

Dipnoan fishes from the Late Devonian Gogo Formation of Western Australia

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Abstract – The Frasnian Gogo Formation of Western Australia has yielded nine species of dipnoans assigned to six genera and two subgenera; all specimens were discovered within a very limited area. No other Devonian area has such an abundance of dipnoans within a small stratigraphic range. In addition, most of the specimens come from similar rock matrices. It is reasonable to interpret the animals as having lived off a deeply embayed reef, the best specimens coming from Paddy's Valley, an embayment partly sealed by a small atoll. Other specimens from outside this embayment were found in similar sediments. This high abundance of organisms provides an opportunity to analyse the different ways in which dipnoans adapted to a variety of different habitats within a narrow ecological range. Emphasis is placed on a number of features which are displayed by these animals – marine environment, air-breathing, dental apparatus, axial structures, pectoral and pelvic girdles, and feeding types – all of which give information on the state of evolution and function of dipnoans at an important stage of their evolution.

INTRODUCTION

The first work on the dipnoans from Gogo was published by Miles (1977) who described the specimens collected on an expedition in 1967 organised by the then British Museum (Natural History), the Hunterian Museum, and the Western Australian Museum. The outcrops sampled (for map see Miles 1971) form a line along the Emanuel Ranges, the three main localities being the Stromatoporoid Camp, the Long's Well area, and Paddy's Valley. Occasional specimens come from the first two areas, but most come from Paddy's Valley. Australian National University collections were made by two subsequent excursions; on one trip we were accompanied by Dr Alex Ritchie of the Australian Museum, and on the other by Dr John Long of the Western Australian Museum. Just as with the original collection, most of our dipnoan specimens come from Paddy's Valley, though an occasional specimen was found at the other two localities. The Australian Geological Survey Organisation collections were made by Dr Gavin Young. Several excursions by Dr John Long added many specimens to the Western Australian Museum collections. We have been able to examine all these collections over a number of years, and we express our thanks to the curators for their cooperation.

Miles (1977) described four species of dipnoans. Although the specimens were all accurately located, our own field work has shown that most

specimens must have been collected from nodules lying in a deep black soil, or in shallow valleys where the nodules containing the specimens had been transported. No exposures of the formation are available in Paddy's Valley, but sections through the rocks are well known from the work of mineral exploration companies and the Geological Survey of Western Australia. These show that shale makes up the main body of the rock, and that the nodules containing the fishes occur at several levels through the shale. Consequently, the precise location of the blocks in the soils and the valleys within it, are not of value in interpreting the environment.

On the other hand, deeper erosion south of Lloyd's Hill has produced better exposures in gullies and across intervening spaces. At one locality it is possible to trace the remnants of a stratum across about 200–300 m, with nodules being relatively abundant. Most of these specimens are well preserved; multitudes of small Devonian molluscs are also preserved in the area. We interpret this occurrence as indicating the fauna was living close to the bottom of the sea and that it was overcome by a cloud of sediment that was deposited down the front of the reef, smothering the animals and burying them in the same episode. If this is an accurate account of the way in which fossilization took place, it explains the wholeness of the specimens and the way in which their mineralization occurred. The preservation of some

dipnoans in three dimensions is a problem which requires special explanation. The points involved are outlined in the next section. It is possible to distinguish placoderms and dipnoans in this one stratum, but actinopterygians were not observed. Presumably this means that the more heavily armoured species were living close to the bottom and the more free-swimming actinopterygians could avoid the flood of bottom sediment. Unfortunately we have not found specimens in sections where sedimentary structures can be used to support this mode of burial, but this is a result of lack of information in the sequences we have examined.

Institutional abbreviations are given at the end of the paper.

PRESERVATION

The processes by which the mineralization of some dipnoan species took place was described by Campbell and Barwick (1988a). These depend on the covering up of the specimens at the time of fossilization, and the decomposition of the soft parts within days of burial. The bones of the head and the scales were quite unaltered. During the early stages of decomposition, radially arranged carbonate crystals were deposited between the bones of the head and the scales on the body (Figure 1). This enabled the animal to retain its three-dimensional shape and made it able to withstand the weight of the thin sediment overlying it. The space within the body of the

animal could then be filled by several episodes of sediment entering through holes in the wall, and from separate episodes of calcium carbonate precipitation. Of course, not all dipnoans are preserved in this way, because some of them were dead and partly decomposed when they were entombed by the sediment. Moreover, some species did not have the dermal bones fused together, and consequently fell apart shortly after death. We note that placoderms, although preserved with all the bones of a single specimen within the one nodule, are usually collapsed. This is because, although they were buried by being engulfed, they had no scale overlap to cause the body to be able to withstand the weight of overlying sediments, and their dermal bones were not fused together.

ABUNDANCES

It is not possible to determine precisely the relative abundances of the species. There are several reasons for this. Specimens are now spread among several institutions, some collected nodules have not been etched, and not all specimens observed in the field have been collected. Despite this lack of data, our own collections and those in the Western Australian Museum, and the Australian Geological Survey Organisation, give a reasonable account of the relative abundances of species. In addition, Miles (1977) indicated how many specimens he dealt with in doing the original descriptions. By far the largest numbers in all three

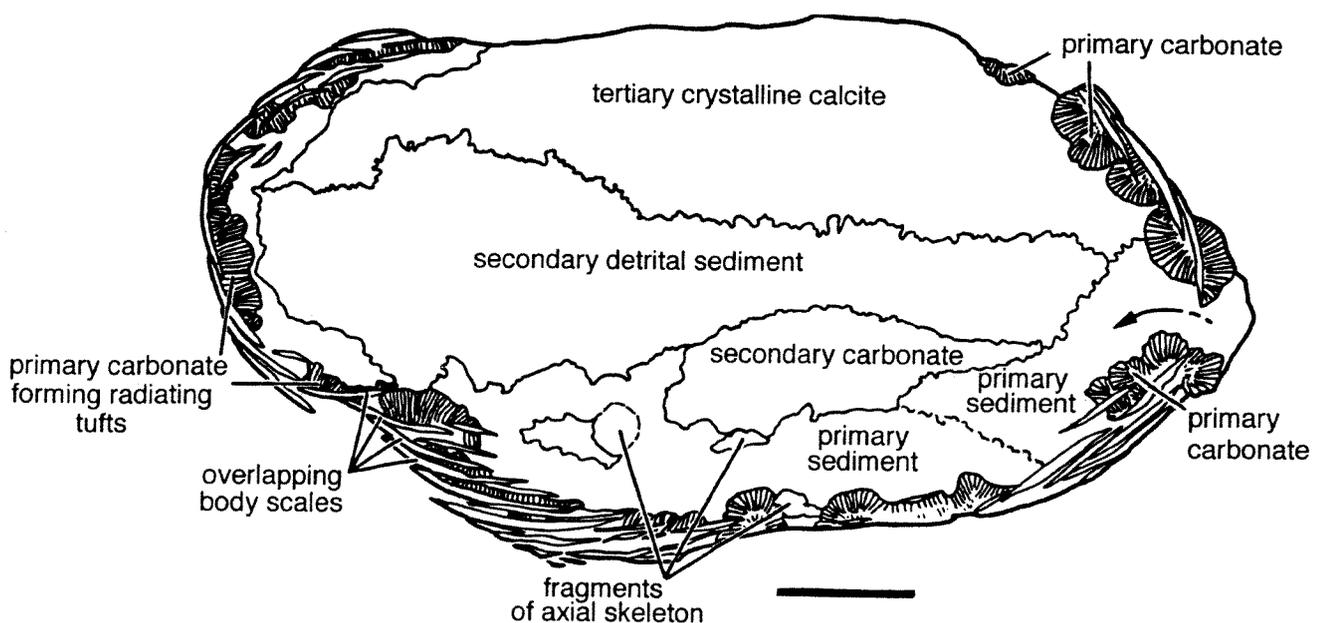


Figure 1 Transverse section of the body of *Chirodipterus australis* Miles in which the body is preserved in three dimensions, ANU 49497. The section shows how infilling has taken place as described in the text. Dorsal direction to the top. Scale bar = 10 mm.

collections belong to *Chirodipterus australis* Miles and *Griphognathus whitei* Miles. These are preserved as both adult and juvenile specimens. *Holodipterus gogoensis* Miles is the third most abundant (Pridmore *et al.* 1994), but it is only about one fifth as abundant as the two previously mentioned species, and the specimens are not complete. The other species of *Holodipterus*, such as *H. longi* Campbell and Barwick, *H. (Holodipteroides) elderi* Pridmore *et al.*, and *H. (Asthenorhynchus) meemanna* Pridmore *et al.* are represented by two or three individuals. *Gogodipterus paddyensis* (Miles) and *Pillarrhynchus longi* Barwick and Campbell, are each known from two adult individuals. A new genus of tooth-plated dipnoan, *Adololopas*, is known from one juvenile and two adult specimens (Campbell and Barwick 1998).

What are we to make of this disparity of abundances among species? In the first place, *Adololopas* has much the same form as *Chirodipterus* and is preserved in much the same way. We conclude from this that preservation is not a determining factor in the small number of individuals counted. Nor can we accept that collection methods account for the differences, because we have been careful to collect any specimens which show signs of true tooth plates. There can be little doubt that the new genus represents a form which occurred in small numbers in comparison with *Chirodipterus australis* and *Griphognathus whitei*.

Holodipterus is poorly represented in the Natural History Museum, London (N.H.M.) collections, and Miles used only eight incomplete specimens for his descriptions. Our collections have a small number of individuals also. Could this be the result of the breakdown of individuals because the bones of the head were not fused and did not hold together? We do not accept this interpretation because *Holodipterus* scales are easy to recognize, and we would have recognized them in the matrices examined. Clearly they were not abundant in the fauna.

The only known specimens of *Gogodipterus* are in the N.H.M. collections. We have searched our collections for another specimen, but without success. John Long has not found any further specimens in the Western Australian Museum collection. It must be a species of low abundance in the original fauna.

Pillarrhynchus Barwick and Campbell (1996) was collected by two field parties which were specifically looking for genera which were known from only a small number of individuals. Hence we can be assured that the genus occurs only in limited numbers.

We draw the conclusion that the following list gives a rough approximation of the abundances of the various species. The numbers given refer to the

relative abundances using *Griphognathus* and *Chirodipterus* as equal in number and rated as 50.

<i>Griphognathus whitei</i>	50
<i>Chirodipterus australis</i>	50
<i>Holodipterus gogoensis</i>	10
<i>H. (Holodipteroides) elderi</i>	10
<i>Adololopas moyasmithae</i>	5
<i>Pillarrhynchus longi</i>	5
<i>Gogodipterus paddyensis</i>	5
<i>Holodipterus longi</i>	2
<i>H. (Asthenorhynchus) meemanna</i>	2

So far as completeness and detail of morphology are known, this must be one of the best Devonian occurrences in the world. No doubt there are biases based on the collection and the location of material. However, it should be possible to outline the interrelationships between the fishes and the presence of other organisms in the environment.

WHAT CONCLUSIONS CAN WE DRAW FROM THIS OCCURRENCE?

The great number of dipnoans provides a basis for examination of the ecology of members of the group in a limited environment. Although many members cannot be exactly located in the section, their abundance and the uniformity of the formation suggests that they can be interpreted in terms of an homogeneous assemblage.

Marine Environment

Most workers now agree that the early evolution of dipnoans took place in marine waters. All the dipnoan species in the Gogo Formation have been interpreted as having lived in the sea in the area where they were found. Some people have suggested to us that the animals actually lived up among the reefs and were washed down into the basin. Even if that were possible, which we doubt, it would still indicate that they were of marine origin.

The possibility must be considered that they were fresh water animals washed in from adjacent rivers. Examination of the maps of the region shows that the Devonian marine sediments covered an extensive part of the area, and in Late Devonian times the nearest land would have been many tens of kilometres away (Playford and Lowry 1966). The greatest abundance of lungfish is in the Paddy's Valley embayment, where there is no evidence of adjacent streams. Moreover, the sediment in the embayment shows no sign of fresh water influence, and its invertebrate fauna is entirely marine.

We conclude that the dipnoan fauna was deposited in the marine environment in which it lived. The environment contained abundant marine

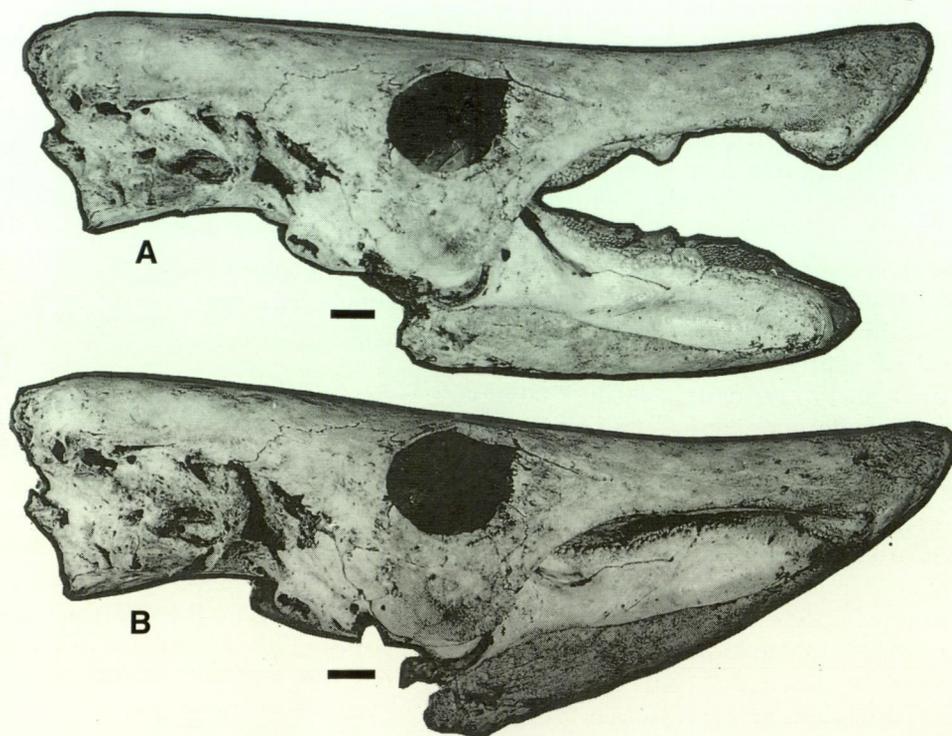


Figure 2 Two lateral views of the skull of *Griphognathus whitei* Miles, CPC 21186. A. The mandible is open more extensively than was possible in the living animal. It shows the excrescences for the marginal structures and the extent to which the muscle attachment area must have fitted up into the cheek. B. The same specimen with the mandible closed, and showing the size of the cheek pouch and the flat ventral surface of the head. Scale bars = 10 mm.

invertebrates, many of which were benthic in habit. In addition, nautiloids were common, indicating the presence of organisms which lived in the water column at a variety of levels. The abundance of reefs and the palaeomagnetic evidence (about 10–15°S in the Late Devonian; Scotese and McKerrow 1990), shows that the temperature was tropical to subtropical.

Where Did They Live in the Water Column?

Three lines of evidence can be used in this argument – one is preservational and the other two are morphological. As we have indicated above, many specimens show evidence of being engulfed in a bottom sediment flow and quickly buried. This would mean that they were at or near the bottom of the sea at the time of sediment flow.

Specimens of *Griphognathus whitei* have a lateral profile (Figure 2) that indicates that they were bottom feeders (Miles 1977; Campbell and Barwick 1987). The flattened mandible fits high up into the base of the skull, so that the whole ventral surface would have been in contact with the substrate. The snout is turned under the front of the head, so that it has the characteristic snout shape of a sediment feeder. The snout and the front end of the mandible both enclose tubules (Figure 3), some of which open directly to the external surface. We consider that these tubules contained electrosensory systems

(Miles 1977; Campbell and Barwick 1987; Cheng 1989). Bemis and Northcutt (1992) have recently described ampullary electroreceptors in *Neoceratodus forsteri* Krefft, though they do not accept that the tubule system in the snout is used for electroreception. Electroreceptive systems are found at present in some primitive mammals such as *Ornithorhynchus* (Scheich *et al.* 1986; Bohringer 1992), in which they are used for searching out prey in the sediment. No matter what we consider is the function of the tubule systems, we consider that *Griphognathus* was a bottom-dwelling, sediment-searching feeder.

