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FIRST COMPLETE SPECIMEN OF THE DIPNOAN *GOSFORDIA TRUNCATA* WOODWARD FROM THE TRIASSIC OF NEW SOUTH WALES.

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SUMMARY

Gosfordia truncata Woodward is based on several incomplete specimens found in the 1880's. The recent discovery of the first complete specimen of *G. truncata* in a Triassic shale lens near Gosford, New South Wales, makes possible the first restoration of the species and clarifies its relationships with other dipnoans, living and extinct.

INTRODUCTION

Of all the continents, Australia has the longest documented record of lungfish (or dipnoan) evolution (Hills 1958, 103) ranging from the early Devonian marine genus *Dipnorhynchus* (Thomson and Campbell 1971) to the extant Queensland freshwater form, *Neoceratodus forsteri* (Krefft 1870). Until the recent discovery of well-preserved, articulated dipnoan remains in the marine late Devonian Gogo Formation of the Kimberleys, Western Australia (Miles 1979) and in the late Devonian continental deposits of the Mt. Howitt Province, central Victoria (Marsden 1976, 122) few Australian fossil dipnoans have been represented by material sufficiently well-preserved to allow complete restorations to be made.

This certainly applied to *Gosfordia,* a poorly known, early Triassic dipnoan recovered in the 1880's from a shale horizon near the top of the Gosford Formation in the Narrabeen Group of the Sydney Basin (cf. Packham *et al.,* 1969, 407). The original material of *Gosfordia* (and of several other species of Triassic fishes) was uncovered near the town of Gosford, 50 km north of Sydney, N.S.W. during the excavation of a quarry for railway ballast materials. The Railway Ballast Quarry yielded over 400 fossil fish specimens and a labyrinthodont amphibian. Included amongst the fish specimens, which were predominantly actinopterygians, were five incomplete specimens which Woodward (1890, 4-6, Pl.1 figs 1, 2, Pl. II figs. 1, 2) attributed to a new genus and species of dipnoan which he named *Gosfordia truncata.*

Ninety years after the discovery of *Gosfordia,* and almost exactly 110 years after William Forster, a Queensland squatter, sent to Gerard Krefft in Sydney the first specimens of the living lungfish which now bears his name, *Neoceratodus forsteri* (Krefft), The Australian Museum unexpectedly acquired another remarkable lungfish specimen — the first complete example of the Triassic dipnoan *Gosfordia* (AM F.60621).

The new specimen of *Gosfordia* (Fig. 1) was discovered by an observant quarryman, Mr John Costigan, employed by Glendale Wash Sands Pty. Ltd. which operates a quarry in the Somersby Falls area, west north west of Gosford and only 6-7 km away from the type locality. Mr Costigan noticed a small part of a largish fish exposed on a block of shale and split it to reveal a complete and remarkably well-preserved specimen of unusual type. Shortly afterwards the fish fossil was acquired by an amateur collector, Mr Colin Chidley of Sydney who recognised its unique scientific importance and passed it, in turn, to The Australian Museum for safe-keeping and scientific study.

The quarry from which the *Gosfordia* specimen came works an extensive shale lens in the Hawkesbury Sandstone. The massive, grey silty shale, up to 3.4 m thick, is used for brickmaking materials whilst the considerable thickness of overlying, weathered yellow

Records of The Australian Museum, 1981, **Vol. 33 No. 11,** 606-616, Figures 1-3.

sandstone is stripped off and processed for building sands. Fish fossils have turned up on several occasions during the quarrying of the shale but, because of the extraction methods, it has not yet proved possible to locate the level (or levels) from which the fish come.

Recent investigations by the N.S.W. Geological Survey (Uren 1974) have shown that this particular shale lens lies within the Hawkesbury Sandstone, at least 60-70 m above its base. It is thus stratigraphically higher and geologically later than the original fish-bed in the Railway Ballast Quarry which lies near the top of the underlying Narrabeen Group. Shale lenses in the Hawkesbury Sandstone throughout the Gosford area cover areas of up to 8 hectares and vary in thickness from 2-6 m. They appear to represent temporary lakes or cut-off loops of large river systems in Triassic times.

