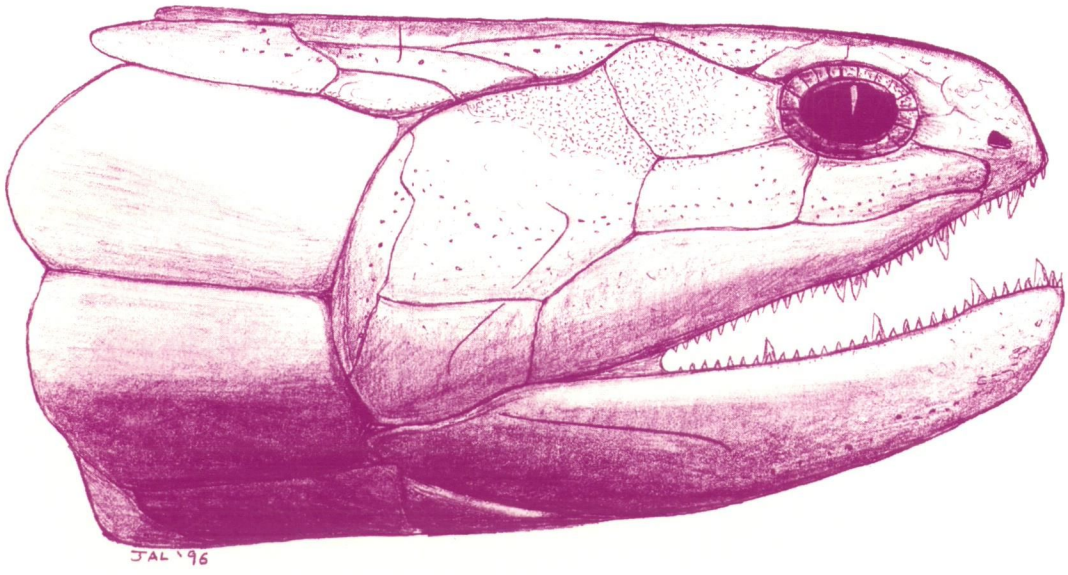
ISBN 0 7309 8794 9
ISSN 0313 122X

Osteology and Functional Morphology of the Osteolepiform Fish *Gogonasus andrewsae* Long, 1985, from the Upper Devonian Gogo Formation, Western Australia

by
J.A. Long, R.E. Barwick and K.S.W. Campbell



Records of the Western Australian Museum
Supplement No. 53

Records
of the
Western Australian Museum

The *Records of the Western Australian Museum* publishes the results of research into all branches of natural sciences, and social and cultural history, primarily based on the collections of the Western Australian Museum and on research carried out by its staff members.

Collections and research at the Western Australian Museum are centred on Earth and Planetary Sciences, Zoology, Anthropology, Archaeology and History. In particular the following areas are covered: systematics, ecology, biogeography and evolution of living and fossil organisms; mineralogy; meteoritics; anthropology and archaeology; history; maritime history and maritime archaeology; and conservation.

Western Australian Museum
Francis Street, Perth, Western Australia 6000
Tel. (09) 328 4411
Fax. (09) 328 8686
E-mail ouseya@muswa.dialix.oz.au

Minister for the Arts The Hon. Peter G. Foss MLC

Chair of Trustees Dr Robert L. Vickery AM, B.Sc., Dip.Ed., M.S., Ed.D., F.A.C.E., F.W.A.I.E.A.

Executive Director Mr Andrew P. Reeves B.A. (Hons), M.A.