The case of *Chirodipterus australis* is not so clear cut (Miles 1977; Smith and Campbell 1987). The preservation suggests that it lived near the bottom, but the genus (Figure 4) lacks the depressed profile and the underturned nose characteristic of *Griphognathus*. On the other hand, *C. australis* has a well-developed electrosensory system in its snout and mandible (Figure 3) suggesting bottom-feeding, but its capacity to feed on sediments is not supported by the shape of its snout, the shape of its dental apparatus, or the large adductor muscles that activate the mandible. All these features suggest a harder diet that had to be reduced by grinding the prey. Such prey organisms are found in the short molluscan cones, and nautiloids found in the Gogo Formation. It seems that *Chirodipterus*

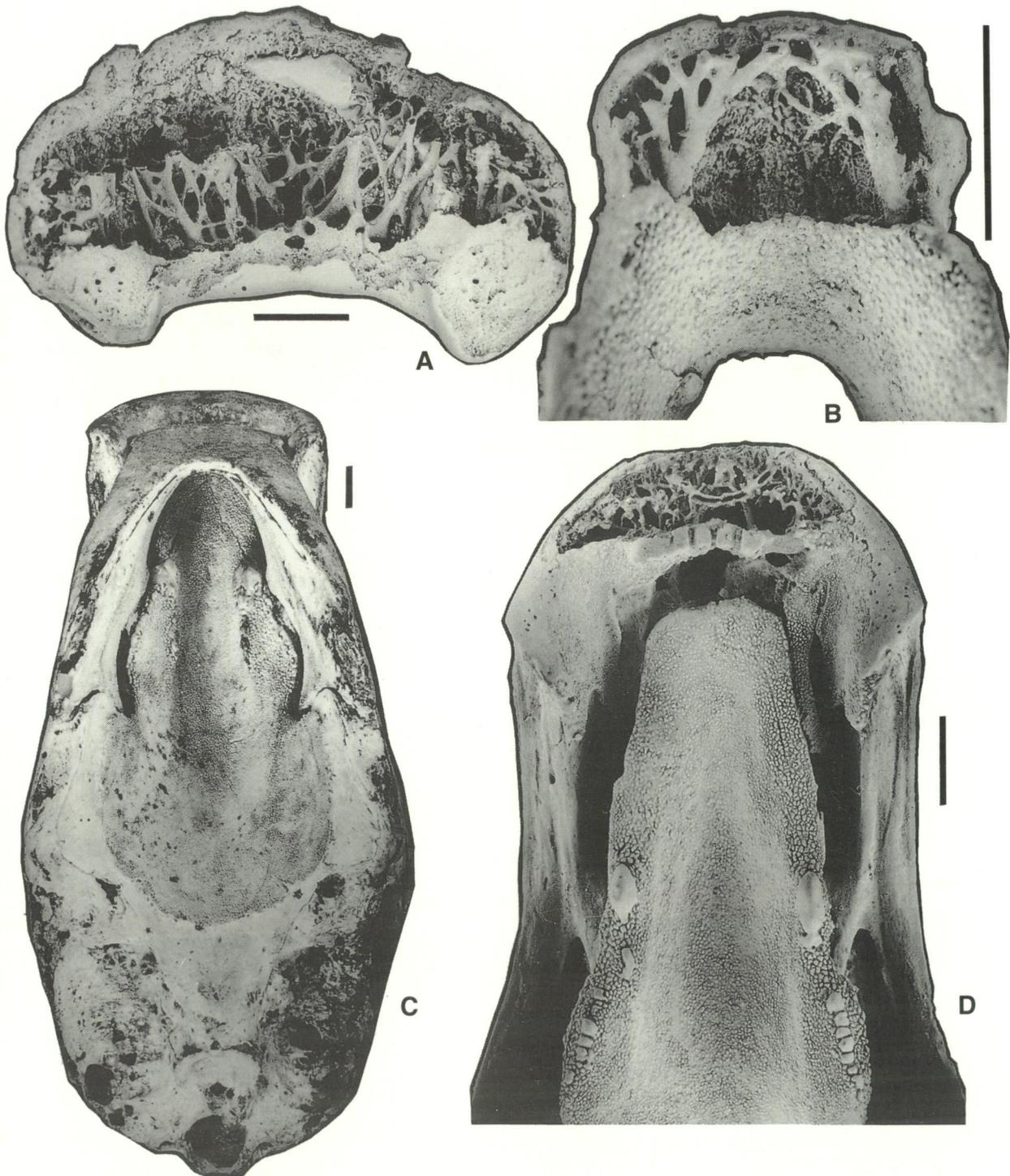


Figure 3 A. Internal view of the snout of *Chirodipterus australis* Miles, showing the tubules of the electrosensory system, ANU 35636. B. The anterior end of the mandible of *Griphognathus whitei* Miles, showing electrosensory tubules, ANU 35644. C. Ventral view of *G. whitei* with the mandible in occlusion. Note that the dental apparatus of the palate and the mandible are not in contact, CPC 21186. D. Anterior end of the head of *Griphognathus whitei* with similar structures, and the transverse band of the lateral line system across the mid-line. Also note the excrescences and the enlarged irregular excrescences along the palatal margin, CPC 25742. Scale bars = 10 mm.

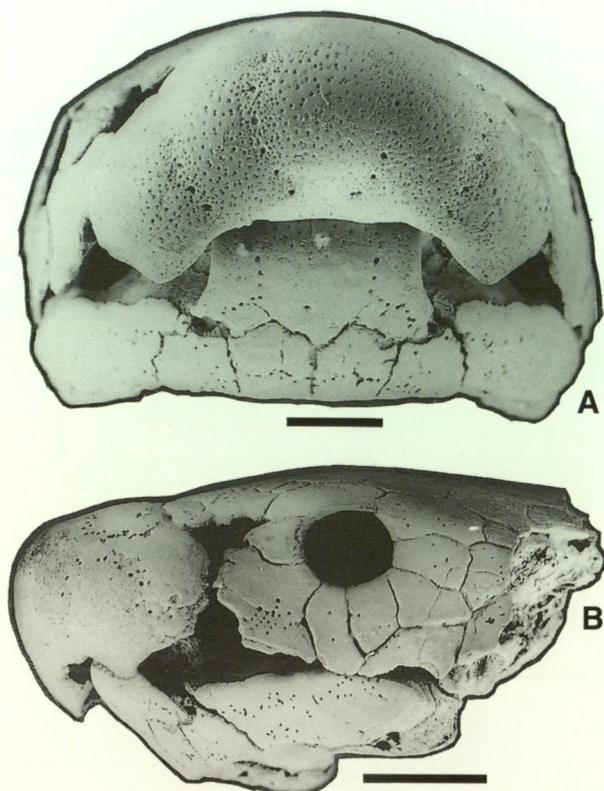


Figure 4 Anterior (A) and lateral (B) views of the skull of *Chirodipterus australis* Miles, ANU 21634. Note the rounded snout, the large pores of the lateral line system, and the closure of the mandible into the snout. Scale bars = 10 mm.

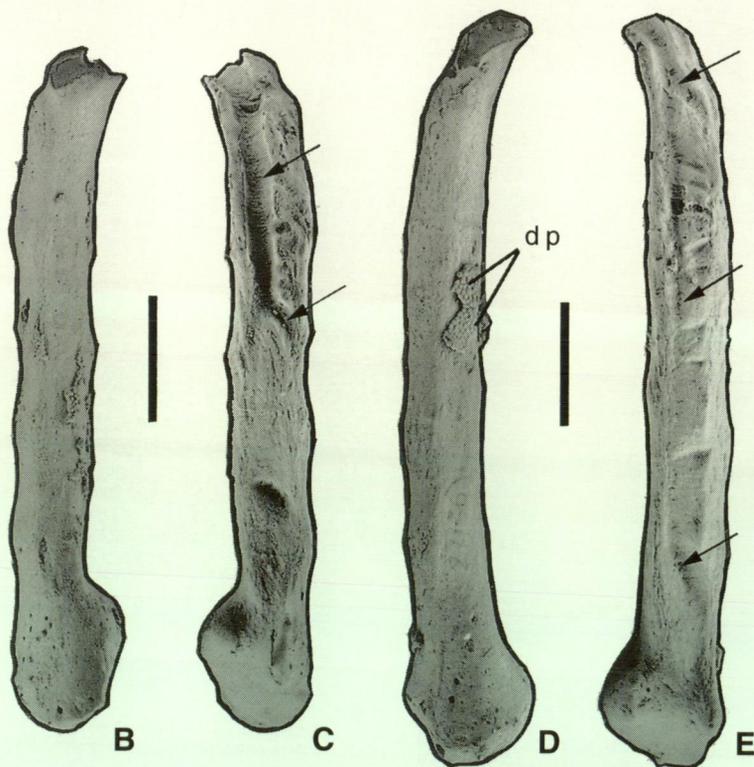


Figure 5 Branchial arches of *Griphognathus whitei* Miles. A. Ceratohyal and the four ceratobranchial arches of ANU 35645. All plates were found in natural articulation in the one specimen. Note the ceratobranchial grooves, and the processes for the junction of the arches. B-C. Views of ceratobranchials of CPC 21186, showing the ceratobranchial furrow for the efferent artery and branches, and the branchial nerve. D-E. Two other ceratobranchials. Arrows indicate the ceratobranchial furrows. dp shows some denticulated plates still attached to the surface. Scale bars = 10 mm.

lived above the water base, but fed on unattached invertebrate faunas that covered the floor, and circulated in the lower water profile.

The other species are more difficult to interpret; however, holodipterids have the structure and dental capacity to bite and comminute both soft and hard prey.

Were They Air-breathing?

Several specimens are well enough preserved to show the gill arches. All of these have grooves that contained the branchial vessels and nerves. Some specimens also show branches for the gill filaments (e.g. *Griphognathus*, Figure 5). Although these specimens demonstrate the animals were gill-breathing, could they have been air-breathing as well? If we are correct in considering that these animals lived near the bottom of the sea, as argued above, it becomes necessary to discover the depth of the sea-water. The work of stratigraphers shows that in the Paddy's Valley embayment the water must have been more than 100 m deep (Campbell and Barwick 1988a). Such depths would make it impossible for dipnoans to rise to the surface of the sea to breathe. In addition, it has been shown by Pridmore and Barwick (1993) that the scaly skeleton of dipnoans gave them a relatively stiff body (Figure 6), and they would not have been able to swim rapidly by body undulation.

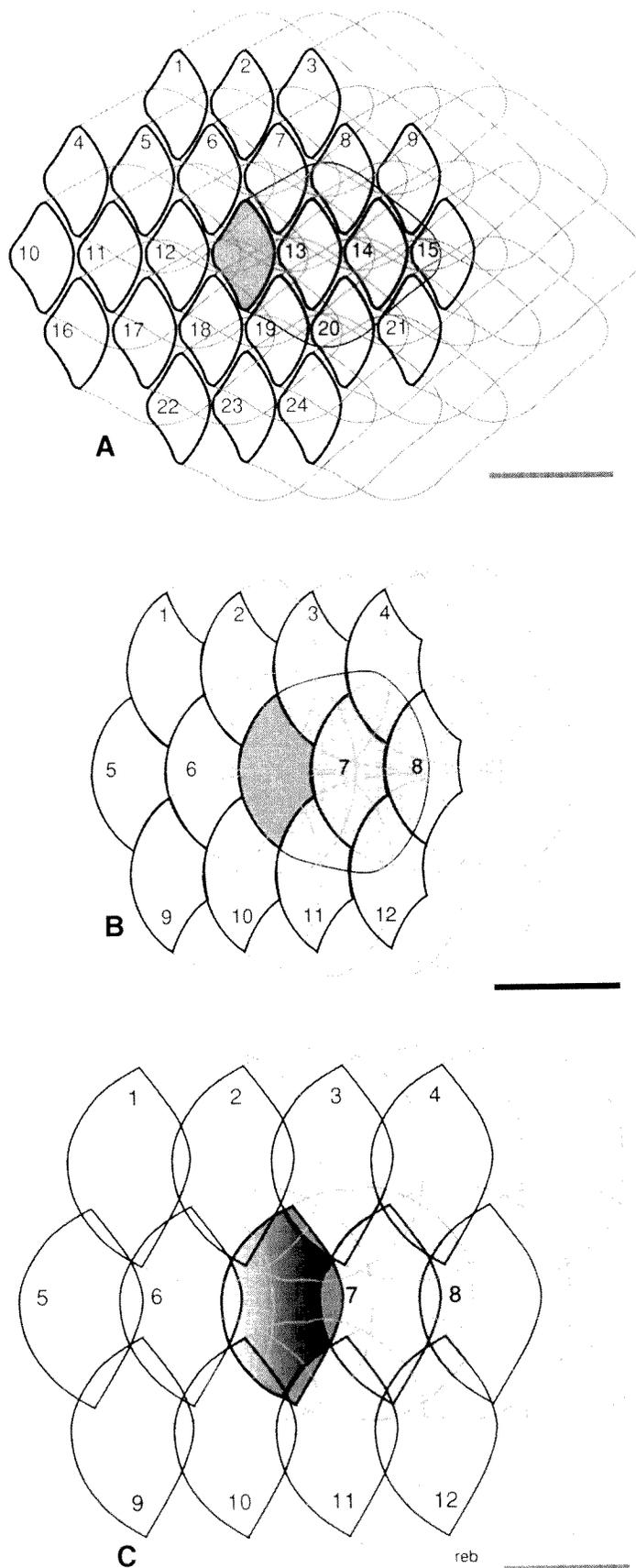


Figure 6 Reconstruction of the scale pattern developed from a single scale in each species along the medial part of the lateral line. The single scale is darkened, and the exposed part is more heavily darkened. All the scales that are in contact with the control scale are numbered. A. *Chirodipterus australis* Miles. B. *Griphognathus whitei* Miles. C. *Holodipterus (Asthenorhynchus) meemannae* Pridmore *et al.* In C, portions of the exposed cosmine-covered area of the scale are overlapped posteriorly by adjacent scales. Scale bars = 10 mm.

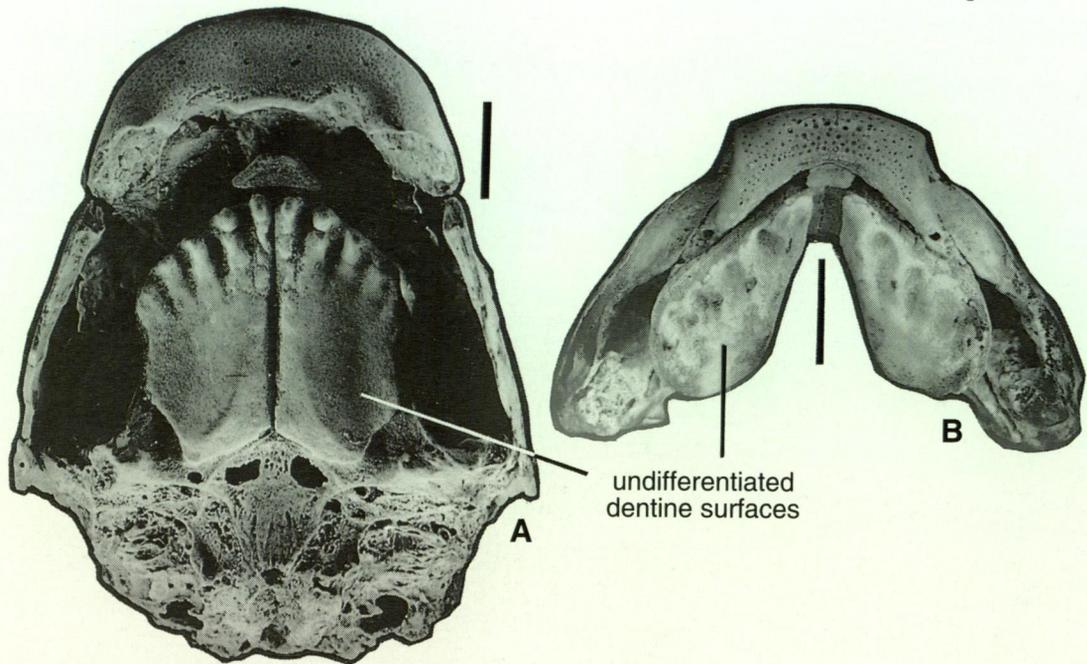


Figure 7 View of the palate and the buccal surface of the mandible of *Chirodipterus australis* Miles, ANU 21634. Note the hard posterior part of the plates, and the anterior part with roughly outlined radial ridges. Scale bars = 10 mm.

Campbell and Barwick (1988a) argued that the dipnoan faunas in the Gogo Formation lacked the tooth plate structure necessary to have formed a seal to the anterior end of the mouth during breathing, that they lacked the long posterior part of the buccal cavity used for holding air before it was pushed into the lungs, and that the hyoid and pectoral arches were not able to rotate to produce a force pump mechanism to relocate the air (Bishop and Foxon 1968). So far as we can see these arguments remain valid. Panchen and Smithson (1987), using independent argument, have supported a similar view. Thomson (1993) considered that our supporting arguments are 'contorted special pleading', but offered no supporting evidence for his statement. Previously, Thomson (1980) decided that early dipnoans and other lobe-finned fishes were air-breathing, his data being speculative physiological concerns based on an indefinite interpretation of Palaeozoic environments. No morphological arguments were presented in his statement. Since he provided no firm argument to support his views, we consider that his comment cannot be refuted by normal scientific dialogue. The positive morphological evidence, the stratigraphic evidence from Gogo, and the functional evidence from extant dipnoans, supports the view that the marine species we have discussed here were not air-breathers.