DESCRIPTION OF THE SPECIMEN

The entire fish is clearly visible on the larger of the slabs of grey shale and most of the counterpart (with the exception of much of the head) was recovered on various large flakes which have since been reassembled into a smaller block. Like all the other fish fossils from the Gosford area this latest specimen is largely reduced to a carbon film with very little surface relief. By good fortune the specimen of *Gosfordia,* which measures 50 cm from nose to tail, lies neatly just within the margins of the enclosing block, having been narrowly missed both by the bulldozer blade and by the quarryman's chisel!

The fish is seen entirely in lateral view, confirming Woodward's interpretation (1890,5) that the animal was laterally compressed in life. The median fins are beautifully preserved with a minimum of disturbance and with even the finest of fin-rays visible. The paired fins are also visible, projecting clear of the ventral margin of the trunk.

HEAD REGION

As observed by Woodward (1890,5) the head of *Gosfordia* is subtriangular and very small relative to the size of the animal, measuring only 6 cm from the posterior margin of the opercular plate to the snout. Because of the crushed, heavily carbonised nature of preservation the fine details of the bones in the head region are difficult to identify and trace and the new specimen, unfortunately, adds little to that figure by Woodward (1890, Pl.I fig. 1; AM F.50975). The outline of the cleithrum is reasonably clear (Figs. 1, 2B) as a longish, narrow, curved plate. With less certainty one can determine the position of the orbit and the outline of a subcircular operculum bordered ventrally by narrow subopercular plates (Fig. 2B). In the skull roof, normally one of the most useful regions for dipnoan comparative anatomy, very little can be determined with accuracy.

The only possible evidence of the crushing toothplates consists of several indistinct ridges disappearing under the head. If correctly identified as a toothplate these must have been much more weakly developed in *Gosfordia* than in its contemporary, *Ceratodus,* or in the extant *Neoceratodus.*

TRUNK

The new specimen of *Gosfordia* reveals the fish to have been remarkably deep-bodied for a lungfish and, presumably, laterally compressed. Most of the area of the fossil is covered by an evenly carbonised film which probably represents the original squamation. Woodward (1890,6) noted that the scales were "evidently very small, and all are marked by fine longitudinal striations" but was unable to distinguish their precise outlines. It seems probable that the squamation extended distally over much of the lateral surface of the median fins as depicted by Goodrich in *Neoceratodus* (1904, Pl.35, fig. 3) and by Jarvik (1959 figs. 17A, B) in both *Scaumenacia* (late Devonian) and

Neoceratodus (Recent), forms separated by about 350 million years. The new *Gosfordia* (Fig. 1) displays a marked, narrow zone of disturbance and minor crumpling extending right around the median fin between the outer margin and the axial skeleton. This line may mark the transition between the more fleshy proximal region and the thinner distal part of the fin.

The presence of a long narrow, clear strip running the length of the trunk indicates that the notochord was persistent and unconstricted and that none of the associated vertebral structures were ossified. Distally it tapers to a sharp point at the termination of the caudal fin.

The ribs are moderately well-preserved. They were long, slender and gently arched and, in several places, both left and right ribs are visible and superimposed. Allowing for this there appear to be about 25-27 pairs of ribs in *Gosfordia* (Fig. 2B) compared with some 26 pairs in *Neoceratodus* (Fig. 2A).

The neural and haemal arches and rods were lightly ossified and, although their general arrangement is quite clear, some details are difficult to determine accurately. In *Gosfordia* (Fig. 2B) as in *Neoceratodus* (Fig. 2A) there appear to be three series of ossified rods in the dorsal axial skeleton and in the ventral region posterior to the rib-cage. In *Gosfordia* the middle row is extremely faint and has thus been more tentatively restored.

The greatest depth of the trunk (not including the fins) is about 15 cm but a marked bulge along the ventral margin probably indicates that the soft, unsupported underbelly collapsed in the mud during burial. In restoring *Gosfordia* (Fig. 2B) the writer has allowed for the original roundness of the trunk and has reduced the overall depth to 14 cm.