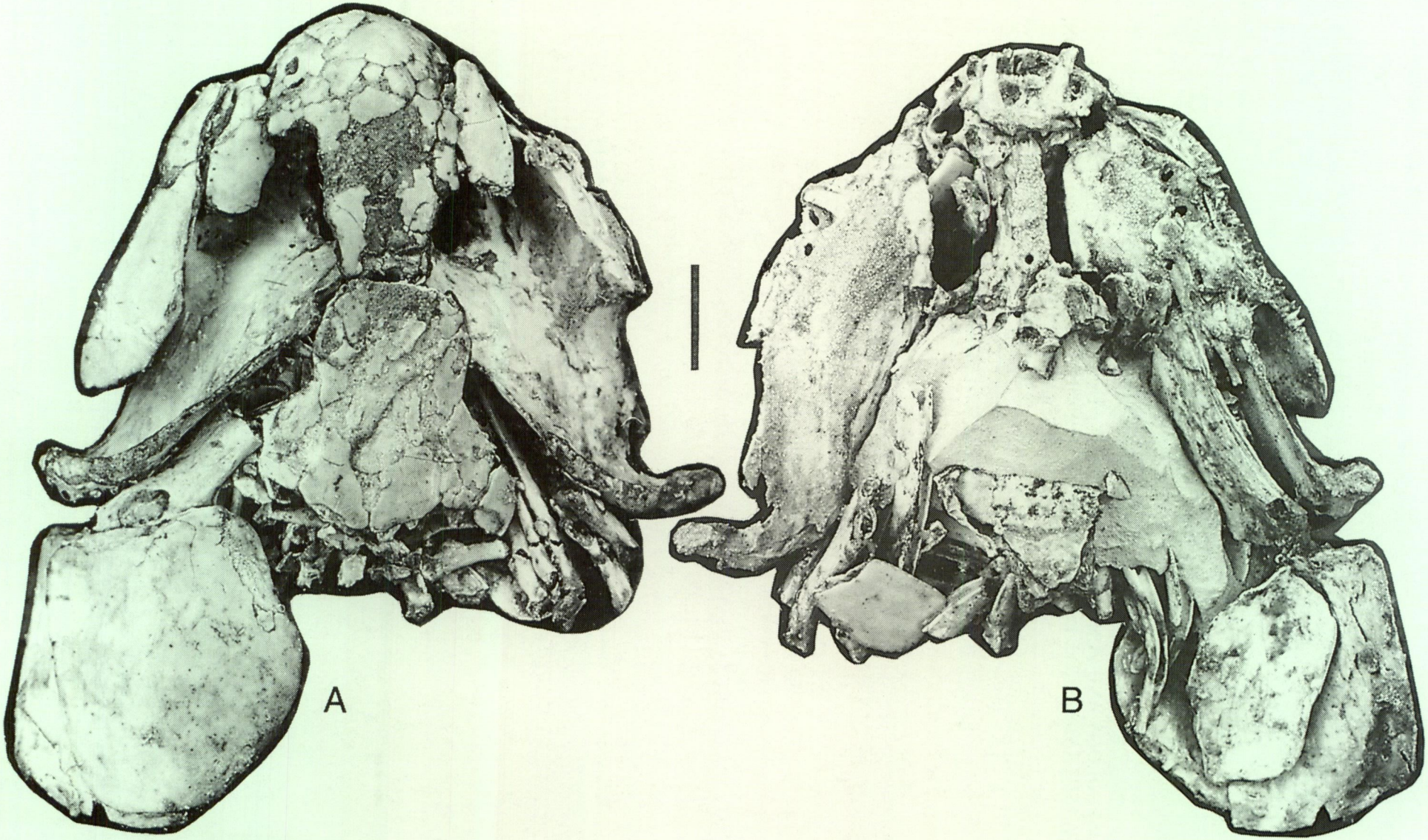
Editors Dr Kenneth J. McNamara B.Sc. (Hons), Ph.D.
Dr Mark S. Harvey B.Sc., Ph.D.

The *Records of the Western Australian Museum* is published twice a year. A series of *Supplements* are also produced. The *Records* are available for sale and exchange, the current price being $10 plus postage per part. Each volume comprises four parts. Subscriptions can be taken out for whole volumes at a rate of $30 plus postage. Supplements can be purchased from the W.A. Museum Bookshop. Prices on request.

Printed and published by the Western Australian Museum
© Western Australian Museum, June 1997
ISBN 0 7309 8794 9

Cover: Reconstruction of the head of *Gogonasus andrewsae* in lateral view by John Long. Pencil drawing.

OSTEOLOGY AND FUNCTIONAL MORPHOLOGY OF THE OSTEOLEPIFORM FISH *GOGONASUS ANDREWSAE* LONG, 1985, FROM THE UPPER DEVONIAN GOGO FORMATION, WESTERN AUSTRALIA



Frontispiece.
A, B. Dorsal and ventral views of ANU 49259 during the etching process. These views show the relative positions of all the preserved parts and, in particular, the orientation of the branchial skeleton and the opercular series.

Records of the Western Australian Museum
Supplement No. 53

Osteology and Functional Morphology of the Osteolepiform Fish *Gogonasus andrewsae* Long, 1985, from the Upper Devonian Gogo Formation, Western Australia

J.A. Long, R.E. Barwick and K.S.W. Campbell

Western Australian Museum
1997

© Western Australian Museum, June, 1997

World List Abbreviation:
Rec. West. Aust. Mus. Suppl. No. 53

ISBN 0 7309 8794 9
ISSN 0 313 122X

Printed and published by the Western Australian Museum,
Francis Street, Perth, Western Australia 6000

TABLE OF CONTENTS

Page

ABSTRACT 1

INTRODUCTION 1

SYSTEMATICS 3

- Order Osteolepiformes 3
- Family Osteolepididae 4
- Genus *Gogonasus* Long, 1985 5
  - Diagnosis 5
  - Remarks 5
- *Gogonasus andrewsae* Long, 1985 6

Description 6

- Skull Roof 6
  - Ethmosphenoid Unit 7
  - Otico-occipital Unit 16
- Cheek 17
- Extrascapulars 21
- Palate 23
  - Parasphenoid 23
  - Vomers 24
  - Palatoquadrate complex 25
  - Endopterygoid 27
  - Dermopalatine and Ectopterygoid 29
- Opercular series 29
- Gulars 32
- Submandibulars 34
- Mandible 34
  - External Dermal bones 34
  - Internal Dermal Bones 35
  - Articular and Meckelian Bones 36
  - Vascularisation and Innervation of the Mandible 38
- Shoulder girdle 39
- Endocranium of ethmosphenoid unit 42
  - Gross Features 42
  - Brain Cavity 42
  - Lateral Wall of Braincase 43
  - Ventral Endocranium 45
  - Nasal Capsules 47
- Endocranium of Otico-occipital unit 49
  - Posterior and Ventral Faces 49
  - Lateral Face 55
  - Otic Apparatus 57