Ex cathedra statements of the kind used by Thomson have a contrary effect on further development of argument. In a recent book by

Graham (1997), it is said that Campbell and Barwick (1988a) argued that because most Early Devonian dipnoans were marine, they could not have been air breathing. This is not a correct representation of our views as presented in that paper. We indicated that the morphology of the marine Devonian Dipnoi, the thickness of their skeletons, the probability that they were poor swimmers, combined with the evidence that Late Devonian species at Gogo lived in moderately deep marine water, provided support for our contention that gill breathing was their normal respiratory method. This conclusion is further supported by the fact that the earliest Dipnoan burrows occur in rocks that are of Late Carboniferous (or Permian) age (McAllister 1992). Also Graham noted that the unpublished thesis of Yu (1990; not seen by us) "shows a pattern of divergence . . . which suggests that a functional lung was likely present in all of the earliest lobefins". Without supporting evidence, this adds nothing to the discussion. Even if it could be shown that the antecedents of actinopterygians and sarcopterygians had air bladders, this would not allow us to assume that lungs were present in primitive dipnoans. As Graham (1997, p. 10) has pointed out, "air breathing has been independently and frequently acquired in a variety of actinopterygians during the 400 million years evolutionary history of this group . . .". The real problem is to show that the primitive dipnoans had the morphology to be air-breathers from their earliest origins.

One further point is worth comment. Long (1993) mentioned the absence of cranial ribs in the Gogo

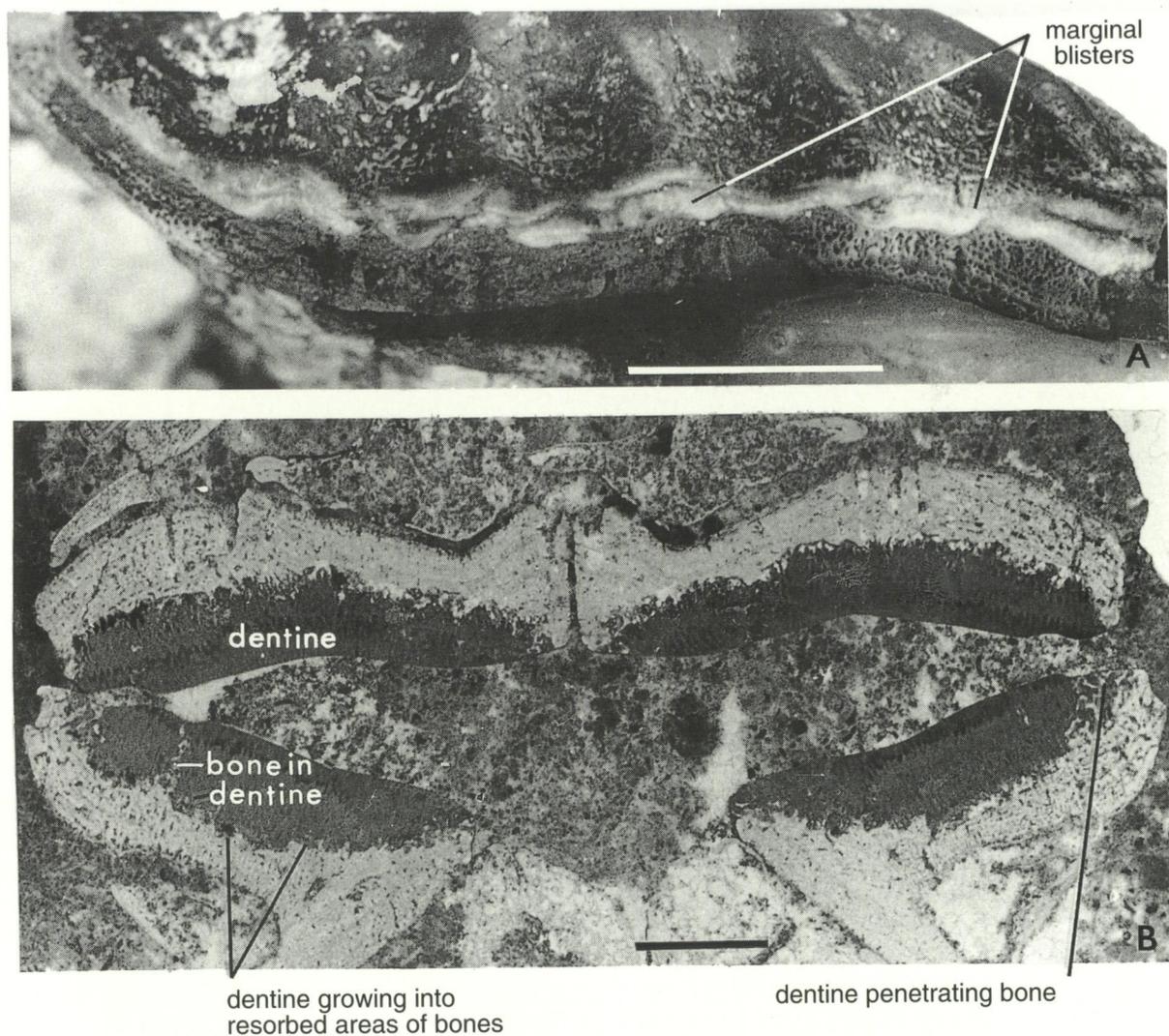


Figure 8 Dental plates of *Chirodipterus australis* Miles. A. The margin of a prearticular plate showing solid dentine at top, margins with blisters, and bone forming the prearticular. Anterior to right, ANU 35639. B. Cross section of a head with palate above. Note the dark dentine growing into the pterygoid and prearticular bone, the gaps where dentine replacement is not complete, the extent of the growth of the prearticular to a more lateral position than the pterygoid, and the growth of the prearticular around the end of the dentine, and particularly the growth of the dentine into the bone laterally on the prearticular. CPC 22592. Scale bars = 5 mm.

dipnoans, though they are present in the Middle Devonian *Dipterus* from Scotland, and in *Howidipterus* and *Barwickia*, late Givetian-early Frasnian genera from Victoria (Long 1992a). He commented that in extant dipnoans, cranial ribs are associated with air-breathing, being involved with hyoid depression. Such ribs are found in genera with forwardly placed teeth, and long parasphenoids indicating a long posterior end to the buccal cavity. So far, dipnoans with cranial ribs have been found only in sediments deposited in fresh water.

The Formation of Dental Apparatuses

Some work has been done on the deposition of dental apparatus in extant dipnoans (Kemp 1977, 1979; Smith 1985, 1988), and it has been assumed

by some workers that these modes have always been adopted by dipnoans at all stages of their evolution. In fact, extant dipnoans are the end products of a limited number of dipnoan lines of evolution. As is shown below, we consider that other modes of formation existed in early genera, and have since become extinct.

Some workers have also attempted to show that some forms of apparatus such as teeth, have evolved once only, and to use those characters as indicators of phylogenetic lines (Smith 1988). The Gogo fauna is so well preserved, that it is possible to describe the development of characters in several species, as well as their histology during part of their development.

Three types of dental apparatuses have been described. The first is based on *Chirodipterus*

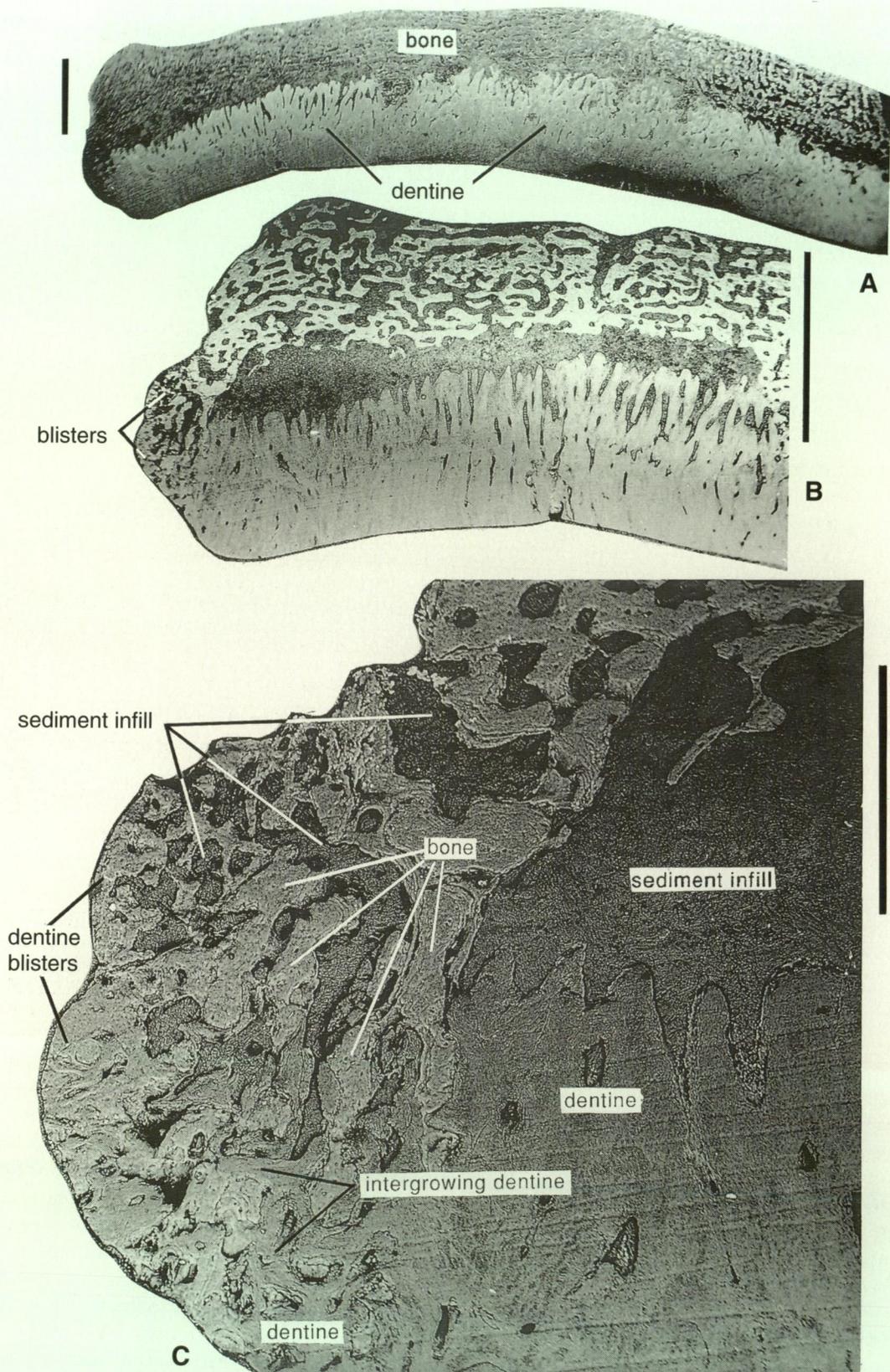


Figure 9 Sections of a dental plate of *Chirodipterus australis* Miles, cut approximately along a row of tuberosities. A. Length of plate with bone at top and dentine at bottom. Dentine is solid at the buccal surface, shows open pulp canals dorsally, and passes into spaces where the bone has been resorbed. B. The left lateral edge of the same specimen showing two blisters with the smaller one dorsal and overlying the earlier one and adjacent bone. The bone dorsally shows the bone extending down adjacent to the dentine, the fine dentine structures of the blisters, and the intergrowing dentine occupying spaces in the primitive dentine of the blisters. ANU 56248. Scale bars: A = 1 mm; B = 2 mm; C = 0.5 mm.

australis, the second on a new species described elsewhere, and the third on *Griphognathus whitei* and *Holodipterus* spp.. These are now described.

Chirodipterus australis (Campbell and Barwick 1983; Smith and Campbell 1987), and *Pilliarhynchus longi* (Barwick and Campbell 1996) have thick dental plates made up of hypermineralized dentine (Figure 7), but they have no isolated, enamel-covered teeth at the margins of the plates. Additions to the lateral and anterior margins of their plates were made first by the growth of bone, followed by the development of new blisters of enamel-covered dentine in layers over the bony surface. Once these were built out to form a new surface, they were intergrown from the plate by resorption and penetration by hypermineralized dentine (Figures 8, 9). This penetration did not occur in a continuous series. Rather it occurred as hard nodules along lines which were arranged to make radial rows along the plates (Figure 7). This gives the rough appearance of tooth plates as in *Dipterus*. Subsequent development took place by thickening of the dentine basally. This occurred not by addition from a basal pulp cavity, but by resorption of the underlying bone and intergrowth by new dentine into the available space (Figure 8). The proximal part of the plate also shows modification by the lateral extension of the nodules forming the plate, so that the lines of ridges become joined to form a hard undifferentiated surface. This kind of plate is termed a dental plate rather than a tooth plate (Smith and Campbell 1987).

A new Devonian genus, *Adololopas*, has true tooth plates with new enamel-covered teeth at the lateral and anterior margins of the plates (Figure 10). Each new tooth in this species has a basal pulp cavity and deposition into this cavity allows the tooth to develop much of its thickness; when this thickness is reached, further growth allows the cavity beneath the new tooth to be joined to the cavities under the previously formed teeth in the same row, to make a continuous cavity beneath the tooth rows. Beneath the gaps between the tooth rows, the situation is different. The dentine in the valleys is in contact with the underlying bone in an irregular fashion. This differs from what is seen in adult *Neoceratodus*, in which the basal pulp cavity is continuous across the whole tooth plate except at the margins. Thus, in *Neoceratodus*, the dentine increases its thickness by deposition across the whole plate at the same time. In the new Devonian form, addition to the thickness of the newly formed teeth took place from the basal pulp cavity, but the dentine in the valleys between the rows is formed by the addition of coarse dentine superimposed directly on bone.

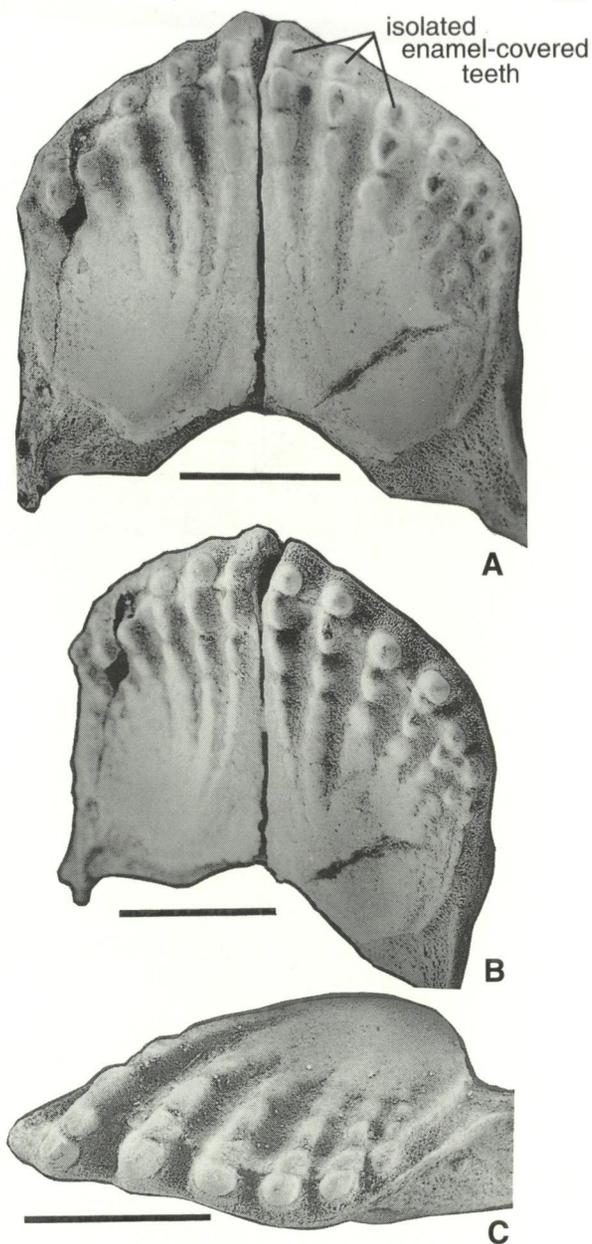


Figure 10 The palatal plate of *Adololopas* which shows the addition of real teeth covered with dentine at the ends of the rows. A, ventral view and B, oblique view to show the dentine along the edge and infilling dentine between the tooth rows. C. Oblique view of the left prearticular plate of the same specimen showing the teeth on bone at the margins and the layer of enamel-covered dentine formed between the teeth. All views of ANU 49213. Scale bars = 10 mm.

Griphognathus (Campbell and Barwick 1983) and *Holodipterus* (Campbell and Smith 1987) show a third type of growth. They are not identical, *Griphognathus* being the primitive style. We describe it first.