MEDIAN FINS

In *Gosfordia,* as in virtually all post-Devonian dipnoans (Fig. 3) the caudal, dorsal and anal fins have so completely fused as to leave little evidence of their former extent. The caudal fin of *Gosfordia* (Figs. 1, 2B; Woodward 1890 Pl.I, fig. 2) is diphycercal and very large, even by dipnoan standards. It extends along the dorsal margin for 30 cm (60% of the total length) and along the ventral margin for 20 cm. It is also very deep, reaching about 16.5 cm between the highest point on the epichordal (dorsal) lobe which lies slightly anterior to the lowest point on the hypochordal (ventral) lobe. Posteriorly the caudal fin terminates in a blunt point which subtends an obtuse angle of about 115° in contrast to all other dipnoans (Fig. 3) where the termination of the caudal fin is acute-angled.

PAIRED FINS

One example of each of the pectoral and pelvic fins is preserved and clearly visible outside the remains of the trunk. The proximal portion of the pectoral fin was later excavated in the counterpart and, although not particularly well-preserved, appeared to indicate that the fin was inserted about halfway along the posterior cleithral margin. The pectoral fin is extremely long (15-16 cm), narrow (1.8 cm) and lanceolate, tapering to a fine point. The fin-rays are equally well-developed along the anterior and posterior margins of the fin but no trace remains of the axial elements of the fin endoskeleton. In shape and structure the pectoral fin of *Gosfordia* more closely resembles the very specialised pectoral fin of *Protopterus* (Fig. 3) than the shorter, more powerfully built fin of *Neoceratodus* (Fig. 2A). It is now clear that the specimen tentatively identified by Woodward (1890 Pl.II fig. 2) as a pectoral fin of *Gosfordia* does not belong to this genus; it is more likely to belong to the long-bodied actinopterygian, *Saurichthys,* which is also present in the same horizon.

The pelvic fin of *Gosfordia* is similar in shape to the pectoral but much shorter (about

8 cm) and presumably less mobile in life. There is no visible evidence in the *Gosfordia* material of a pelvic girdle similar to that still present in *Neoceratodus* (Fig. 2A).

The pectoral and pelvic fins of *Gosfordia* were clearly rather feeble structures which, like those of *Neoceratodus,* were used in sculling during slow locomotion and probably also for "walking" along the bottom or in resting on the bottom with the head raised up. This would only apply of course, when the fish was totally submerged and the weight supported by the water. It is also possible that the *Gosfordia* pectoral fins acted as sensory feelers (similar to those of *Protopterus* and *Lepidosiren)* which would have been of considerable use in very murky waters as suggested by Thomson (1969a, 118); the lithology of the Hawkesbuy shale lens indicates rather muddy bottom conditions at the time of deposition.

ASSOCIATED FAUNA

In 1972 quarrying operations in the same general area, and working the same shale lens, as the latest find brought to light numerous, well-preserved specimens of fossil fish. A joint party from The Australian Museum and the N.S.W. Mines Department collected several specimens most of which appear to belong to *Zeuchthiscus australis* (Woodward). This species was based initially (1890, 3l, p1.IV, fig. 2; *Semionotus australis* Woodward) on a single imperfect specimen from the Railway Ballast Quarry. Wade subsequently recognised other specimens in the same collection and redescribed and renamed the species as *Zeuchthiscus australis* (Wade 1939, 214-6, Pl.IX, fig. 4). The only significant difference between 1890 and 1972 finds (which are now housed in The Australian Museum; AM F.55094-55107), is in their relative sizes. The specimens from the Railway Ballast Quarry apparently reached a length of about 16.5 cm whilst the 1972 finds from the new quarry included several specimens around 25 cm in length.

The only other fossil fish recorded from this horizon, to date, is a very fine specimen of *Saurichthys gigas* (Woodward) which was discovered in 1972 by the same Mr J. Costigan who found the latest *Gosfordia.* This *Saurichthys* (AM F.55091-2), as preserved, extends from the tip of the snout to just posterior to the pelvic fins and is 70 cm. long. Using the earlier Railway Ballast Quarry specimens of *Saurichthys* as a guide (Woodward 1890, Pl.IX, figs. 1,2; *Belonorhynchus gigas* Woodward) it is possible to estimate that the original total length of the specimen from the new quarry must have been half as long again, around 105 cm from nose to tail. Woodward's material indicated a length of around 49 cm for *S. gigas* but he mentioned (1890,23) that it probably attained "sometimes much more".