Hyoid arch elements 57
Hymandibular 57
Interhyal 58
Ceratohyal 58
Hypohyal 59
Basihyal/Basibranchial 59
Urohyal 63
Branchial arch elements 63
Hypobranchials 63
Scales 65
Teeth and tusks 67
FUNCTIONAL MORPHOLOGY 69
Intracranial Kinesis 69
Attachment of Palate to Maxilla and its possible limitation of movements 76
Respiration 78
Height of Skull 78
Angle of Hyomandibular and Palatoquadrate 79
Movement of Opercular Series 81
Feeding 83
Opening and Closing the Mouth 83
Tusks and their Fossae in Opposing Jaws 83
Sensory systems 83
Distribution of Tubules from Lateral-line Canals 83
Absence of Sensory Pore Clusters 84
Prenasal Fossae 84
Locomotion 85
ACKNOWLEDGEMENTS 86
REFERENCES 86

Records of the Western Australian Museum Supplement No. 53

Osteology and Functional Morphology of the Osteolepiform Fish *Gogonasus andrewsae* Long, 1985, from the Upper Devonian Gogo Formation, Western Australia

J.A.Long [1], R.E.Barwick [2] and K.S.W.Campbell [2]

[1] Western Australian Museum, Francis Street, Perth, Western Australia, 6000
[2] Geology Department, Australian National University, Canberra City, A.C.T. 0200

Abstract - *Gogonasus andrewsae* Long is a Frasnian (Late Devonian) osteolepiform which was described from a single ethmosphenoid unit which lacked the cheek. Since the first description in 1985, two more complete specimens have been found, and are described herein. They are of particular significance in that they have been etched from limestone and are virtually undistorted. As a result they provide detailed information on the anatomy of the Osteolepiformes previously available only from interpretations of ground sections, and from etched specimens of the genus *Cladarosymblema*, which comes from the much later Early Carboniferous (Viséan) of Queensland, and *Medoevia*, which comes from an unknown, probably Late Devonian, locality in Russia. Particular items of significance are the notch in the anterior end of the maxilla defining the posterior margin of the choana; the absence of prenasal fossae; the very high crista suspendens; the foramen for the ophthalmica magna situated at the anterior edge of the basisphenoid process; the pair of large rounded processes at the edge of the fossa Bridgei; the proximal part of the hyomandibular is horizontal; the basibranchial/basihyal is short, broad and flat, making a single unit; and the posterior edge of the palatoquadrate making a high arch.

An attempt is made to show how the total structural complex of the head can be interpreted in functional terms. *Gogonasus* probably had a very limited degree of intracranial kinesis, and the amount of vertical movement between the maxilla, palatoquadrate complex and the rostral part of the ethmosphenoid was also very small. The high position of the hyomandibular, and its distal end being adjacent to the opercular bone, is here suggested as not being directly related to the high position of the stapes in primitive tetrapods, but to the high shape of the head, and enlargement of the buccal cavity, and as a new means of opening the opercular series. Closure of the mouth was achieved largely through the adductor mandibulae, without a need to involve basicranial muscles for initiation.

INTRODUCTION

The fish fauna of the Gogo Formation is now well documented. It consists of about twenty-five species of placoderms, nine species of dipnoans, two species of actinopterygians, the rhipidistian *Gogonasus* and the onychodontid *Onychodus* (Long 1988). With such a rich fauna it is surprising that only one species of rhipidistian crossopterygian has been found, and that this is represented by only three known specimens among the thousands of fish collected and prepared. Each specimen came from a different locality within the same general area. The holotype was found by the 1967 British Museum (Natural History) expedition within the Paddy's Valley Embayment at their locality 93B (Miles 1971); the second was found at the southern end of Bugle Gap; and the third on the southern side of Lloyd Hill in a loose nodule on a gully bank (Figure 1).

Gogonasus andrewsae was first described from a single ethmosphenoid unit housed in the Geology Department, Australian National University (Long 1985a). Subsequently a second specimen, WAM 86.9.661, was found in 1986 by Long during field work sponsored by the National Geographic Society, and initiated from the Geology Department, University of Western Australia. This specimen was used by him as the basis for a preliminary re-assessment of the species in 1988; that work took advantage of the fact that the new specimen had the palatoquadrate, the mandible, and most of the otico-occipital unit preserved, though its posterior part was dorsoventrally crushed. One notable aspect of the work was the

