to the centre of the bone, and well developed overlap ridges along both anterior and posterior margins (Figure 5). The fine pitting on the lateral surface does not indicate that the bone was necessarily part of the externally exposed shoulder girdle, instead it probably functioned as a roughened attachment area for skin or ligaments. In *Chirodipterus australis* the anterodorsal tip of the anocleithrum articulates to the rear of the braincase (Prof. K. Campbell, pers. comm.), where it was probably joined by ligaments in life. The long dorsal process of the anocleithrum of *Eoctenodus* and *Scaumenacia* indicates that this may have been a specialised condition for dipnoans as in other osteichthyans which possess an anocleithrum it serves merely as a surface to accomodate movements between the dorsal and ventral divisions of the pectoral girdle (Andrews and Westoll 1979*a, b;* Andrews 1972; Long 1985*a,* 1985*b*).

There is a small bone preserved in mesial view on the same rock as the holotype upper jaw. It is rectangular in shape, having a breadth/length index of 65 with a well rounded posterior margin, and a broad overlap surface at the anterior of the bone which narrows posteriorly along the dorsal margin terminating at the presumed posterodorsal corner. This bone (Figure 5-C) corresponds both in size (assuming it is associated with the holotype upper jaw which gives an estimated head size of 6 cm), shape and overlap margins to being either a subopercular or branchiostegal ray (cf. Campbell and Barwick 1984, fig. 27-C). There are no indications of ligamentous attachment areas as occur inside the opercular bones (Campbell and Barwick 1984). The mesial surface is smooth with a shallow depression running parallel to its long axis in the centre of the bone.

The scales of *Eoctenodus* have been described and figured by Hills (1929, plate 18, figs. 3, 5, 6). In addition to Hills' description it may be added that the ornamentation comprises very fine wavy ridges which are sparsely distributed over the externally exposed portion of the scale, which comprises about one-third of the scale length (Figure 7). In this respect they differ noticeably from scales of the *Scaumenacia* type (Jarvik 1950, fig. 33) which have a higher density of ornamental ridges.

Relationships of *Eoctenodus*

The presence of a long, narrow occipital stalk on the parasphenoid, similar form of the toothplates and tooth ridges, and cleithrum with very broad branchial lamina indicate that *Eoctenodus* is probably closely related to *Ctenodus* and other ctenodontids. The presence of a similar type of parasphenoid, dentition and cleithrum in *Sagenodus,* which shows more derived features of the skull roof pattern than for *Ctenodus* (Miles 1977), would suggest placement of *Eoctenodus* close to the base of the group containing ctenodontids and sagenodontids. Its exact relationship remains indeterminate due to the paucity of present material. The Frasnian occurrence of *Eoctenodus* would make it the oldest known member of the ctenodontid-sagenodontid group, which are otherwise restricted to the Carboniferous and Permian periods. *Delatitia (Ctenodus breviceps* Woodward 1906), from the Lower Carboniferous of Victoria, is the only other member of this group which has been described from Australia (Long and Campbell 1985). As this genus and *Eoctenodus* are both primitive relative to other ctenodontids it is possible that the ctenodontid group may have originated in the East Gondwana region.

Comments on other Australian records of the genus *Dipterus*

As *Eoctenodus* has now been shown to be a valid genus the presence of *Dipterus* in the Australian Devonian remains to be shown. Two other reported occurrences of *Dipterus* are from the Late Devonian (Frasnian) Gneudna Formation, Western Australia (*Dipterus* cf. *D. digitatus,* Seddon 1969) and from the Famennian Hervey Group, NSW (*Dipterus* sp. Hills 1936).