GOSFORDIA AND THE EVOLUTION OF DIPNOI

Dipnoan evolution has long been a subject of interest and debate, and there remain conflicting opinions as to the relationships of dipnoans and other groups of bony fishes which appeared about the same time in the early Devonian. Fortunately the dipnoans have left us a fairly good fossil record and three living genera which allow us to study their soft parts and living habits. A representative selection of dipnoan genera for which there are good body fossils available is presented (Fig. 3) for comparison with *Gosfordia.* Many other genera and species are represented only by isolated toothplates, or by skulls or cranial roofs. There are also conflicting views on the possible interrelationships of the various lines of dipnoan evolution which have been identified (e.g. Bertmar, 1968; and Thomson and Campbell 1971, 102, fig. 35, who have attempted to depict the phyletic relations of known Palaeozoic Dipnoi).

The examples used here (Fig. 3) are arranged both stratigraphically and (from left to right) to illustrate the range in body forms from more "conservative" to more "progressive" genera. As Westoll (1949) and others have demonstrated the Dipnoi evolved rapidly during the Devonian and by Permo-Carboniferous times had achieved a basically "modern" body form.

The earliest well-known genera, *Uranolophus* (Denison 1967) and *Dipnorhynchus* (Thomson and Campbell 1971) from the early Devonian, were marine fish as were many other Devonian dipnoan genera but the majority of later forms have been freshwater inhabitants (Thomson 1969b, table 1, 461). *Dipterus* and *Pentlandia* (Fig. 3) from the Middle Devonian do not differ greatly in their external morphology from contemporary crossopterygians (e.g. *Osteolepis*) in which the two dorsal fins and the single anal fin were separate and the caudal fin was normally heterocercal. By late Devonian times several lines of dipnoan evolution had produced a wide range of body forms ranging from the "conservative" *Rhynchodipterus* (Fig.3) through *Fleurantia* and *Scaumenacia* (with enlarged posterior and reduced anterior dorsal fins) to more "progressive" forms such as *Phaneropleuron*. In the last genus the dorsal fins had merged with the caudal and only the anal fin remained separate.

By Carboniferous and Permian times even this fin had been incorporated in the caudal fin complex as in *Uronemus* and *Conchopoma*. Major changes were still taking place in the skull, dentition, axial skeleton etc. but the body form was essentially modern.

Although *Gosfordia* is usually placed in the family Ceratodontidae (Thomson 1969a, 93) it is now clear that it must be considered an aberrant offshoot from the main line of ceratodontid evolution. The genus *Ceratodus* was already in existence by early Triassic times and a contemporary of *Gosfordia*. *Ceratodus,* which survived into late Cretaceous times, has been recorded from North America, Europe, Asia, Africa and Australia (Schaeffer 1969) although most of the occurrences, unfortunately, consist only of isolated toothplates and complete body fossils of the genus are rare.

Two occurrences of *Ceratodus* have been recorded from the Triassic rocks of the Sydney Basin. A small lungfish specimen, only 9.5 cm long, was described by Wade (1935, 1-3, Pl.I) from the Middle Triassic fish-bearing shale lens in the Hawkesbury Sandstone formerly quarried on Beacon Hill, Brookvale, a Sydney suburb. The unique holotype of *Ceratodus formosus* Wade (B.M.N.H. P16828) may well be a juvenile (Wade records the findings of several large, isolated dipnoan scales in the Brookvale horizon) but the relative proportions of the head, trunk and fins rule out any possibility of a close relationship to *Gosfordia*.