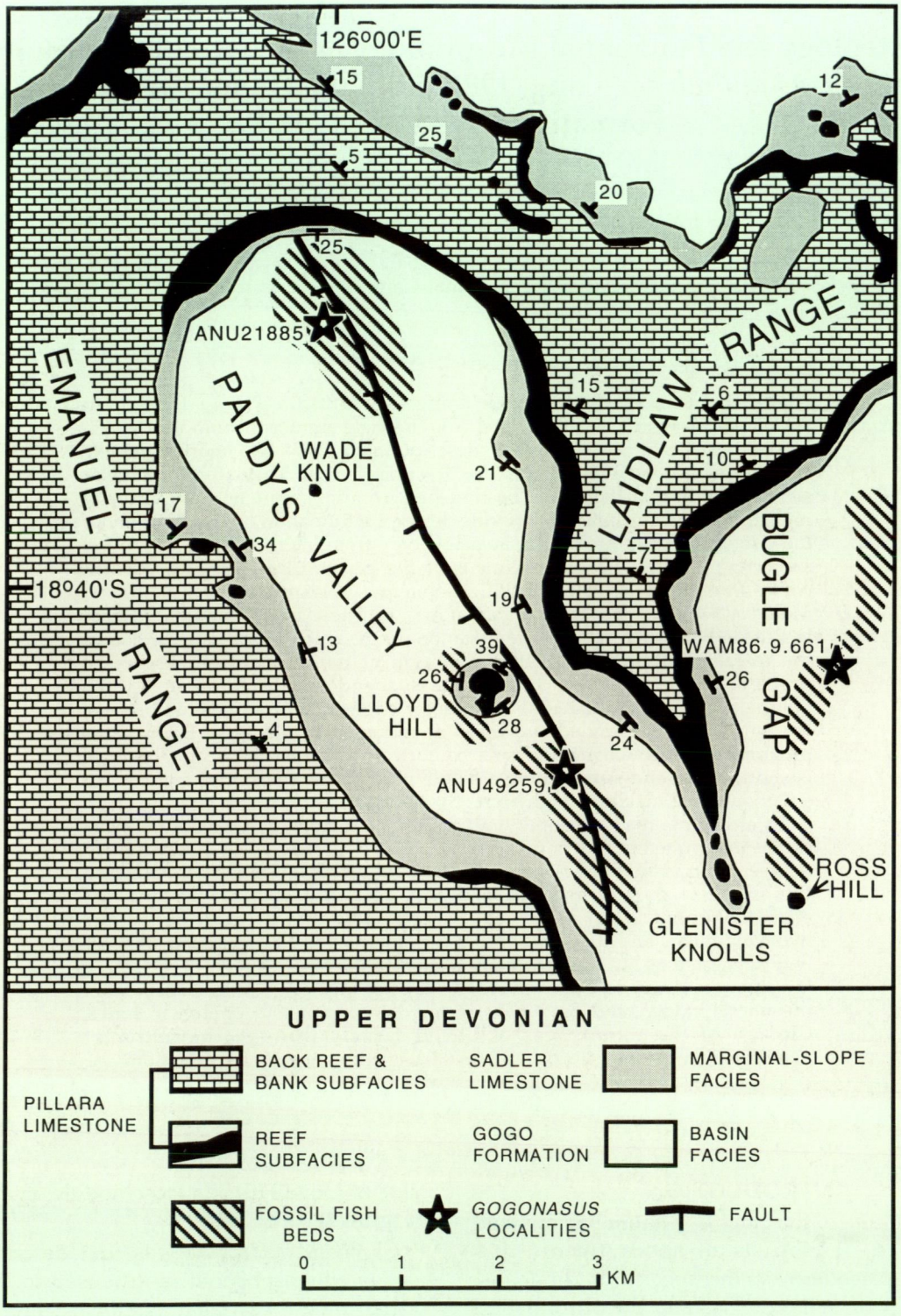


Figure 1 Map of Paddy's Valley and Bugle Gap, east of Fitzroy Crossing, Western Australia, to show the local geology and the localities where the three specimens of *Gogonasus andrewsae* were found.

revelation that a choana was present on the specimen, thus offering strong evidence against the assertion of Rosen *et al.* (1981) that osteolepiforms lacked a choana, and that the structure previously interpreted as such was an opening in the palate to receive one of the mandibular tusks on full occlusion. Full description of the species, however, was left in abeyance in the hope that further and more complete material would become available with further field work.

In 1990, on an Australian National University expedition, Barwick found another specimen, ANU 49259. This was in an isolated and somewhat eroded nodule. On preparation, it produced the

best otico-occipital roof and mandibular ramus known. All three specimens together make it possible to describe the whole head of the species. Apart from the clavicles, an anterior vertebral element, and several broken centra from WAM 86.9.661, most of the postcranial skeleton is still lacking.

At the time of the first description of the species, it was the only known osteolepiform skull unit that could be freed from its matrix by etching with acetic acid. Since then a new megalichthyid genus and species *Cladarosymblema narrienense* has been described from a freshwater limestone in the Lower Carboniferous Raymond Formation, Drummond Basin, Queensland, by Fox *et al.* (1995). Although the specimens of this genus were freed from the limestone with acid, they were not nearly as complete as the Gogo specimens, and the parts were all dissociated. No complete individual head was ever found. As a result, although many details of the morphology could be reconstructed, complete individual specimens could not be reassembled.

Lebedev (1995) described an acid-freed skull of a new Late Devonian or possibly Early Carboniferous rhipidistian, *Medoevia lata*, from an unknown locality in Russia. This specimen was of a single individual, and it is comparable with the Gogo specimens in completeness, though because of the cosmine cover, the roofing bones could not be distinguished; they may be amenable to examination by X-radiography.