Fully articulated and undistorted specimens show that the two jaws did not occlude when fully closed (Figure 3C). The mandible passed

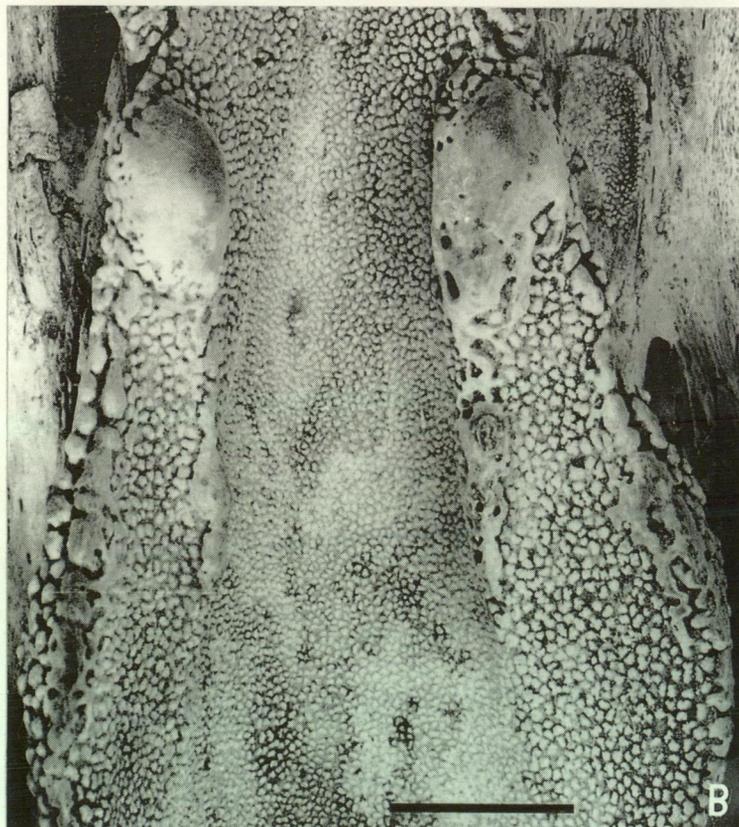


Figure 11 The anterior part of palates of *Griphognathus whitei* Miles. A. Showing the excrescences on the pterygoids medial to the dermopalatines, and the differences in the denticles along the groove bordering the mid-line, and those bordering the palate, ANU 21636. B. Similar view of CPC 21186. Compare with Figure 3C-D. Scale bars = 10 mm.

outside the margin of the palate. What is more, the jaw is so tightly articulated at the glenoid fossa, and the anterior end of the mandible is so confined by the ridges on the snout, that no lateral movement of the mandible was possible (Figure 3C). It can be shown conclusively that the two jaws were not in contact, even at full occlusion. The question then is – how was the food reduced?

First we comment on the largest and best preserved specimens. The pterygoids have a large bulbous excrescence just behind the dermopalatines (Figures 3D, 11). This was illustrated by Miles (1977), Campbell and Barwick (1983), and Smith (1988). Behind this excrescence is a ridge of small denticles which may or may not be continuous (Figure 11A,B). Some adult specimens have another row of similar structures extending posteriorly from the main excrescence. These rows

are not fixed in position; the margins of each surface show resorption and replacement by small denticles. The mandible has a major excrescence situated on the prearticular where that bone meets the dentary (Figure 12). Along the crest of the prearticular posterior to the excrescence is a row of irregular excrescences which become smaller posteriorly. Like those on the pterygoid they were resorbed laterally and were replaced on both sides by a row of irregular denticles. Anterior to the main excrescence, the dentary has a row of hard tissue within which can be seen small centres representing a row of small excrescences (Figure 12C). This tissue is replaced on both sides by resorbed surfaces and small denticles. The dentary surface fits up into a cavity formed by the small plates covering the floor of the nasal capsules. Note that the dentary does not meet the small group of

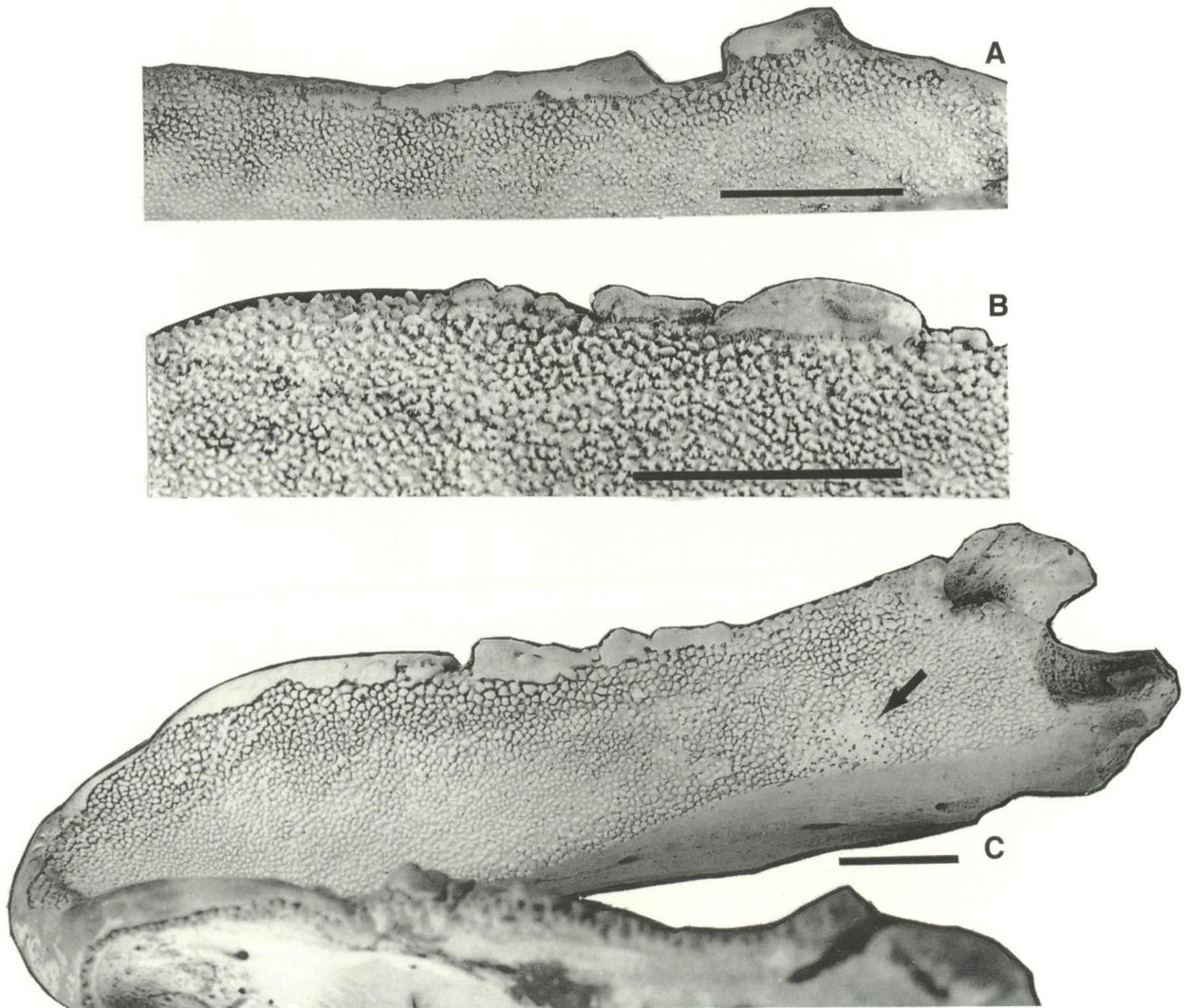


Figure 12 Three views of the margins of palates and mandibles of *Giphognathus whitei* Miles. A and B have the anterior to the right, C anterior to the left. A. Internal view of the mandible of ANU 35644. B. Internal view of palate of same specimen, further enlarged. C. Internal view of mandible of CPC 21186. Note that the denticles on the ramus are in places joined by a layer of primitive dentine, arrowed. Scale bars: A, B = 5mm; C = 10 mm.

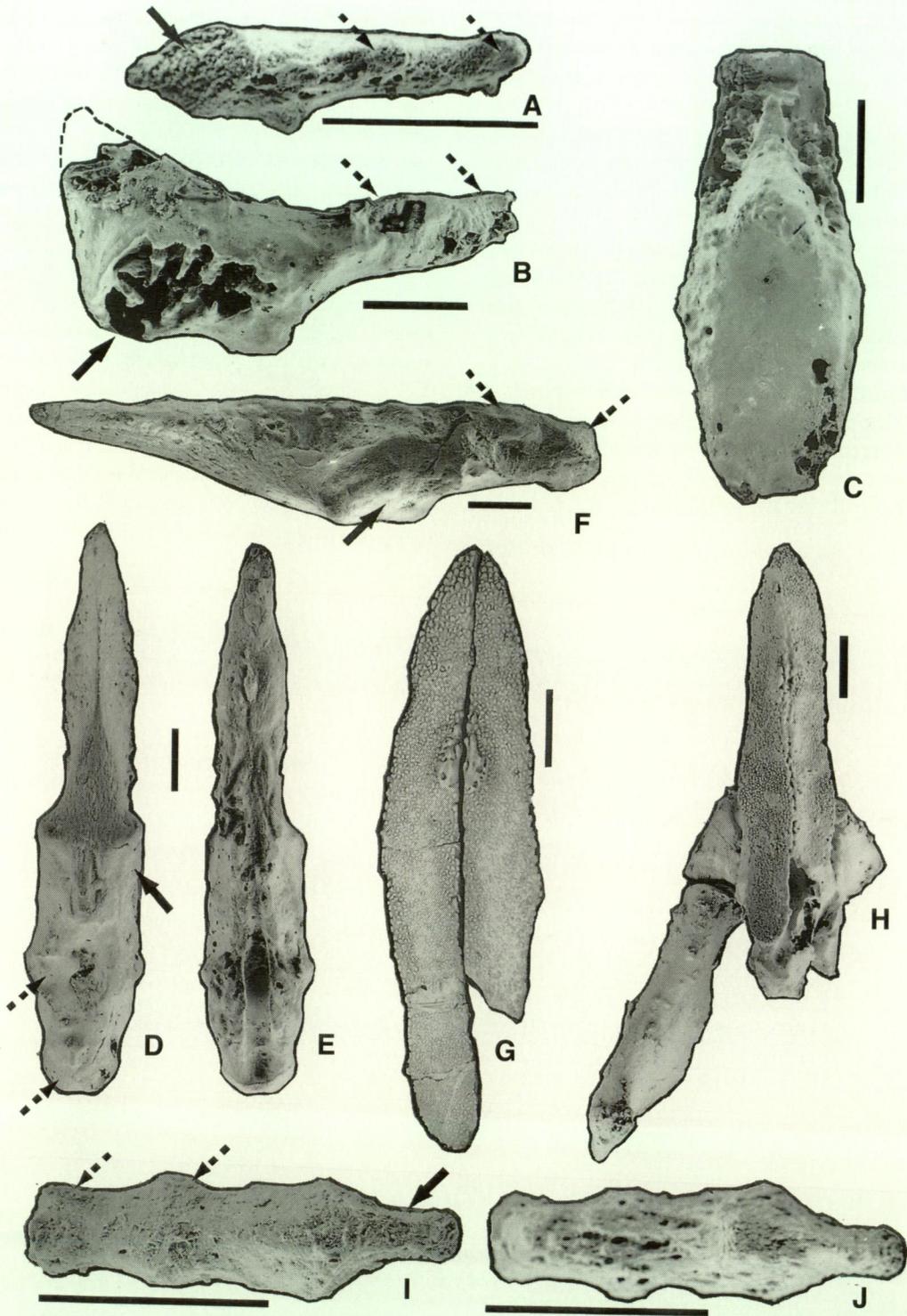


Figure 13 A, I–J. Basihyal/basibranchial plate of *Chirodipterus australis* Miles, ANU 49200. A. Lateral. I. Dorsal and J. Ventral views. Note that the anterior end is depressed, the articulation of the hypohyal (black arrow) is large and dimpled, and the first and second attachments (dashed arrows) for the ceratobranchials, are well inserted. B–C. Basihyal/basibranchial plate of *Holodipterus (Holodipteroides) elderi* Pridmore *et al.*, ANU 49101. B. Lateral view of the plate. Note that the large attachment area for the hypohyal and much smaller ones for the attachment of the ceratobranchial arches, are well shown. The anterior dorsal end was lost during preparation, but note that it was formed as an extension of the outline presented. C. Ventral view of same. D–F. Basihyal/basibranchial of *Griphognathus whitei* Miles, CPC 21186, in ventral, dorsal and lateral views. Arrows show the attachment of hypohyal and first and second ceratobranchials as in previous figures. G. Dorsal views of dental plates attached to the surface of E. Note the enlarged denticles along the mid-line. H. An isolated basihyal/basibranchial plate in dorsal view with the two hypohyals and the left ceratohyal. Denticulate plates are still attached, but the posterior one on the right side is missing. Scale bars = 10 mm.

tooth-like structures placed between the external nares of the snout. It passes behind them, and could not occlude with them at any stage of the jaw opening.

We have several juvenile specimens with skull lengths down to 63 mm. Though these have no mandibles attached, the palates give a good indication of the total dentition. The distribution of the excrescences is as in the adults, and the development of ridges of hard dentine running posteriorly to outline the median groove on the palate, begins at an early stage of growth. Variations of some other features are common. For example, the edges of the palate have long complete ridges of hardened dentine, whereas at the other extreme are those which are reduced to slightly enlarged denticles. Some specimens have a

uniform mode of denticles over the pterygoid body, whereas others have finer denticles medially and larger ones laterally (Figures 3C-D, 11A-B). These differences indicate only minor changes in function between individuals.

At occlusion the excrescences pass adjacent to their opposing structures and overlap them (Campbell and Barwick 1983); although they did not grind prey, they would have been useful for shearing any large particles that entered the mouth. Consequently, an alternative method for breaking down small particles must have been used. This required the special adaptation of the basihyal/basibranchial plates. These plates formed a large strong structure which extended forwards between the excrescences towards the anterior end of the pterygoids. On their dorsal surfaces they

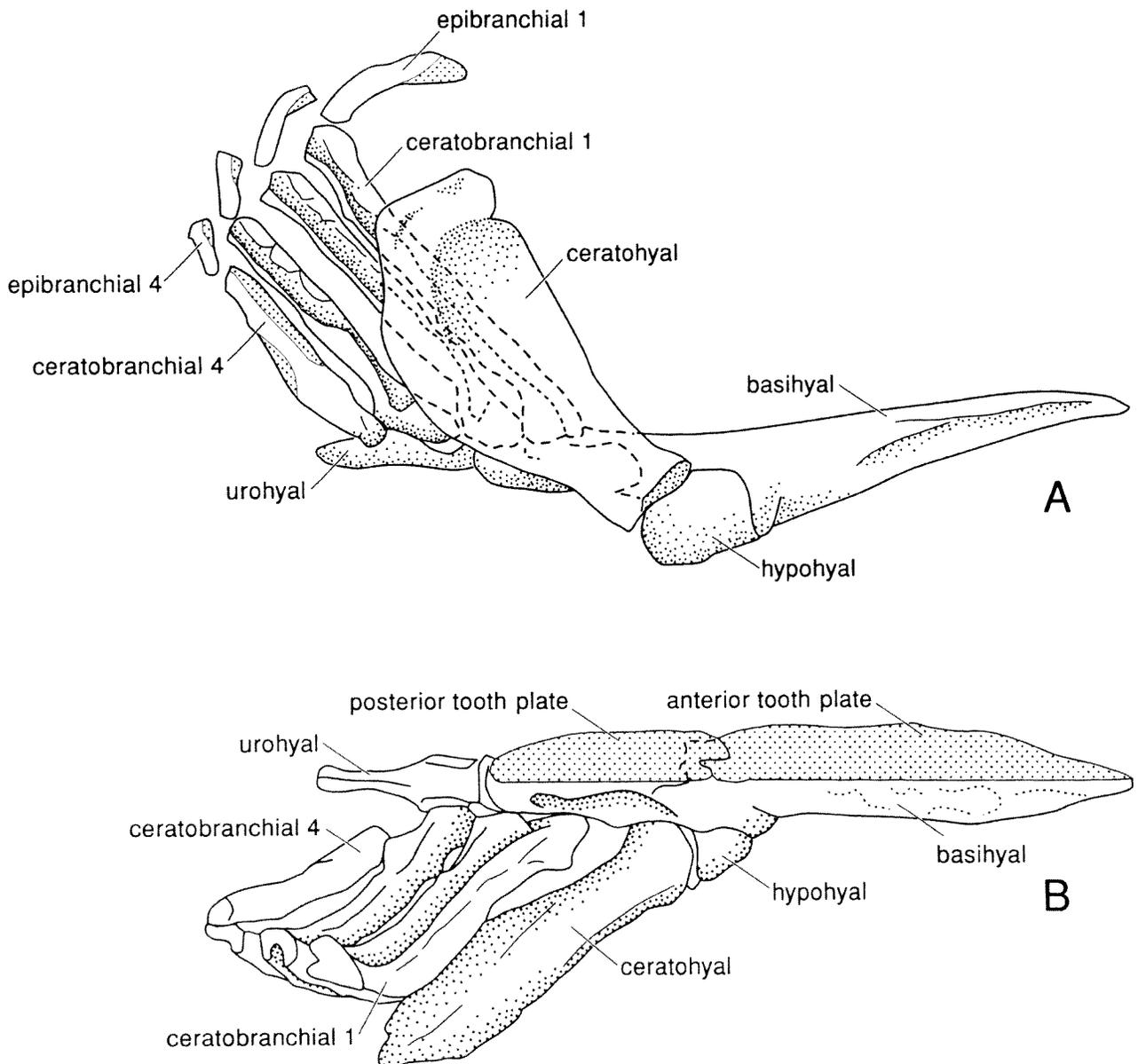


Figure 14 Reconstruction of the basihyal/basibranchial bones of *Griphognathus whitei* Miles, the hyoid arch and the branchial arches. Modified from Miles (1977) and Campbell and Barwick (1983).