The other Sydney *Ceratodus* record came from the Middle Triassic shale horizons in the later Wianamatta Group, from now disused quarries in the suburb or St. Peter's. *Sagenodus laticeps* Woodward (1908, 6-8, Pl II, figs. 1, 1a) was later reassigned to *Ceratodus* by Wade (1931, 123) in his review of Australian Mesozoic fishes. *Ceratodus laticeps* (Woodward) is represented by a single incomplete specimen consisting of the central region of the trunk of a rather large, deep-bodied dipnoan. The head region is not well preserved but clearly displays a fused pair of fairly massive palatal toothplates which indicate that the proportions of the head must have been considerably more substantial than the head of a *Gosfordia* individual of comparable body size.

Whether or not these two occurrences have been correctly assigned to *Ceratodus* remains uncertain. There is no doubt, however, of the validity of Woodward's genus *Gosfordia,* a distinctive, deep-bodied dipnoan of early-Middle Triassic times. In many respects *Gosfordia* is more specialised than either *Ceratodus* or its descendant *Neoceratodus,* which has remained essentially unchanged at least since Cretaceous times and probably much longer.

From our knowledge of the mode of life of the three living lungfish genera it would appear that *Gosfordia* had most in common with *Neoceratodus*. Both *Protopterus* and *Lepidosiren* possess the ability to burrow and aestivate (or hibernate), a dipnoan survival device which is known to have been employed by some members of the group as early as Permo-Carboniferous times (e.g. *Gnathorhiza*). Although some workers (e.g. Thomson 1969, 128-9) have noted physiological evidence which might indicate that the ceratodontid (as well as the lepidosirenid) dipnoans may once have been able to aestivate, the extant *Neoceratodus* does not possess this ability. From its shape it seems quite unlikely that *Gosfordia* could either burrow or aestivate; on the contrary it gives the impression of having been a rather active, powerfully built swimmer and the size of the caudal fin suggests it could move quite fast when necessary.

ACKNOWLEDGEMENTS

The discovery of a complete *Gosfordia* illustrates dramatically the major contributions to science which may be made by excavation workers in quarries, mines, roadworks etc. who are in an unrivalled position to observe and save unique geological specimens for scientific study and for public display in State museums. All too often such specimens are ignored and needlessly destroyed. The writer wishes to acknowledge the contributions of Mr John Costigan (discoverer of the new *Gosfordia*), Mr C. Chidley, Sydney (who passed it to The Australian Museum), Mr R. Munday, Manager, Glendale Wash Sands Pty. Ltd., Mr John Fields, The Australian Museum photographer (for Fig. 1).

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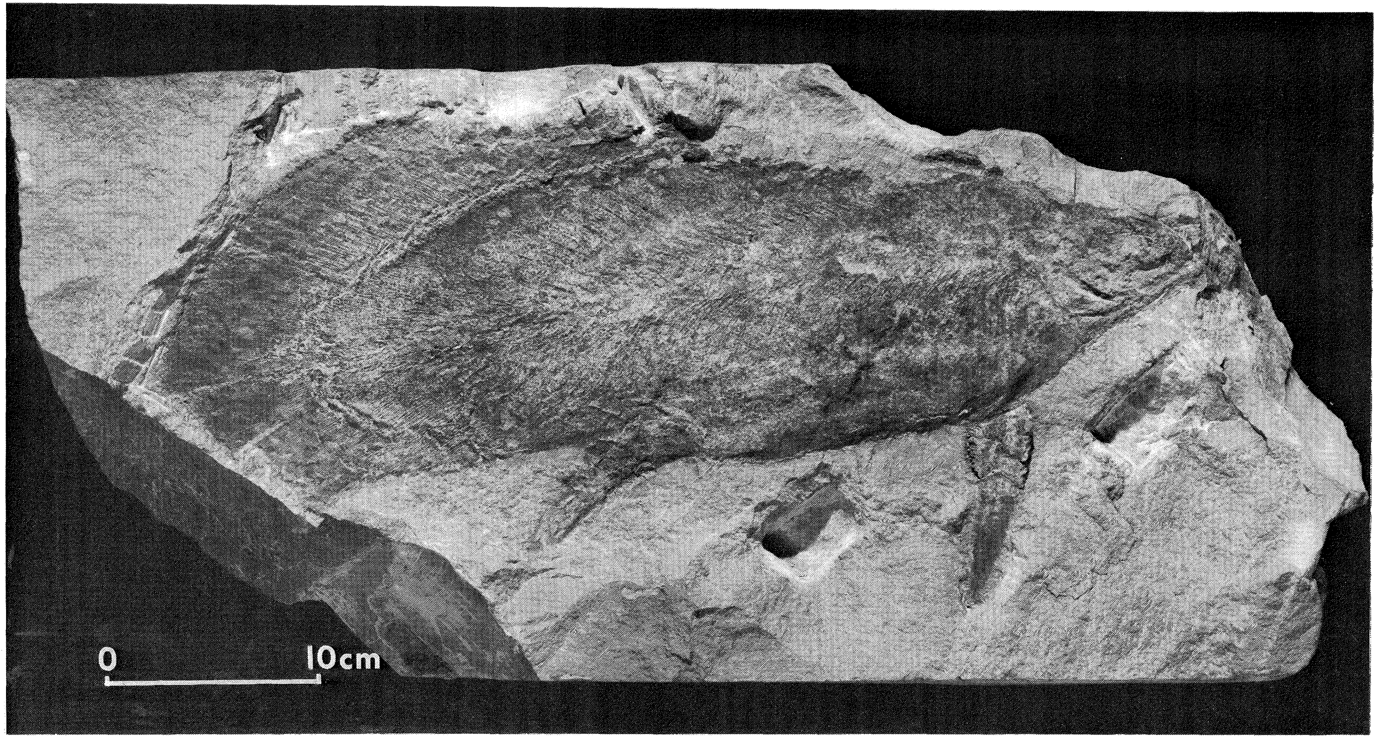