With this accession of new data on Late Devonian and Early Carboniferous osteolepiforms, we are now in a position to be certain of a number of osteolepiform features that were previously in contention. Foremost among these is the presence of the choana as mentioned above. Furthermore the arrangement of bones in the snout roof and their relation to the lateral line canals has become clearer, the position of some of the nerves and vessels on the posterior of the skull is better understood, and the structure of the mandible is clear.

SYSTEMATICS

Order Osteolepiformes Berg, 1937

Remarks

There has been much dispute about the usefulness and even the validity of this taxon. The matter has been discussed by us and our colleagues on previous occasions Long (1985a–c), Young *et al.* (1992) and Fox *et al.* (1995) and, having expressed our views so recently, further comment may seem superfluous. In this current discussion we consider that the Osteolepiformes includes the Osteolepididae, the Megalichthyidae, the Tristicopteridae and the Rhizodopsidae.

However, three recent papers have raised points that necessitate further discussion. The first, by Cloutier and Ahlberg (1995), is an attempt to examine the extent to which a consensus has been reached on the interrelationships of sarcopterygians. In one of their analyses these authors have included 28 genera, four of which have conventionally been regarded as osteolepiforms; these four genera fall in a monophyletic group in their new analysis. In a second analysis, which is 'an Adams and strict consensus tree based on three most parsimonious trees found using successive weighting on the rescaled consistency index of the implemented analysis.....', they included 30 genera, six of which have been regarded by previous authors as members of the osteolepiform group. This analysis also produced a monophyletic osteolepiform group including all six genera. At present we are unable to assess the value of this work because the data matrix on which it is based is still unavailable to us. However, we mention the work because it seems that no matter how one handles the data, the osteolepiform group is sufficiently robust to fall out as a monophyletic entity. Despite this, we are of the opinion that so many morphological data are lacking for members of this group that a satisfactory scheme of interrelationships which can be confidently sustained, remains to be supported.

The second paper is by Schultze (1994), who was concerned with the relationships between sarcopterygians and tetrapods. He assumed that the osteolepiforms were a natural group and, using cladistic methodology, he attempted to find unique characters to define the group. He listed three such characters (Schultze 1994: 156) – (1) the jugal equal to or smaller than the lachrymal, (2) the presence of basal scutes on the fins, and (3) the position of the nerve V_{2-3} foramen. Of these characters only the last one is sustainable at present. Both *Medoevia*, *Gogonasus*, *Canowindra* and a new tristichopterid from near Canowindra, New South Wales (Johanson and Ahlberg in press) have the jugal larger than the lachrymal, and it is probable that *Cladarosymblema* has no large scutes at the base of its fins. Of course it is possible that these three genera are not osteolepiforms, but they share so many osteolepiform features, and lack so many features of any other group to which they could be assigned, that we consider such a possibility to be negligible. Once again, these new data point to the futility of trying to define higher taxa on the basis of unique shared derived characters applicable to the whole group. All that is possible is to define the characters of the taxa at the base of a clade, and then identify the subgroups within the clade as the characters within it evolved. Our views on this topic have been expressed in the Remarks section

dealing with the Family Megalichthyidae by Fox *et al.* (1995: 107–110).

The third paper is by Lebedev (1995), in which the author discussed the central issues again, and gave an historical account of the arguments involved. This account, like those that preceded it, assumed that it was necessary to provide a list of autapomorphies to define a higher taxon, and concluded that there were three such characters for the Osteolepiformes: basal scutes on all except the caudal fins; unjointed radials on the median fins; and a large ornamented anocleithrum. We point out that on this basis alone neither *Medoevia* nor *Gogonasus* could be assigned to the Osteolepiformes, because the first two of these characters cannot be recognised in either genus; the relevant parts are not preserved. Despite this, we are in no doubt that the two genera are osteolepiforms.

The present authors are of the view that little if anything has been gained in the study of sarcopterygian relationships by the application of a variety of new analytical methods to old data; any real advance has been made by the discovery and description of more and better preserved material which allows the description of a wider range of characters. This view is sustained by observing the remarkable change in the topology of cladograms when even a single new taxon is added to the taxonomic units analysed, especially if this new unit is near the base of a clade. A good example is the addition of *Diabolepis* to the cladograms presented by Schultze (1994).

We adhere to the view that major taxa should be defined in terms of a functional complex of characters found in the basal taxa of the major taxon. In future, therefore, particular emphasis must be placed on the discovery and analysis of new Devonian material of sarcopterygians.

Family Osteolepididae Cope, 1889

Remarks

Long (1985a,b) stated that this family is difficult to define because genera customarily assigned to it are characterised by a number of primitive features. Lebedev (1995) also reached the conclusion that no apomorphy could be found to define the family.