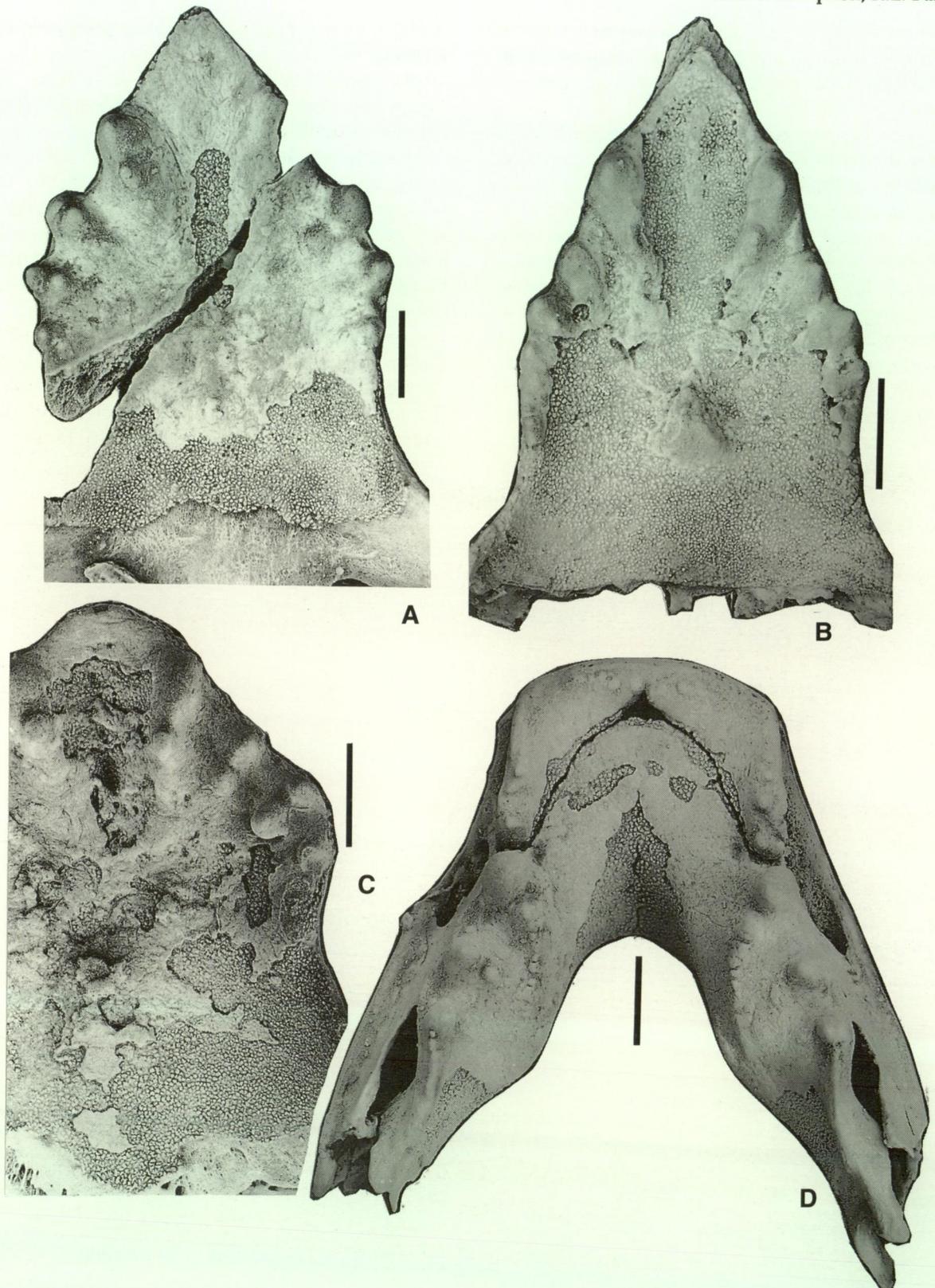


Figure 15 Dental plates of *Holodipterus gogoensis* Miles. A–C. Three palatal tooth plates showing the different views of resorption of the primitive dentine and the growth of replacement denticles. A. Palate of CPC 25738 in full ventral view showing extensive primitive dentine. B. Shows the large median callus left after several resorptions have not removed all the primitive dentine layers. C. A larger specimen showing extensive resorption patches in the primitive dentine with denticles occupying the vacated spaces. Both show resorbed marginal teeth. D. Mandible showing teeth along the top of the dentary, partly resorbed teeth on the prearticulars, denticles replacing the teeth and the primitive dentine, the foramen medial to the dentary, and the small open space for the adductor muscles. A = CPC 25738. B = CPC 25740. D = BMP 52569. E = CPC 28738. Scale bars = 10 mm.

supported four plates on which were situated denticles (Figure 13G–H). In places these denticles joined together and had a hard core of hypermineralized dentine. Hypohyals were joined to ceratohyals (Figure 14) which were attached to the posterior end of the skull (Miles 1977; Campbell and Barwick 1987). The ceratohyals and hypohyals were unusually strong and carried attachment surfaces for muscle and ligament attachment. They were able to move the basihyal/basibranchial plates, so that the surface denticles on the plates they bore would move against the palatal denticles and break down food particles. Such a mode of food reduction would be expected to have other

modifications. These will be considered in the next section.

In *Griphognathus* we have found several gill arches which have small patches of bone with denticles like those on the palate (Figure 5D). The etches also show occasional small conical bodies covered with denticles. These are interpreted as having fallen off the gill arches; they have the appearance of gill rakers such as are found in extant fishes. These structures no doubt prevented larger food particles that had passed through the buccal cavity, from passing down into the gills.

Holodipterus (Figure 15) has a similar kind of denticles on the palate and on the inner surface of

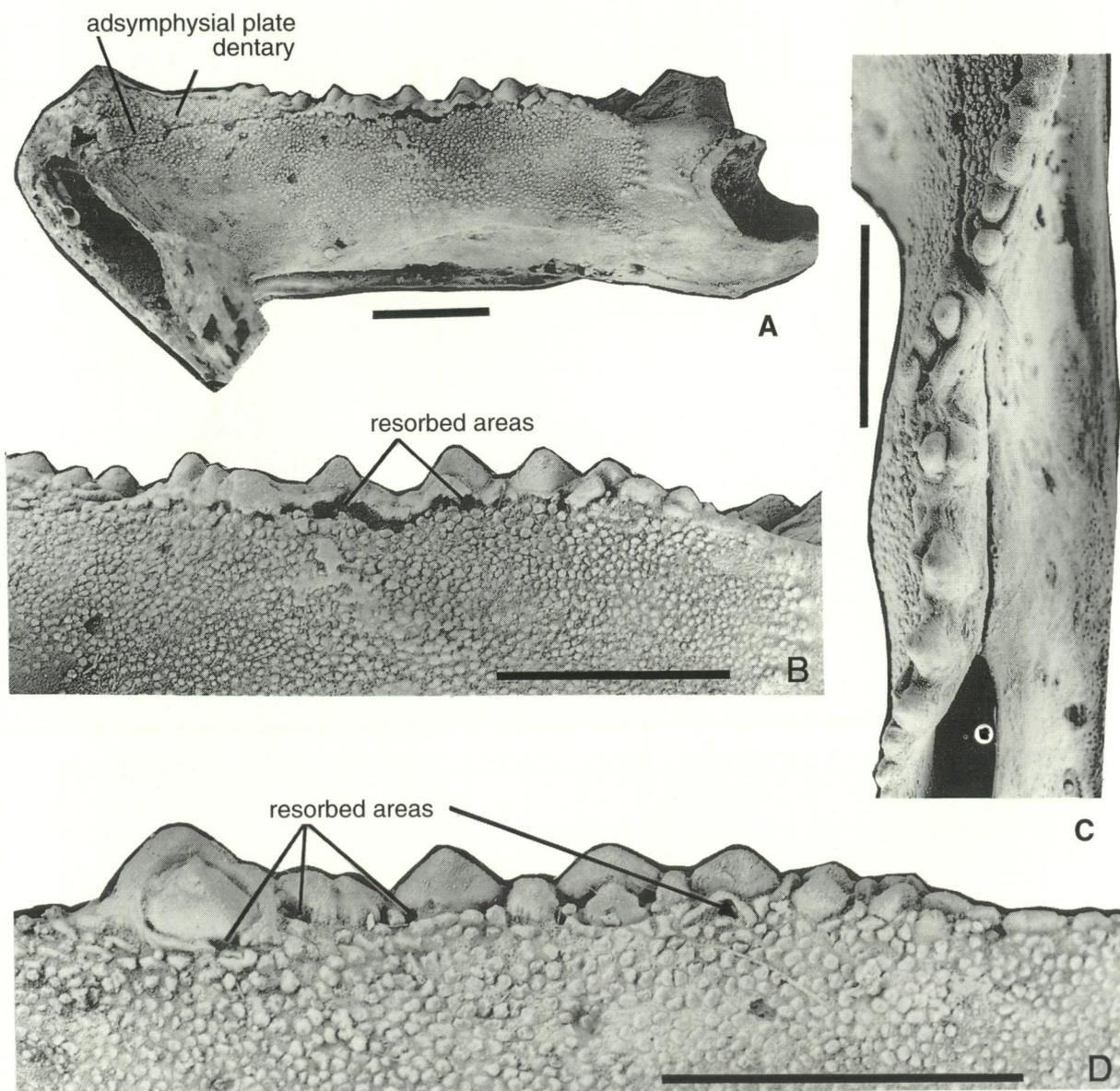


Figure 16 Dental plates of *Holodipterus longi* Campbell and Barwick, WAM 86.9.684. A. Internal view of half a mandible. B. Enlargement of same to show the partial resorption of the marginal denticles, and the small patch of primitive dentine joining some of the denticles. C. Dorsal view of the mandible to show the adductor opening, the teeth along the prearticular, the dentary with a row of teeth along its edge, and the infradentary bones along the right side. D. Medial view of the left side of the palate showing the interrelationships of the marginal teeth and the resorption patterns. Note that the teeth decrease in size posteriorly and become irregular. Scale bars = 10 mm.

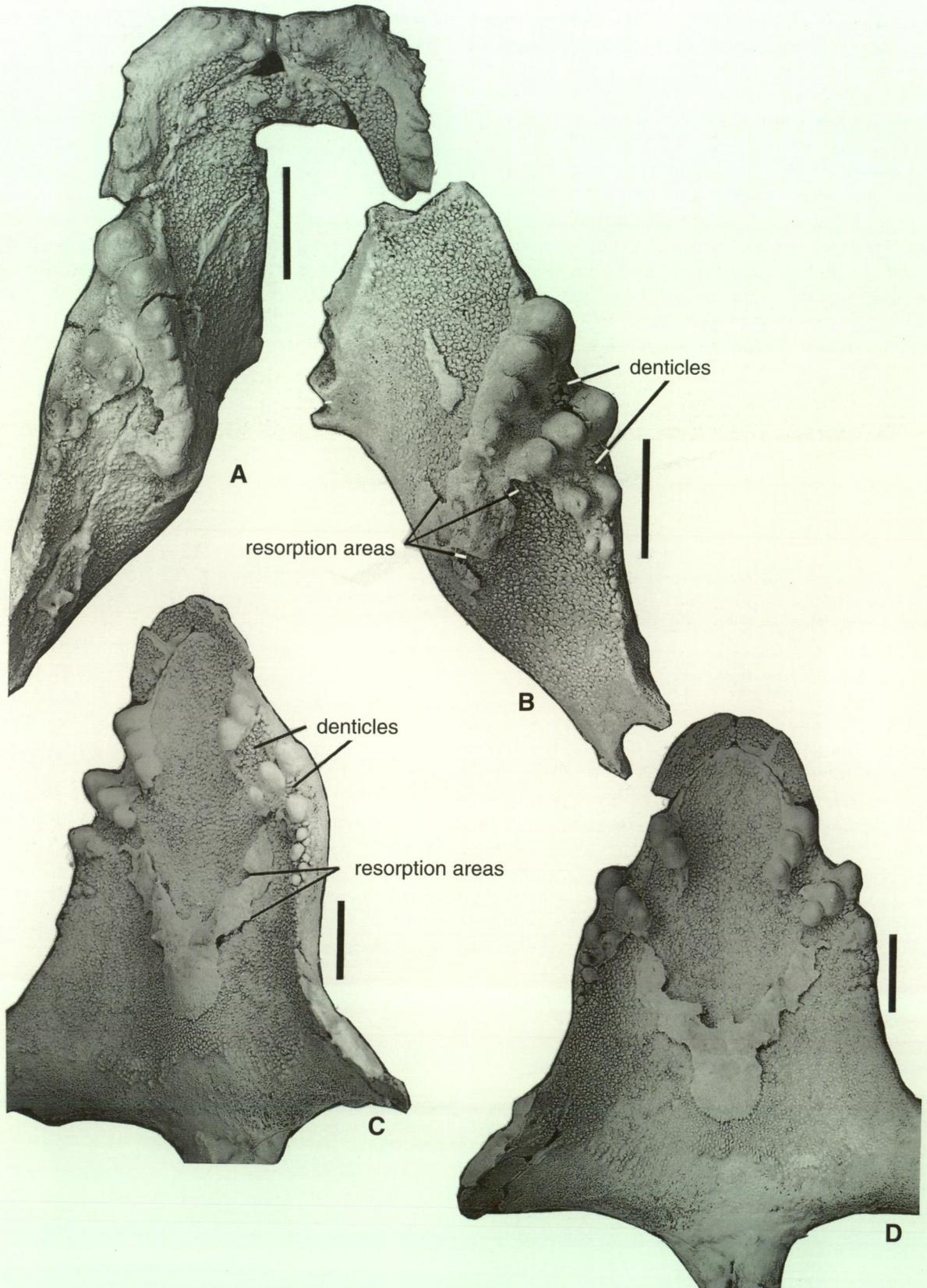


Figure 17 Views of the buccal surfaces of the mandible and head of *Holodipterus (Asthenorhynchus) meemannae* Pridmore *et al.* ANU 49103. A. Mandible with large gaps for the ventral edge of the external naris and irregular row of teeth on the dentary, and the partial resorption of the teeth. B. Right mandible of same specimen. In A and B small patches of sediment remain on the surface. C–D. Oblique and ventral views of the palate showing the arrangement of denticles and teeth, the more advanced resorption of the main teeth in comparison with the mandible of the same specimen, and the unresorbed dentine which will make the callus. On the posterior edge of the callus, it is possible to identify the overgrown denticles. Scale bars = 10 mm.

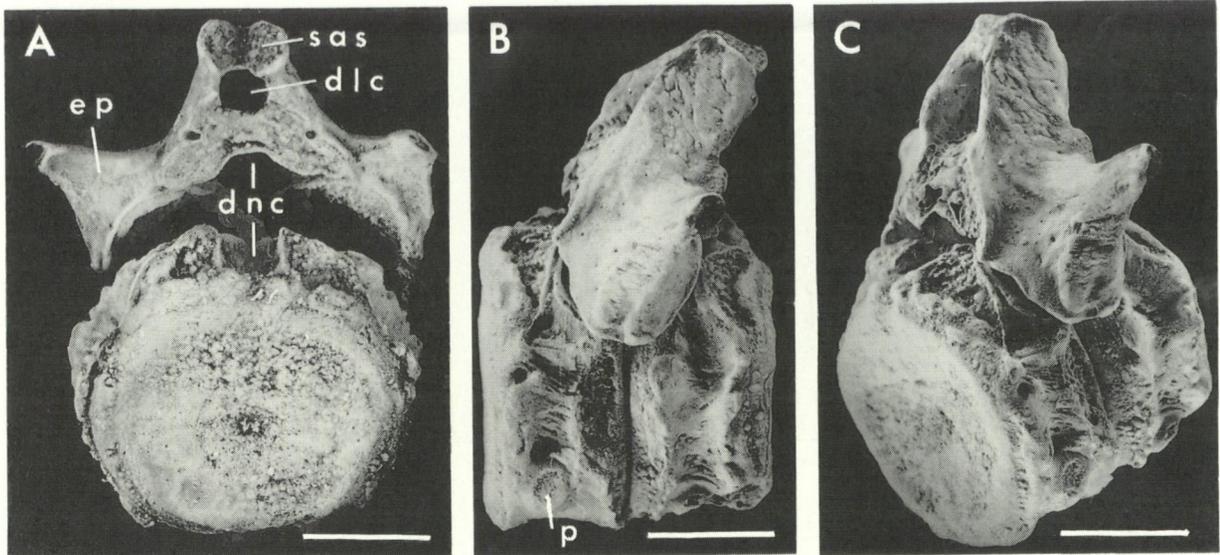


Figure 18 *Griphognathus whitei* Miles. Three views of the second and third vertebral centra with a neural arch, ANU 35645. A. Posterior view. B. Lateral view. C. Oblique view. See Figure 20 for notation. Scale bars = 5 mm.

the mandible (Campbell and Smith 1987; Pridmore *et al.* 1994). The margins of the plates have enamel covered teeth, some of which are arranged in radial fashion like those of a tooth-plated genus. However, we note that within the Gogo fauna there are several different types of tooth arrangement in holodipterids. The simplest is in *H. longi*. It has a row of teeth along the margins of the pterygoids behind the articulation of the dermopalatines (Figure 16). These are not just isolated irregular excrescences as in *Griphognathus*, but are regularly arranged, circular in section, and are bounded by ridges of dentine in others. The median edge of the teeth shows evidence of resorption, some relicts of more medial teeth being preserved. The median posterior part of the pterygoids is covered with continuous dentine layers, but this probably contained a slight thickening. The mandible has a similar row of teeth along the margins, and strong evidence of resorption along the medial edges of the teeth (Figure 16). The edge of the dentary has a row of denticles which extend to the mid-line. Unlike *Griphognathus* the mandible has a sharply inturned denticulated edge on the dentary, a well-defined adsymphysial plate, parts of the surface where the denticles are covered with a thin layer of primitive dentine, and a distinct cavity is present for the adductor muscles (Figure 15D).