The two upper jaw toothplates from the Gneudna Formation which were figured by Seddon (1969, plate 2) have been re-examined. The largest and better preserved of the two specimens is shown in Figure 3-F. Both Miles (1977, page 292) and Dring (1980, unpublished Ph.D thesis, Geology Department, University of Western Australia) have remarked on the similarity of these specimens to the dentition of *Chirodipterus australis,* which occurs in the Gogo Formation, of similar age to the Gneudna Formation. The chirodipterid type of dental plate is generally distinguished from those of other Devonian dipnoans in lacking well formed rows of discrete cusps, as in dipterid or ctenodontid tooth-plates, instead showing bulbous, well-rounded ridges or swellings at the anterior end of the plate which merge into the smooth depressed area comprising the posterior half of the tooth-plate. The histology of the chirodipterid dental plate is also distinctive (Dr Moya Smith, pers. comm.). In their shape, development and number of grooves present, and approximate relative size of tooth-ridges the Gneudna dipnoan dental-plates can be assigned to *Chirodopterus australis* with reasonable confidence. *Chirodipterus paddyensis* Miles, also from the Gogo Formation, can be distinguished from *C. australis* by the deeper grooves and higher, sharper tooth-ridges (Miles 1977), and *C. wildungensis* Gross differs from both of these species in possessing well formed tubercular cusps along the tooth rows (Save-Soderburgh 1952). Other chirodipterid-type toothplates, such as those reported from the Middle Devonian of Iran by Blieck *et al.* (1980, plate 1-18, 19) differ from *Chirodipterus australis* by their narrower form and more pustulose, shorter tooth rows.

Dipterus sp. was reported by Hills (1936) from Gingham Gap, in the Hervey Range, NSW on the basis of a single left upper jaw toothplate (Figure 3-E). In having discrete round cusps set in rows which are well separated, and radiate out to form almost a right angle from the first to last rows this specimen does appear to be close to *Dipterus* in as far as dentition may allow such comparisons. A radiating pattern of numerous separate cusps forming the tooth ridges also occurs in *Rhinodipterus,* (Ørvig 1961), and *Scaumenacia* (Westoll 1949). However, other dipnoan toothplates which are identical to the Gingham Gap specimen in their shape, arrangement of cusps and angular radiation of tooth ridges are common in the Famennian Hunter Siltstone, near Grenfell, New South Wales. This fauna is of similar age and geographic location to the Gingham Gap fauna, and it would not be unlikely that the dipnoan toothplates from these two locations could be congeners or even conspecific. The resemblance to *Dipterus* in toothplate morphology is, however, offset by the shape of the parasphenoid in the Hunter Siltstone dipnoan. Two specimens of the parasphenoid (Australian Museum F 56323, F 56155) from the Hunter Siltstone occur with the *Dipterus*-type of toothplate, and as there is no evidence suggesting that more than one form is present in the fauna it can be assumed that the parasphenoids belong to the same species which possessed the toothplates. The parasphenoids have no similarities to that of *Dipterus* as they have a square-shaped corpus and a very long occipital stalk (ratio of corpus length to overall length being between 30-37%), thus being closer in form to the parasphenoid of *Ctenodus.* A further distinction from *Dipterus* is in the apical angle of the parasphenoid which is close to 90 degrees in the Hunter Siltstone dipnoan (approximately 70 degrees in *Dipterus*). If the Hunter Siltstone dipnoan and the Gingham Gap dipnoan are congeners then they do not belong to the genus *Dipterus*, but are more apomorphic than this genus in the development of the parasphenoid. In conclusion the presence of *Dipterus* in Australia cannot be confidently demonstrated.

The genus *Dipterus* is known from complete material only from the Middle Devonian of Britain (Forster-Cooper 1937, Westoll 1949), and from partial skulls and toothplates from Germany and Baltic Russia (Gross 1934, 1951, 1964), from inland Russia (Obruchev 1940) and dubiously from North America (see discussion in Denison 1951; Denison 1968). The reported *Dipterus* toothplate from Alaska (Perkins 1971) appears to be similar to the chirodipterid dental plate type and needs further investigation. Reed (1985) recognised the difficulties in determining isolated dipnoan toothplates to genera and preferred to assign material from the Late Devonian of Nevada into indeterminate taxa at the *Dipterus* grade of organisation. A single worn, damaged toothplate of *Dipterus* was reported from the Late Devonian of Iran (Janvier and Martin 1978) but does not reliably indicate the presence of *Dipterus* from a Gondwana country when considering the nature of the Hunter Siltstone dipnoan which has *Dipterus*-type dentition with an advanced parasphenoid. The genus *Dipterus* occurs in Laurasian countries during the Middle and possibly Late Devonian, but is not yet proven to occur in Australia or any part of the East Gondwana Province (*sensu* Young 1981) during these times.

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