It would be possible to remove some taxa from the family, as understood by Long, by recognising that some of the more primitive ones do, in fact, have a suite of distinctive, advanced, functionally-related characters. For example, we consider that the genus *Gyroptychius* is not homogeneous, as *G. milleri* Jarvik (1948), *G. groenlandicus* Jarvik (1950) and *G. dolichotatus* Jarvik (1985) are distinguished from the type species *G. agassizi* (Traill, 1841) by a number of obvious characters as follows. They have eyes that are surrounded in front by wide lateral extensions of the premaxilla and lateral rostral bones to form a prominent preorbital corner, and have a more dorsal aspect than those of *G. agassizi* and species of *Osteolepis*. This positioning of the eyes is associated with an ethmosphenoid unit that is much broader than long, a posterior position of the pineal foramen, and a low maxilla (a feature shared with *Gyroptychius* s.s.). The high posterior width of the otico-occipital unit relative to its length is also noted, making a greater space for the adductores mandibulae muscles. All of these features are related to the nature of the bite. Other features that are probably related to the bite or to the buccal pump mechanism, are the wider otico-occipital unit, and the wide supratemporals, making the junction between the ethmosphenoid and the otico-occipital units transverse; the wider and shorter gulars than those in *G. agassizi* and species of *Osteolepis*, as would be expected from the dimensions of the skull; and the extension of the submandibulars around the entire edge of the gulars unlike those of *G. agassizi* and species of *Osteolepis* in which the median gular lies immediately adjacent to the mandibular symphysis. These features are usually related to the passage of water through the buccal cavity, and hence are related to the buccal-pump mechanism. This group of species is similar to *Latvius*, as figured by Gross (1956) and by Jessen (1966, 1973) in respect of the preorbital width and shape of the preorbital corner, the wide gulars, and the transverse otico-occipital unit. On the other hand, the maxilla in the *Latvius* species is higher, and the submandibulars do not extend around the flanks of the median gular. More detailed examination of *Latvius* is required by workers who have access to the material.

It is our opinion that newly discovered characters show that it is possible to separate at least two of the remaining genera after the *G. milleri* group and *Latvius* have been removed. *Gogonasus* and *Medoevia* share high ethmosphenoid units with a high crista suspendens; a large optic nerve foramen; an anterior, non-denticulated part of the parasphenoid situated at a much more dorsal level than the denticulated part; vomers not extending back along the parasphenoid to the denticulated surface; hyomandibular placed high relative to the opercular series, and with a relatively horizontal, straight anterior part, and a posterior part downturned at about 45–55° to it; and the posterior outline of the palatoquadrate standing almost vertically. Details of the functional significance of these features are discussed in the section on Functional Morphology below. Therefore, we consider it possible that another family of

osteolepiforms could be separated from the Osteolepididae as currently understood, but unfortunately it is not possible at present to extend most of this kind of information, because most of the known genera are described from specimens preserved in shale and hence they are depressed post-mortem. Attempts at more realistic reconstructions are necessary before serious advances are possible. Meanwhile, the consideration of superficial characters in isolation in an attempt to define higher taxa does more harm than good, and unnecessarily encumbers the literature.

Genus *Gogonasus* Long, 1985

Emended diagnosis

A blunt-snouted osteolepidid; ethmosphenoid unit high relative to length in comparison with most osteolepidids, the height being 52–54% of length, and having a suture running through the optic nerve foramen dividing the unit into anterior and posterior divisions; external naris equidimensional in outline, not slit-like; bones around external naris being an anterior tectal posteriorly and an a lateral rostral anteriorly; width across preorbital corners ca. 80% of total length of unit; median postrostral large, extending ca.60% the length of the parietals; posterior tectal large; two supraorbitals; posterior nasal large and lying between the median postrostral and the supraorbitals; lachrymal high and extending forwards of the maxilla to fit into a distinct notch in the edge of the premaxilla; ratio of length of dermal parietal shield to length of postparietal shield from 113–142; postparietals extend much further posteriorly than the tabulars; tabulars turned down anterolaterally to make a tight junction with the neurocranium, forming the inner margin of the spiracular slit; extratemporals unusually large with comparison to other osteolepiforms; squamosal with an idented posterior edge to accommodate flexed anterior edge of preopercular; quadratojugal large for osteolepiforms, with a strong pit-line, but the lateral line canal passing across the inner face of the bone rather than penetrating it; denticulated part of the parasphenoid ventrally placed, and with its lateral margins turned dorsally against the crista suspendens to form a concave surface for the articulation for the palatoquadrate complex; crista suspendens high and thin; non-denticulated anterior end of the parasphenoid short and situated much more dorsally than the denticulated part; denticulated part of the parasphenoid not drawn out into an acuminate anterior end; anterior to the parasphenoid the palatal lamina of the neurocranium almost flat, providing the surface of attachment for the vomers; only slight depressions mark the position normally occupied by apical fossae; olfactory tracts divide at a point anterior to the large foramen for optic nerve II; foramen for nerve II, the pineal and the buccohypophysial foramina all approximately in the one vertical plane; dorsal and ventral attachments for the hyomandibular situated one directly above the other, positing an almost horizontal anterior part of the hyomandibular; vomer without a long posterior extension; deep narrow gutter between the endopterygoid on one hand, and the ectopterygoid and the dermopalatine on the other; ectopterygoid and dermopalatine each with one tusk and adjacent replacement pit; lateral occipital commissure well developed; vestibular fontanelle large; mandible increasing gradually in height, or maintaining its height, anteriorly; denticulated surface of parasymphysial plate continuous with denticulated surface of coronoid 1; deep grooves between coronoids and dentary and between coronoids and prearticular.

Remarks

This diagnosis is not a synoptic list of synapomorphies as has been discussed in our introduction. Although some of the features are not unique to the genus, the combination of these characters is what defines *Gogonasus*.