Holodipterus (Asthenorhynchus) meemannae is more complicated in its dental pattern (Figure 17). Its palate has several rows of radially arranged teeth, none of which reaches the mid-line. Medially the rows all show resorption of the teeth, and these resorption areas are all occupied by denticles. In addition to the resorption and replacement by

denticles, the palate shows areas where primitive dentine formed a surface over the denticles, and towards the median line this type of dentine formed a hard callus. Running laterally from this callus, irregular patches of dentine look as though they may have formed part of a tooth plate, but this is not correct. They are an independent layer overlying replacement denticles. A similar arrangement occurs in some specimens of *Griphognathus* species. No tooth plate comparable with that of the extant tooth plate-bearing genera is present. No junction between the pterygoids is present; the callus, which formed because it represented areas of unresorbed primitive dentine which were overgrown in successive phases of growth, demonstrates that median growth of the pterygoids did not take place, at least during the latter phases of growth of the animal. The pterygoids grew by addition to the lateral, anterior and posterior margins, not to the mid-line.

The mandible is partly known. Each half plate has a lingual tooth row extending back to a solid callus. The tooth row is partly resorbed medially. Two other tooth rows are present, but they are not continuous with the callus; they have their early stages resorbed and replaced by denticles. Between the tooth rows of the two sides of the mandible is a deep lingual furrow covered with denticles and in part with a thin layer of primitive dentine. The mandible has a row of denticles along its crest. The mandible fits against the palate, and although the tooth rows interdigitate, the inner row of the palate falls well inside the medial mandibular row. The crests of the teeth are relatively unworn, and there is no evidence that the opposing teeth acted as occluding grinding surfaces. On the contrary, on

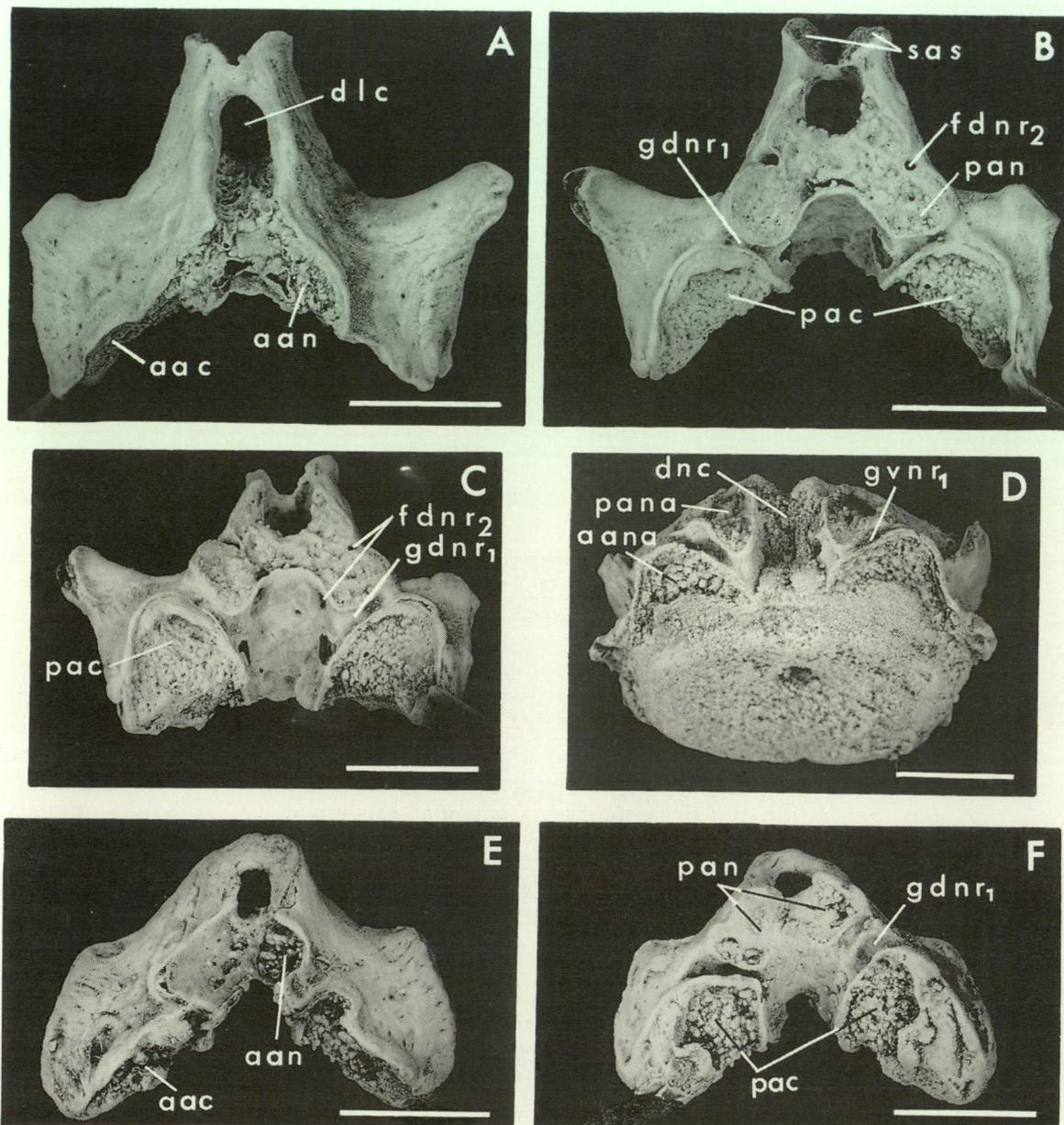


Figure 19 *Griphognathus whitei* Miles. A–C. Anterior, posterior and posteroventral views of the detached neural arch, showing details of nerve canals. Same specimen as in Figure 18. D. Anterodorsal surface of a centrum showing the surface to which C was attached. E–F. Anterior and posterior views of the first neural arch. See Figure 20 for notation. Scale bars = 5 mm.

occlusion, the teeth fit against denticles which lie between the tooth rows, quite unlike any other dipnoan dentition with which we are familiar (Figure 17B–C).

The palate of *H. gogoensis* has the most complex dentition of all the holodipterid species. It has teeth which are well formed marginally but are worn down medially, large parts of the palate covered with primitive dentine, extensive resorption of the surface with replacement by denticles, large coverage of denticles with primitive dentine, and median calluses left when resorptive phases did not remove all the previously deposited primitive dentine (Figure

15A–B). In addition, as the specimen becomes older, the primitive dentine is intergrown by columns of hypermineralized dentine which made a surface that was progressively more difficult to remove by resorption, and strengthened the calluses. The mandible is much the same as in *H. (Asthenorhynchus) meemannae* described above. As is always the case with holodipterids, the opening for the adductor musculature is well developed.

Scale Patterns and Body Form

The scales in *Chirodipterus australis* and *Griphognathus whitei* (Figure 6) have been dealt with

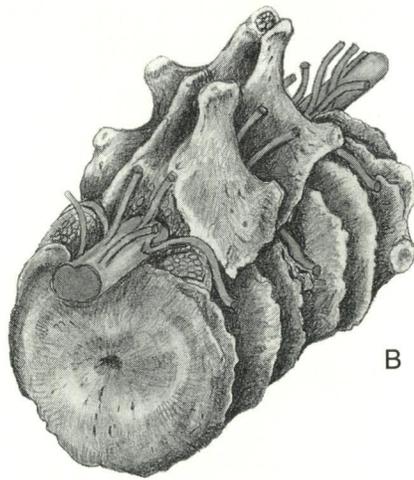
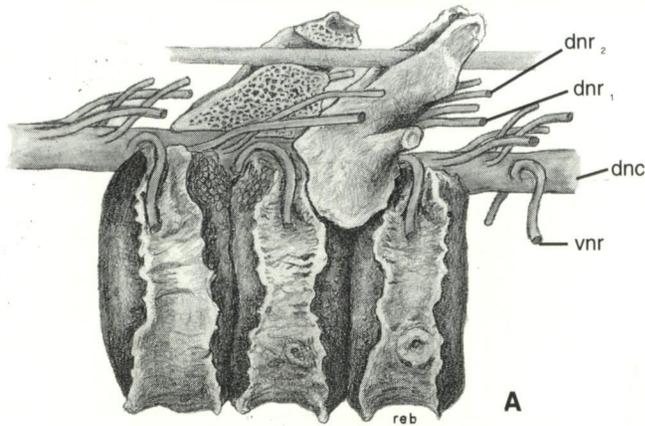


Figure 20 Reconstruction of the vertebral column of *Griphognathus whitei* Miles as shown in Figures 18–19. A. Lateral view with half the first neural arch removed. B. Anterodorsolateral view of same with full neural arches. C. Posterodorsolateral view of two centra with the second neural arch. aac and pac = anterior and posterior arches for the articulation with the centra; aana and pana = anterior and posterior articular surfaces for the neural arches; aan = anterior articulation with the next neural arch; dlc = dorsal ligament canal; dnc = dorsal nerve cord; ep = epineural process; fdnr₁, fdnr₂, gdnr₁, gdnr₂ = foramina and grooves for the first and second dorsal nerve roots; gvnr₁ = groove for the ventral nerve root; p = parapophysis for the attachment of the rib; pan = articulation for the next posterior neural arch; sas = supraneural articular surface; vnr = ventral nerve root. Scale bar = 10 mm.

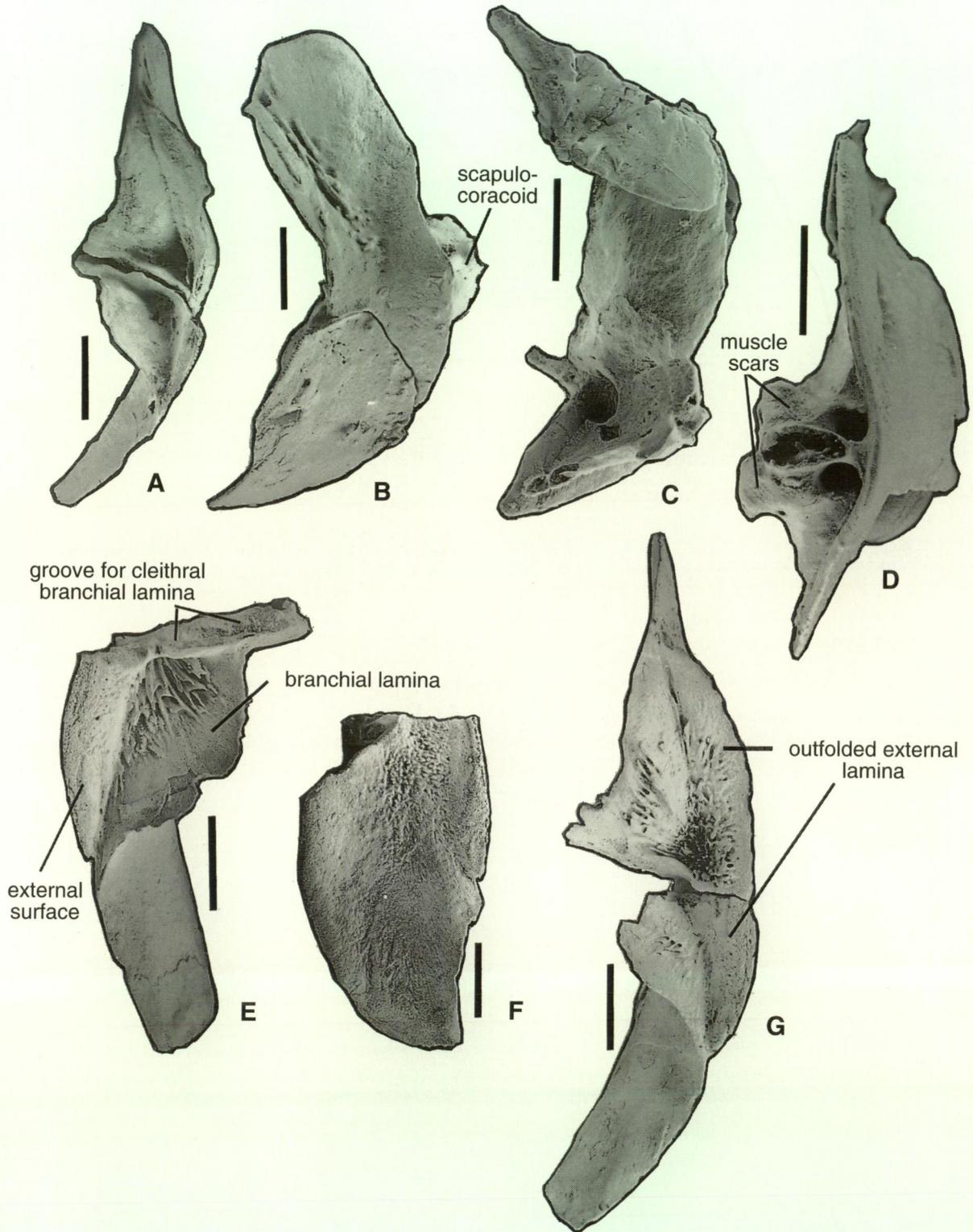


Figure 21 Pectoral girdles of *Chirodipterus australis* Miles. A–B. Anterior and lateral views of the left girdle of ANU 49200. Note the strong branchial laminae in A, and the deep external furrows in B. C–D. Cleithrum, anocleithrum and scapulocoracoid of the right girdle of CPC 26576. C. Internal view. Note the large ventral attachment of the scapulocoracoid, part of which is broken away. D. Anterior view showing the attachment of the fin. Note the shape of the attachment surface and the two foramina in the scapulocoracoid, the supraglenoid (dorsal) foramen and the supracoracoid (ventral) foramen. Muscle scars are visible on the dorsal and ventral sides of the fin attachment. E–F. Isolated right clavicle ANU 35636. E. Anterior view showing the rough tissue against the branchial lamina. F. External view, concave on the surface and showing the line where the external and branchial surfaces meet. G. Left cleithrum and clavicle, but with the branchial lamina on the clavicle partly broken away, ANU 35636. Scale bars = 10 mm.

by Pridmore and Barwick (1993). Holodipterids are less well preserved (Pridmore *et al.* 1994). All the scales have a thick bone layer with layers of dentine and complete or incomplete enamel over the exposed external surface. This makes the scales of all species strong and resistant to wear.

The body form of *C. australis* is approximately ovoid in cross section and it has no ossified centra in its vertebral column. The scales are thick, and are in contact with many surrounding scales (Figure 6). The exposed part of the scale, which occupies about one fifth of the surface area of each scale, consists of a cosmine layer. The overlapped surface consists of highly porous bone. The pores open into canals which radiate out from the centre of the scales. The functional significance of these canals and pores is not known. According to Pridmore and Barwick (1993), the mid-length scales are in touch with 11–13 more cranial scales and a similar number of caudal scales. Clearly the body was not highly flexible, and this affected the style of swimming of which the animal was capable. Pridmore and Barwick considered that *C. australis* moved with an anguilliform to sub-carangiform style. This also confirms what we have decided from an examination of other characters. The pelvic fins are situated farther forward relative to the anal fin than in *G. whitei*.

The scales of *G. whitei* are relatively larger than those of *C. australis*, and they have smaller amounts of overlap with adjacent scales. Pridmore and Barwick (1993) considered that the median flank scales have overlap with six cranial and six caudal scales. Overlap patterns are shown in Figure 6. The exposed part, which makes up about one quarter of the surface of each scale, usually lacks cosmine. Some scales have discontinuous rows of enamel-covered dentine separated by furrows which also contain uncovered dentine. The unexposed part of the scale contains pores which connect to canals, as in *C. australis*.