Fig. 1. *Gosfordia truncata* Woodward. Triassic, from shale lens in Hawkesbury Sandstone, 7 km. WNW of Gosford, New South Wales. Scale equals 10 cm. Australian Museum F.60621.

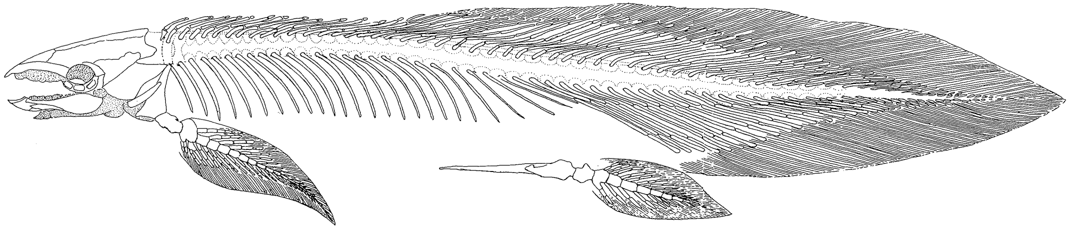

Fig. 2A. *Neoceratodus forsteri* (Krefft). Recent, Queensland. Modified after Günther, 1871 (post-cranial skeleton) and Goodrich, 1930 (cranial skeleton).