Being cosmine covered and clearly an osteolepiform, *Gogonasus* invites comparison with *Osteolepis, Thursius, Medoevia, Latvius* and *Gyroptychius*, although of these genera only *Medoevia* is preserved undistorted; the palatal and endocranial structures of the others are not well known. After due consideration of family relationships outlined above, we tentatively retain *Gogonasus* in the Osteolepididae; hence it is necessary to make comparisons with all the above genera. *Gogonasus* differs from them in the deep embayment in the posterior edge of the skull roof behind the tabular, the large extratemporal, the relatively high ethmosphenoid unit, the strong notch in the rostral shield to receive the lachrymal, and the absence of apical fossae. Reconstructions of the ethmosphenoid units, as summarised by Long (1985a, Figure 7), suggest that *Osteolepis* is also flatter. Thomson's (1965) figure of the braincase of *Osteolepis macrolepidotus* indicates that its optic foramen is smaller than that of *Gogonasus* and its basisphenoid process is much shorter. We are not able to comment, from topotypic material, on these features in *Thursius* or *Gyroptychius*, but the form described as *Thursius estonicus* from the Late Devonian of Estonia by Vorob'jeva (1977) is similar to *Gogonasus* in its high ethmosphenoid unit and its large optic nerve foramen. However, nothing is known of the pattern of its roofing bones, and its assignment to *Thursius* is to be

regarded as tentative, at best. In any case, the shape of its vomers and the peculiar aperture in its endocranium anterior to the parasphenoid, demonstrate that it is not related to *Gogonasus*. Ahlberg (pers comm.) informs us that the structure in the endocranium might be preparation damage. *Thursius* species from Scotland (Jarvik 1948, Figure 22) all have maxillae with a smaller height to length ratio than those of *Gogonasus*. *Latvius* differs clearly from *Gogonasus* by its unique laterosensory-line system of large widely scattered pores on the surface of its cosmine (Gross 1956; Jessen 1973).

Medoevia Lebedev is also comparable, but details of its skull roof remain unknown as a result of cosmine cover, preventing comparison of roofing bone distributions which, in the past, have been regarded as having major significance. The proportions of the ethmosphenoid shield and the otico-occipital shield are approximately the same, but the following differences in detailed structure indicate that *Medoevia* can be readily separated from *Gogonasus*. In comparison with *Gogonasus*, *Medoevia* has a more pointed anterior margin and small orbits; it lacks the deep embayment in the posterior margin of the skull behind the tabular; the maxilla is low relative to its length, its height being 17% of its length as opposed to 31% in *Gogonasus*; the anterior end of its parasphenoid does not rise so abruptly from the denticulated surface, and is relatively much longer; it has definite apical fossae in the anterior palatal lamina; the foramen for the ophthalmica magna artery is placed further forwards and is larger; the denticulated part of its parasphenoid tapers more rapidly forwards; the non-denticulated surface at the anterior end of the endopterygoid is much more extensive than in *Gogonasus*; it has a ventral occipital fissure impinging on the posterior end of the basicranial fenestra; the vestibular fontanelle is smaller and the endocranial plate across the base of the notochordal chamber is wider; the hyomandibular attachments are more laterally directed; the hyomandibular is proportionately longer, lacks a distinct 'opercular process', and has a more distally placed opening for the hyomandibular canal on its lateral face; and the basibranchials 1 and 2 form a single unit with the basihyal.

The only other cosmine-covered genera with which *Gogonasus* might be compared are *Cryptolepis* Vorob'jeva (formerly *Chrysolepis*, see Lebedev 1995) from the Famennian of Russia, and *Kenichthys* Chang and Zhu (1993) from the Late Emsian (Zhu Min, pers. comm. 1995) of Yunnan, China. *Cryptolepis* has a more pointed anterior margin, a more depressed profile of the ethmosphenoid unit, straight-sided parietals, an anteriorly pointed denticulated part of the parasphenoid, and much larger and differently proportioned vomers. *Kenichthys* is less well known, but it can nevertheless be distinguished from *Gogonasus* by its more depressed profile; more anteriorly placed pineal foramen and orbits; fusion of the squamosal, quadratojugal and preopercular in the cheek; short deep profile of the mandible, increasing size of the coronoids posteriorly; and by the very large denticles on the coronoids and the prearticular. Of course, *Gyroptychius* is also distinctive in the proportions of the ethmosphenoid unit and in the shape of the preorbital and postorbital corners, as discussed under the remarks on the family.

Gogonasus andrewsae Long, 1985a

Gogonasus andrewsi Long, 1985a:361–377, figures 1–6, 7E

Gogonasus andrewsi: Long 1987:203, figure 1A, B

Gogonasus andrewsi: Long 1988a:445–6, figure10

Gogonasus andrewsi: Long 1988b:45

Gogonasus andrewsi: Long 1991:388, figure 36F

Gogonasus: Ahlberg 1991:266

Gogonasus: Young *et al.*, 1992: 45

Gogonasus andrewsae: Fox *et al.* 1995:99, figure 52

Gogonasus andrewsae: Long, 1995:192, 195

Gogonasus andrewsae: Lebedev 1995:296, 305

Holotype

ANU 21885, from the Gogo Formation, locality 93B (Miles 1971), Paddys Valley, near the Laidlaw Range, about 100 km east of Fitzroy Crossing, Kimberley region, Western Australia.