Some blocks of scales of *Holodipterus gogoensis* have been preserved (Figure 6C) and these indicate that the overlapped parts of the scales are proportionately much shorter than in either *Chirodipterus* or *Griphognathus*. The overlapped parts of the scales are thin, but still quite inflexible. The scales indicate that the body was more flexible than in the other genera.

Axial Structures

Griphognathus whitei has well-ossified vertebrae which extend from the head to the caudal region. In addition, it has strong neural elements, and posteriorly placed medial fins. The propulsive elements were grouped posteriorly. Only the first few axial units of *G. whitei* have been described (Campbell and Barwick 1988b), but these are the best known axial structures from any Palaeozoic

dipnoan (Figures 18–20). The axial discs are of solid bone. Neural arches are faceted against axial rings anterior and posterior to themselves. The arches are strongly ossified and outline the neural cord. Dorsally, the nerve cord had two branches ($gdnr_1$ and $fdnr_2$, Figures 18–20) on each side, but there was a single ventral nerve root. This passed laterally through a small groove between adjacent arches. Each neural arch has an epineural process on each side, which is pointed laterally. The first neural arch has no sign of an articulation for proximal supraneurals, but the subsequent ones have a pair of articulatory surfaces. These have the appearance of being large facets for a strong element. Low down on the centra is a rounded scar for the attachment of the rib. The ribs around the body cavity are well ossified and bent, indicating a considerable width to the body.

Pridmore and Barwick (1993, figures 7–8) figured two specimens of *G. whitei* which show details of the axial skeleton on the posterior part of the body. More material is now available, and we will be describing it elsewhere.

Pectoral Girdles

The pectoral girdle is well known in *Griphognathus whitei*, *Chirodipterus australis*, *Pilliararhynchus longi*, and less well known in *Holodipterus* spp. All species have a pattern of development which leaves little doubt that they have a similar origin.

The girdles of *Chirodipterus* and *Pilliararhynchus* are very similar, but *Griphognathus* has some distinctive structures. We deal with *Chirodipterus* and *Pilliararhynchus* first. Each has an external surface which is deeply concave (Figure 21). This is because the anterior edge of both the clavicle and the cleithrum are bent outwards to form an edge to which the opercular series was opposed. The deep groove in the surface of the cleithrum has longitudinal ridges which mark the attachment surface for body wall musculature of the trunk. The cleithrum joins the clavicle along an outer edge which is concave to the cleithrum. Internally, the cleithrum has a broad overlap with the clavicle along its posterior part, and they both have a high internal projection, the branchial lamina (Figure 21A,E,G), standing at a high angle to the external surface. These laminae extend inwards to a point where they suddenly terminate in a distinct spine. Together they form a concave posterior barrier to the gill chamber. The scapulocoracoid structure is made of a thin layer of bone over an unossified core (Figure 21C–D). It has a wide basis of attachment which dorsally extends up on the inside of the cleithrum and along the ventral edge of the branchial lamina, and ventrally it extends down onto the lamina against the cleithrum. Anteromedially it has a large subscapular fossa

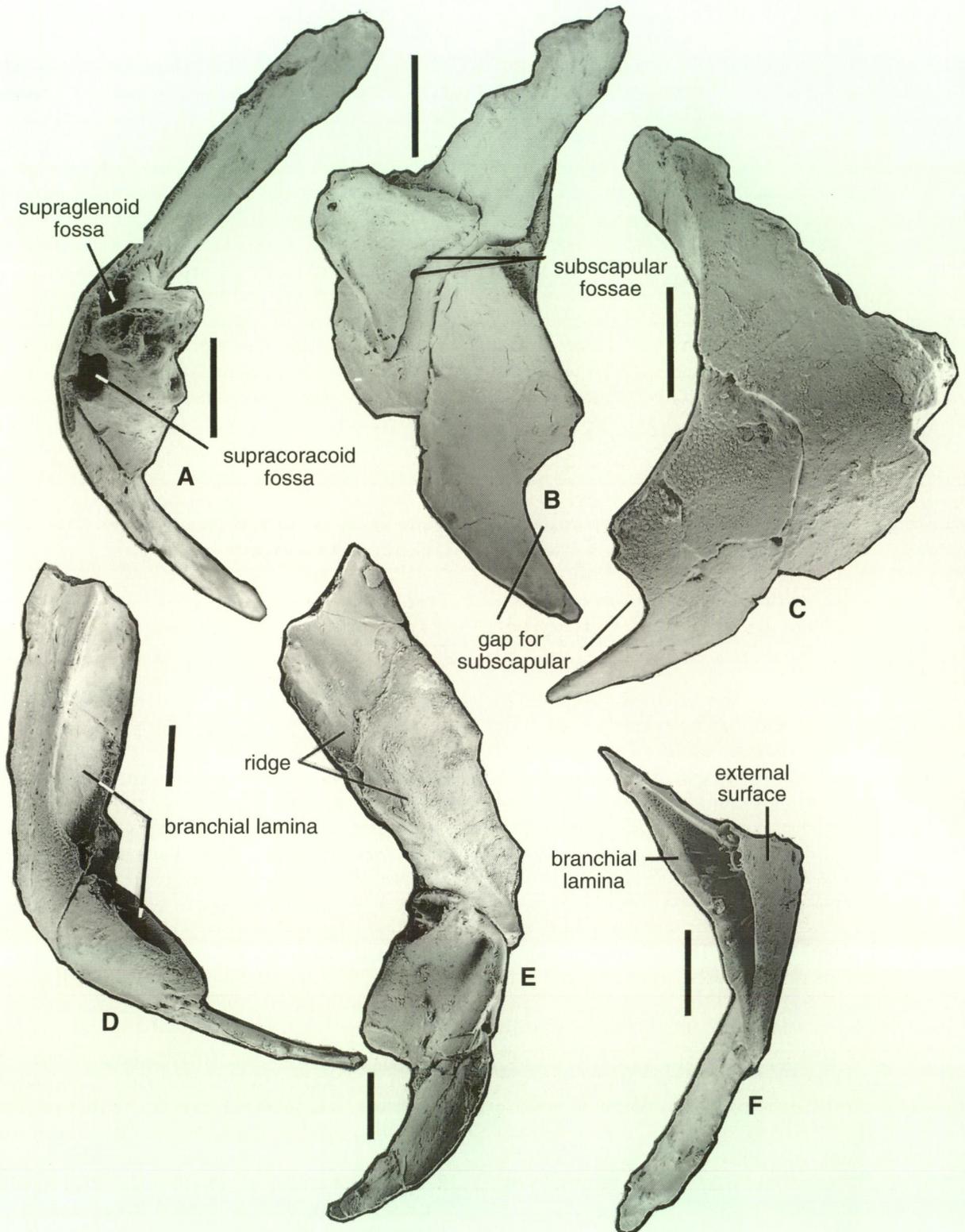


Figure 22 Pectoral girdles of *Griphognathus whitei* Miles. A–C. Three views of ANU 26135. A. Anterior view to show the fin attachment and the supraglenoid (dorsal) and supracoracoid (ventral) foramina into the scapulocoracoid. B. Internal view. Note the two small openings in the subscapular fossa in the scapulocoracoid and the neatness of the attachment to the cleithrum. C. External view. Note the gap for the subopercular. Compare with Figure 21F. D–E. Anterior and internal view of a large specimen, ANU 49117. F. Anterior view of the left clavicle of the same specimen. The ventral end of the cleithrum has been lost. Note the angle of the branchial lamina and the long straight projection for the lamina of the cleithrum. Compare with Figure 21E. Scale bars = 10 mm.

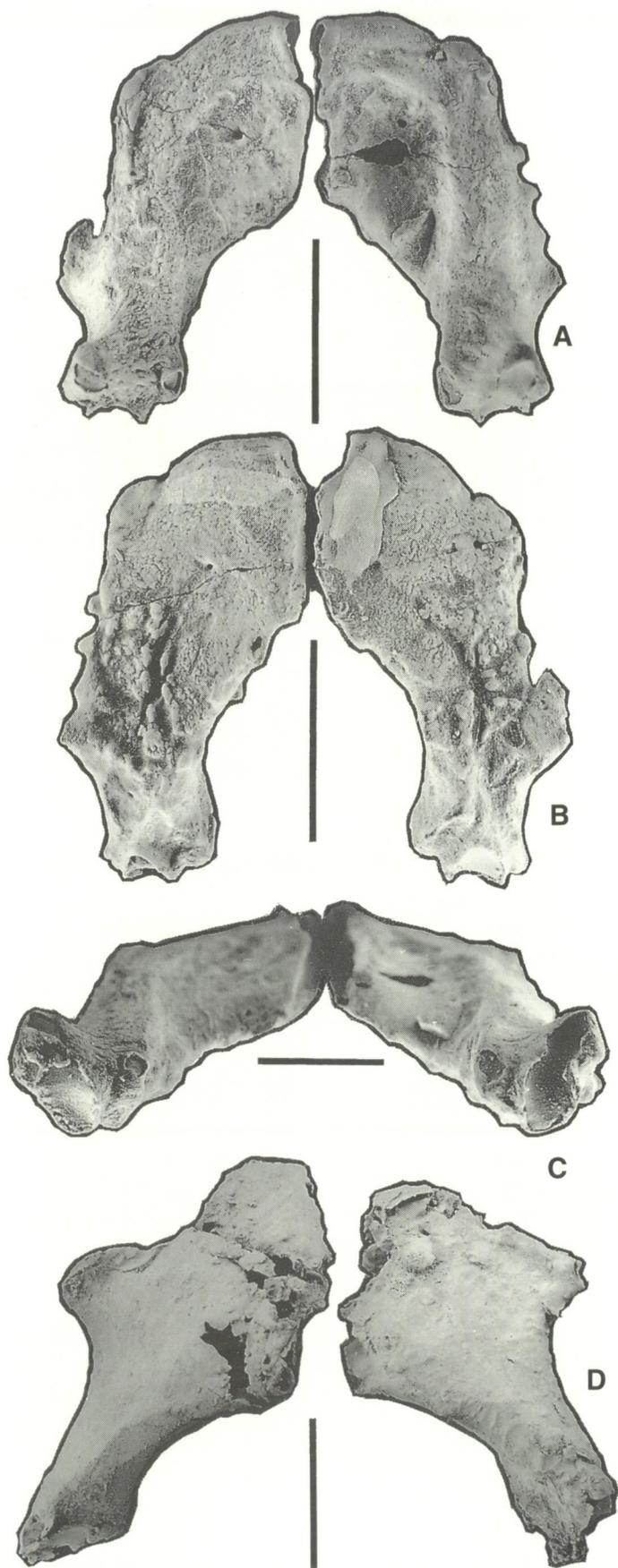


Figure 23 Pelvic girdles. A-C. Dorsal, ventral and posteroventral views of *Chirodipterus australis* Miles, ANU 21639. D. Ventral view of *Griphognathus whitei* Miles, WAM 86.9.645. Scale bars = 10 mm.

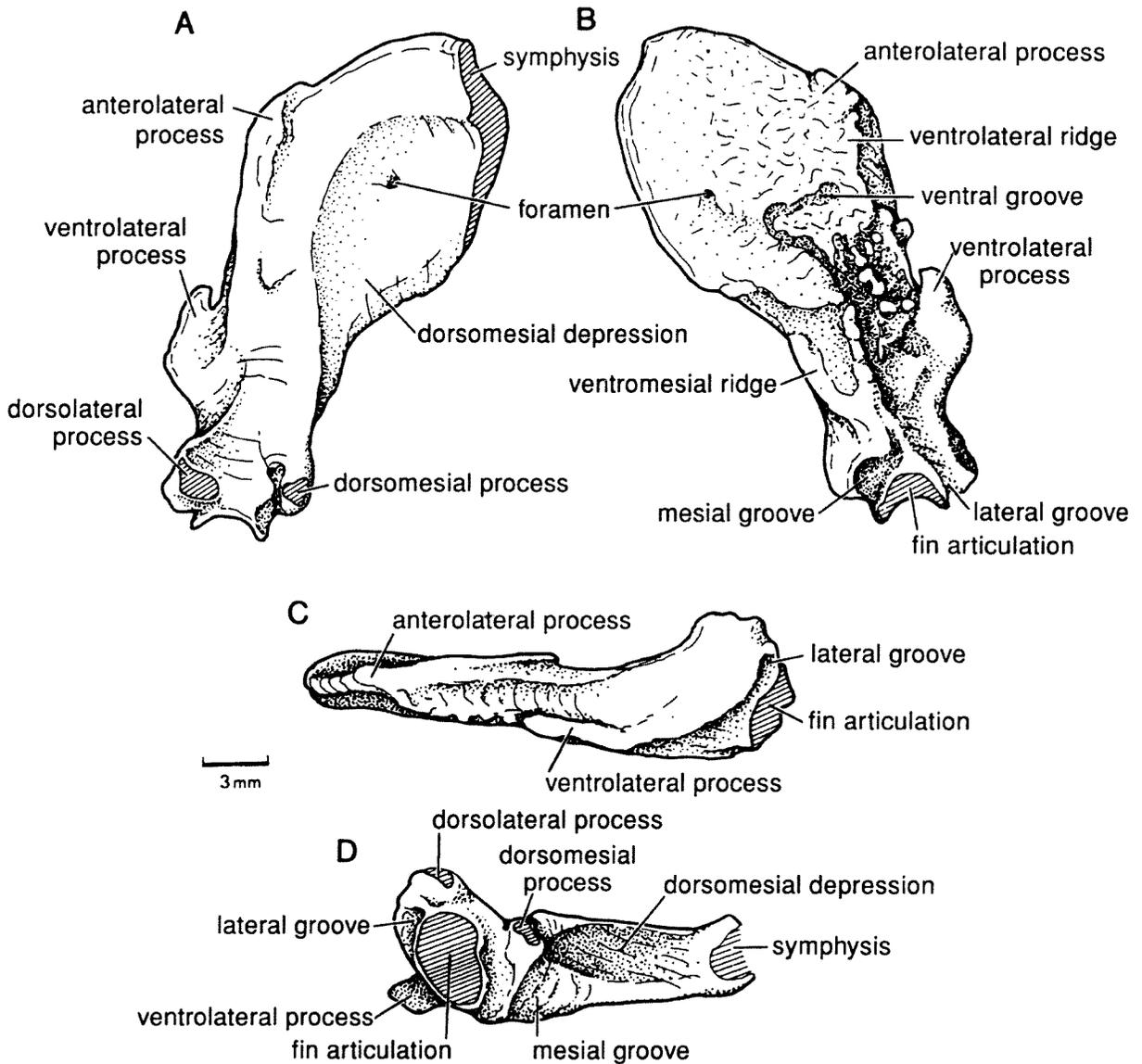


Figure 24 Reconstruction of the pelvic girdle of *Chirodipterus australis* Miles. The structures are named as in Young *et al.* (1989).

which opens into a chamber, which in its turn opens externally to the fin via two large foramina which sit against the cleithrum. The articulation for the fin is ogival in outline, and it is bound by dorsal and ventral processes for muscle attachment. The pectoral girdle is arched so that the maximum width is well up on the side of the animal, the fin therefore being higher than in *G. whitei*.

The pectoral girdle of *G. whitei* has a relatively smooth external surface. The cleithrum on large specimens has a slight but distinct furrow behind the anterior edge to which the opercular was opposed (Figure 22C). This minor external furrow contains weak irregularities to which longitudinal muscles were attached. The clavicle has a deep embayment in its anterior edge to receive the edge of the subopercular; this is a much more pronounced structure than its equivalent in *C.*

australis. In anterior view, the clavicle is inturned strongly, indicating that the body shape was rather flat-sided, and the ventral surface was flattened to match the shape of the head. The branchial laminae are arranged more obliquely to the external surface than are those of *C. australis*, leaving only a small gap for the branchial space (Figure 22F). As with *C. australis*, this space is filled with rough sharp struts. The cleithrum has a strong rounded ridge running along the anterior edge of the branchial lamina. It gradually disappears dorsally. The scapulocoracoid sits against the ventral edge of this ridge making a neat join. The internal surface of the scapulocoracoid is deeply concave; at its base against the cleithrum, there are two small foramina (the subscapular fossae) unlike the single large one in *C. australis*. These foramina open into a small chamber which then opens into a pair of chambers

which run to two openings on the posterior surface. The interior of the scapulocoracoid is supported by a long septum which runs most of the length of the bone, being much more elongate than in *C. australis*. The pectoral fins, judged from the position of the scapulocoracoids, were more ventrally placed than in *C. australis*, allowing the fins to contact the sea floor to propel the animal, as well as allowing them to be used as swimming structures.

Some information is available for *Holodipterus*. The pectoral girdle has a poorly ossified scapulocoracoid, and the shape of the cleithrum and clavicle show that the pectoral fin must have been placed well up on the side of the animal.