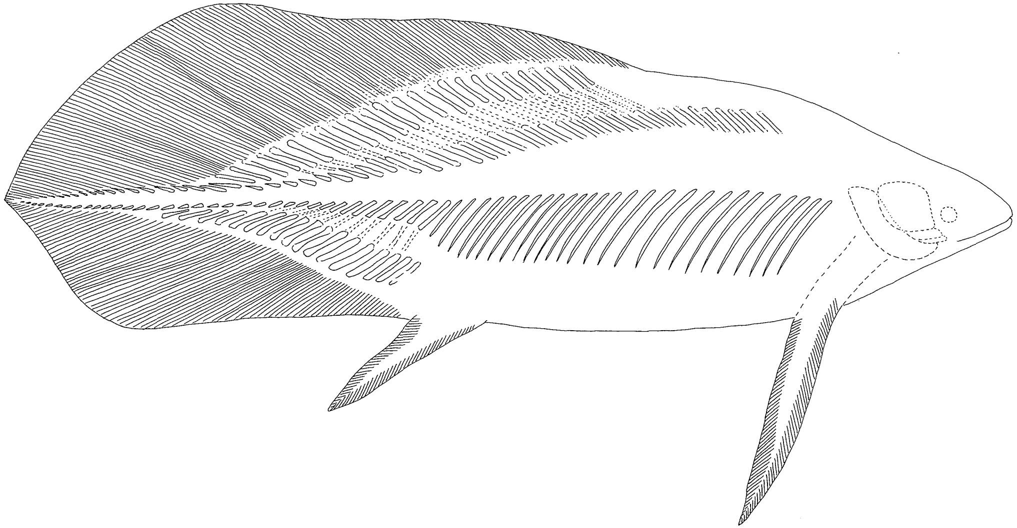

Fig. 2B. *Gosfordia truncata* Woodward. Triassic, New South Wales. Skeletal restoration based on A.M. F.60621 (Fig. 1). Length of original specimen 50 cm.

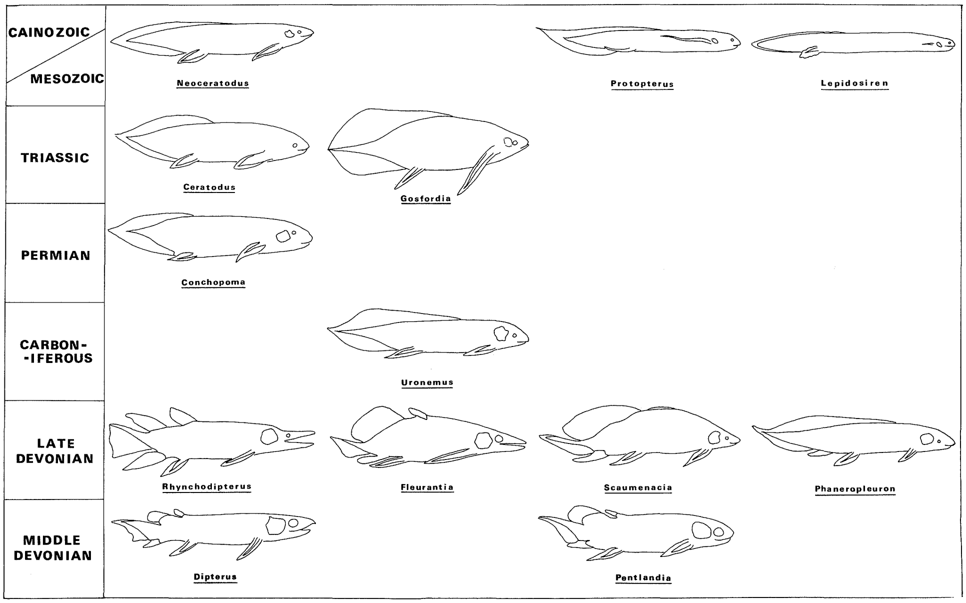

Fig. 3.Outline drawings of representative Dipnoi whose body and fin shapes are well known. All genera reduced to same length for comparative purposes. Stratigraphic ranges and geographical distribution of genera illustrated are as follows:
Dipterus Early-Late Devonian; North America, Europe, Asia, Australia.
Pentlandia Middle Devonian; Europe.
Rhynchodipterus Late Devonian; Europe.
Fleurantia Late Devonian; North America.
Scaumenacia Late Devonian; North America.
Phancroplcuron Latc Dcvonian; Europe.
Uronemus Carboniferous; Europe, North America.
Conchopoma Carboniferous-Permian; Europe, North America.
Ceratodus Triassic-Cretaceous; North America, Europe, Asia, Africa, Australia.
Gosfordia Triassic; Australia.
Neoceratodus Cretaceous-Recent; Australia.
Protopterus Eocene-Recent; Africa.
Lepidosiren Miocene-Recent; South America.

In addition to the stratigraphic arrangement (for convenience the Triassic has been considered separately from the rest of the Mesozoic) the 13 genera figured here are also arranged (from left to right) to illustrate the range of "conservative" to "progressive" body forms displayed by dipnoans of approximately the same geological age. No phyletic relationships are implied (redrawn after Jarvik, Lehman, Thomson and others).