All of these girdles are similar in many respects and different from that of the Late Devonian *Andreyevichthys epistomus* Krupina, from the Tula region of Russia (Krupina 1997). In that species the whole girdle was buried; the cleithrum was reduced; the anocleithrum was high, buried beneath the skin, and connected to a supracleithrum; and the clavicle was turned sharply ventrally beneath the animal. The whole of this structure gives the impression of flexibility, and the inturning of the clavicle suggests that it was capable of vertical movement into the base of the pouch that held air in modern dipnoans. The pectoral girdle of *Andreyevichthys* seems to us to represent the best example of such a structure in an

early air-breathing dipnoan. All the Gogo species have the standard features of gill-breathing species.

Pelvic Girdle

We have pelvic girdles of both *Chirodipterus australis* and *Griphognathus whitei* (Figures 23–24). These are not ossified in other Devonian dipnoans. Young *et al.* (1989) described these elements in which the body of the pelvis consists of a large mass of tissue, internally poorly ossified, but with a more or less continuous perichondrium over it. The pelvis of *C. australis* is better preserved than that of *G. whitei*, and it alone is described herein. In *C. australis* the two halves of the pelvis met in the mid-line where they are joined by a cartilage-filled symphysis. So far as is known, there is no anterior process as occurs in *Neoceratodus*, although if it were present it would have been formed of cartilage. The articulation for the fin is large and posteriorly directed. The large surface available indicates the presence of muscles which can be interpreted in terms of the muscles in *Neoceratodus*. In particular, we recognize the anterolateral, ventrolateral and dorsolateral processes along the lateral side of the pelvis in all genera. In *Neoceratodus* these serve for the attachment of the superficial ventromesial abductor, the dorsolateral abductor levator, the deep ventral abductor depressor, and the

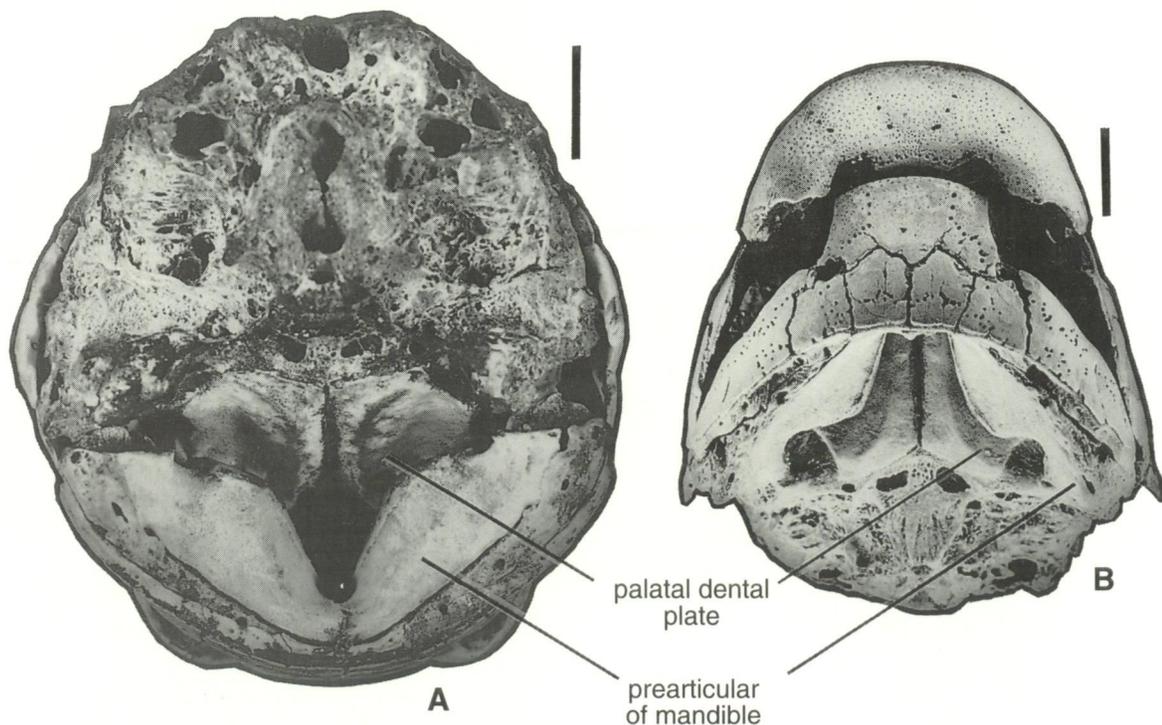


Figure 25 Posterior and ventral views of *Chirodipterus australis* Miles, ANU 21634. A. Shows particularly well the gap between the dental plates of the palate and the mandible. B. Shows the same gap in ventral view. Scale bars = 10 mm

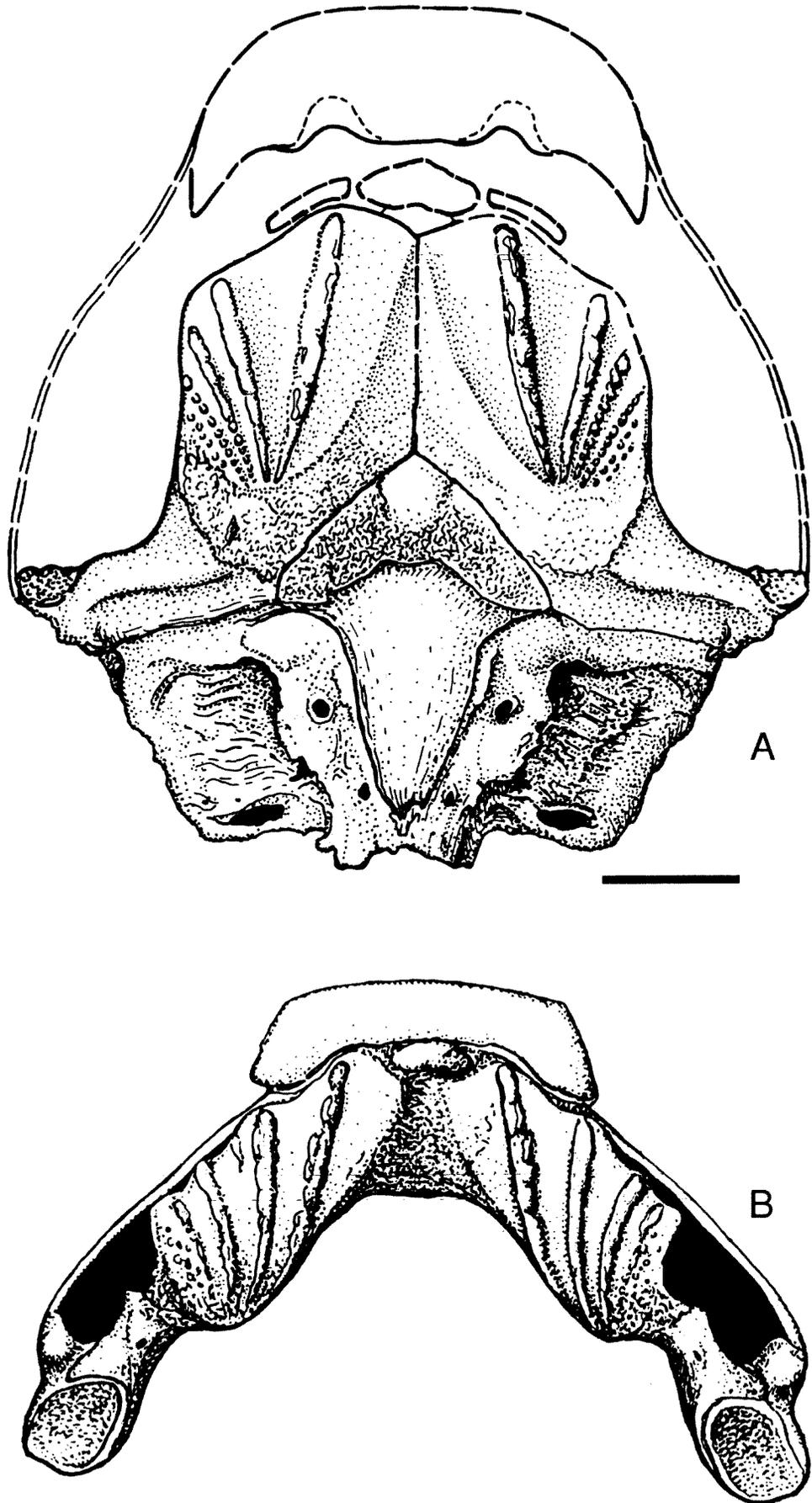


Figure 26 Reconstruction of the ventral view of the palate and the mandible of *Gogodipterus paddyensis* (Miles), refigured and partly modified from Long (1992b). Scale bar = 10 mm.

dorsomedial adductor levator muscles, respectively. The large muscle insertion area on the ventrolateral side indicates that the deep ventral depressor muscle in *C. australis* was larger than in *Neoceratodus*. The large dorsomesial depression shows that the superficial ventromesial adductor was much larger than that of *Neoceratodus*. Naturally we cannot identify all the muscle insertions known from *Neoceratodus*, but sufficient information is available to indicate the conservatism of the system from the Devonian to the Recent. It is possible that the fins were appropriately placed for 'walking' on the bottom as well as swimming (Pridmore 1995).

Feeding Types

The palatal and mandibular plates of *Chirodipterus australis* occlude around the margins (Figures 8, 25). There are no teeth, but the tubercles are short and never sharp; they extend only a short distance in from the plate margins. Medially each of the plates has a relatively smooth surface, and these do not meet the opposing plates on occlusion. In other words, the plates are adapted to biting roughly through prey using the marginal tubercles and passing the remaining hard tissues back in the mouth for further reduction. Another feature is that the snout is high and has a large anterior surface through which open the pores for the electrosensory system (Figures 3A, 4). Few of the pores open ventrally. There is no evidence that the animal searched the surface of the sediment for food. This suggests that the food supply was not soft tissue but rather shelled species which had to be broken open and then processed. The floor of the Gogo ocean contained many invertebrates which would meet these requirements. The basihyal/basibranchial plate has surfaces for the attachment of the hypohyal and the first two ceratobranchials, but these are miniscule in relation to the size of the whole head (Figure 13A,I-J). We note also that the basihyal/basibranchial plate in *C. australis* is very small in comparison to those of *Griphognathus* and *Holodipterus*. The buccal surface would not have served for the attachment of denticulated plates as in *Griphognathus*.

Gogodipterus paddyensis has much longer rows of tubercles (Figure 26) which reach back almost to the proximal parts of the plate (Long 1992b). The posterior parts of the plates have no smooth surface as in *C. australis*. Behind the plates the surface of the buccal cavity is formed of bone rather than dentine. Most tubercles retain some form, though they are worn down to some extent. The whole head is wide in comparison with its length. The lingual furrow is wide in comparison with that of *C. australis* (Figure 25). This species has none of the characters required

for the break down of hard prey. Instead it has the features for eating soft materials such as algae and soft-bodied invertebrates.

The newly described genus *Adololopas* has typical dipnoan teeth. Although the palatal plates are concave and the mandibular plates are convex, the occlusion involves only the marginal teeth. This animal has the features of a feeder which did not live on bottom-dwelling animals, was actively mobile, and ate soft organic matter afloat in the water.

Griphognathus whitei has the overall head shape of a bottom feeder. The electrosensory features in the snout and the mandible are largely ventrally directed as one would expect (Campbell and Barwick 1987). The dentition has no capacity to grind down hard prey, and we conclude that the animal lived on soft tissue in and on the sediment. The food was finally reduced by the movement of the tooth plates on the basihyal/basibranchial plates against the pterygoid. This kind of action apparently required large cheek pouches, the position of which is obvious in any lateral view of the head (Figure 2). These had the ability to collect some broken material which had been through the buccal mill and had passed laterally; then it was returned to the mouth cavity for further processing. The ceratobranchials sometimes have small denticulated plates attached to their surfaces (Figure 5). Their extent is not known, but the etches often show numbers of such small plates suggesting that they were widespread. Some of these are flat, but others are small conical bodies covered with denticles rather similar to modern gill rakers. They served a protective function, preventing finely ground particles from passing into the gill chamber.

Holodipterus provides new data previously undiscussed. Its head is large and high, and the snout is not depressed. The scales are large and more mobile on one another than are those of the other genera. The dentition of the *H. gogoensis* type is adapted to grasping food by rows of teeth mainly at the margins; the adductor muscles were strong to allow this to happen. Some of the crushed material was further reduced by small plates on the basihyal/basibranchial plates. These have been found on *H. (Holodipteroides)* (Pridmore *et al.* 1994). In the whole *Holodipterus* group, the callus on the palate, together with the short nature of the basihyal/basibranchial plates, shows that this secondary reduction was much less effective than in *Griphognathus*. Note, however, that *H. longi* has fewer marginal teeth, a much larger area of denticulation, and a smaller callus on the palate. In the absence of further information, we consider that its mode of feeding was much the same as *Griphognathus*. *Holodipterus* therefore shows a variety of feeding types within the one environment.

Dipnoans include animals which fed on the detritus on the floor of the sea, others that fed on isolated benthic shelled animals, some that fed on soft tissue such as algae and soft invertebrates, and occasional ones that fed on mobile animals, shelled or soft bodied, that swam at various levels in the sea. We consider that dipnoans evolved in the sea, and that all these types of adaptations must have taken place in the sea. In the Gogo Formation, all of the examples of diversification described above are represented in a very narrow environmental zone, and this may indicate that their evolution did not require a major range of environments to produce the changes described.

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ABBREVIATIONS

The institutional abbreviations used with specimen numbers are as follows:

ANU = Geology Department, The Australian National University, Canberra.

BMP = Natural History Museum, London, U.K.

CPC = Commonwealth Palaeontological Collection, Australian Geological Survey Organisation, Canberra.

WAM = Western Australian Museum, Perth.

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ADDENDUM

Since this paper went to press we have received an article by Schultz and Chorn (1997) on *Sagenodus*. In this work a section on air breathing in early lungfish takes a critical view of the hypothesis we have discussed above. It is worth while commenting on this paper because it shows the problems faced in discussion of fossil evidence for functional interpretation.

1. It is said that we have based our views on *Griphognathus*, but that is not correct. In fact our views are focused on the dentine plate bearing genera which are mentioned and described elsewhere in the same paper, but these are not touched upon by Schultz and Chorn. *Griphognathus* is mentioned earlier in the paper as an example of the way in which bottom dwelling fishes are preserved at Gogo, and the structure of the gill supports.
2. It is said that our views are based on the long stalk of the parasphenoid, the shape of the ceratohyal, and the presence of the cranial rib. In fact we considered several other structures which relate to air breathing. On p. 222 we outline seven features (Campbell and Barwick 1988) which support the orobranchial buccal pump mechanism as displayed in *Gnathorhiza*.

These include reduced ossification and mobility of the skull bones, reduced size and increased mobility of the cheek, dental plates on the palate separated and moved forward, cleithrum with a reduced branchial lamina and a small articulation with the clavicle, and gulars and submandibulars either unossified and allowing flexibility to the floor of the buccal cavity. All of these are significant when related to Early and Middle Devonian genera.

3. It is said the we claim that all air breathing is associated with freshwater environments. This is not the case, as we were well aware that *Sagenodus* does occur in marine or marginal marine environments in the USA, as one of us had examined Schultz's material. We have no objection to the view that air breathing may have been initiated in shallow marine or marginal marine environments. We do not maintain that just because the marine water is shallow, the organisms living in it must have been air breathing. Much of the discussion in the paper by Schultz and Chorn on the environments in which early lungfish were deposited, has no relevance to the main discussion of air breathing.

4. "It is a tenuous approach at best to connect a supposed function with a proposed paleoenvironment." This statement cannot refer to our paper. We based our discussion on the morphology of the fossils, and attempted to show how the structure is related to function of the animals. We then noted that the morphological changes that indicated a move to air breathing occurred at a time when most lungfish fossils occurred in freshwater rather than marine deposits. We did not infer that any organism was air breathing just because it occurred in a fresh water deposit.
5. As we have indicated above, the statement lungs "are present in primitive actinopterygians, actinistians, lungfish and tetrapods", tells us nothing about the distribution of lungs in primitive fishes. Graham (1997: 10 *et al.*) has pointed out that "air-breathing has been independently and frequently acquired in a variety of actinopterygians during the 400 million year evolutionary history of that group." The fact

that *Polypterus* has lungs has no bearing on the present problem, as was pointed out by us in the original paper (1988: 225).

6. No morphological evidence has been produced by any author to support the view that Early and Middle Devonian lungfishes had the capacity to breathe air. No amount of argument about environments or about the supposed relationships of lungfishes with other organisms, can ever affect the outcome of the discussion of air breathing.
7. We continue to maintain that *Sagenodus* is one of the best examples of an early air breathing lungfish, and argue that the description of Schultze and Chorn supports this view.

Schultze, H.-P. and Chorn, J. (1997). The Permo-Carboniferous genus *Sagenodus* and the beginning of modern lungfish. *Contributions to Zoology* 67: 9-70.

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