Other Material

WAM 86.9.661 and ANU 49259 from the same formation. Figure 1 shows the localities where all three specimens were found.

Description

Skull Roof

Reconstructions showing the head in lateral and anterior views were published by Long (1988a, 1995). These have now been modified in the light of the new material presented below. The reassembled skull roof, cheek and palate are illustrated photographically in Figure 2, which uses ANU 49259 exclusively (see also the frontispiece for views of the articulated specimen during preparation). Figures 3 and 4 show reconstructions of the head in dorsal and lateral views of the two nearly complete specimens. It should be noted that the ratios of the length of the dermal bones covering the ethmosphenoid (i.e. parietal shield) /

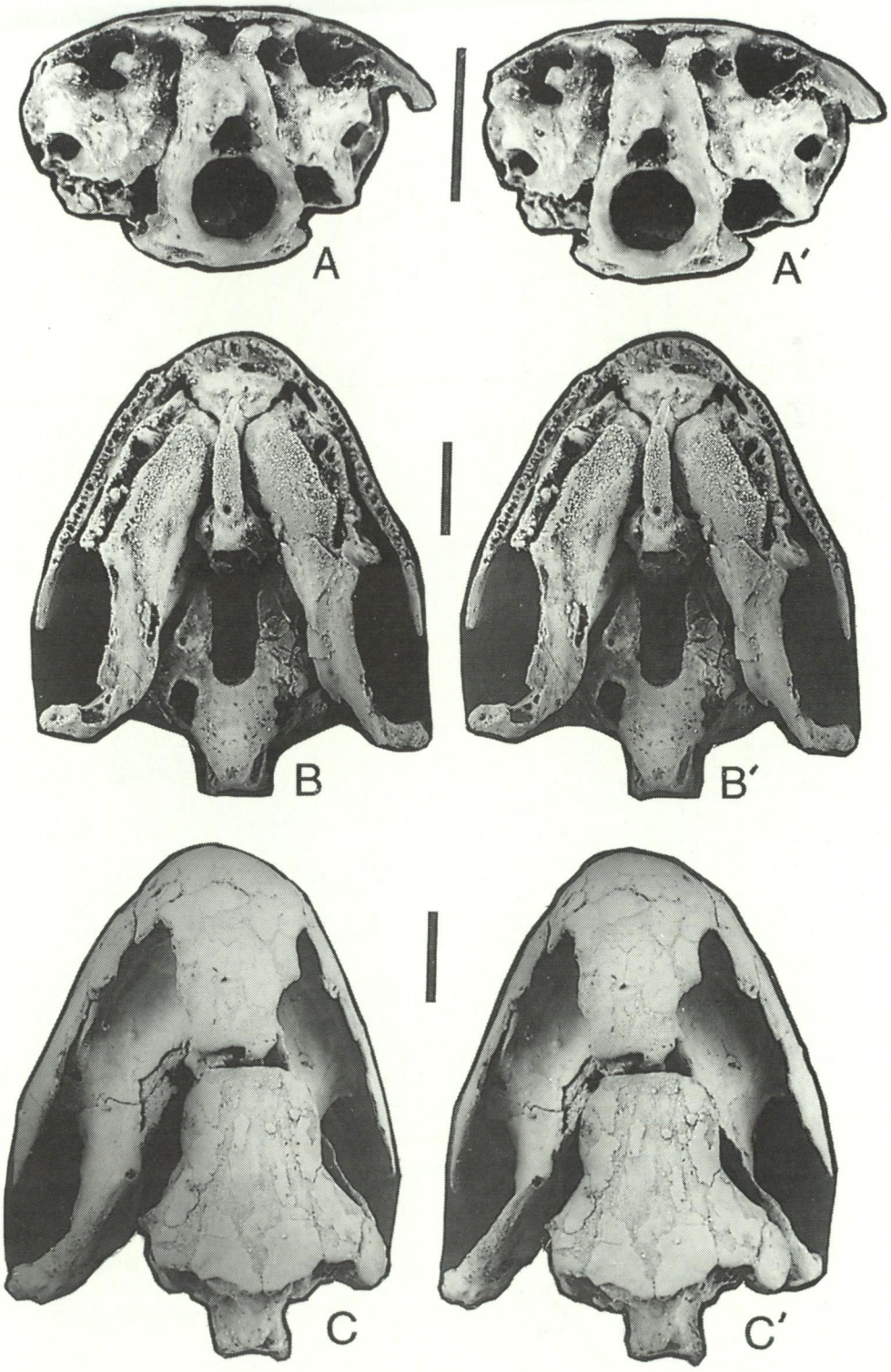


Figure 2 A–A′, stereo-pair of the posterior view of the otico-occipital unit of ANU 49259. B-B′ and C-C′, stereo-pairs of palatal and dorsal views of reassembled specimen ANU 49259. The otico-occipital unit is slightly displaced to the right of the specimen. Scales = 10 mm

the length of the dermal bones of the otico-occipital (postparietal) shield varies enormously, as in WAM 86.9.661 the ratio is 1.42, becoming 1.13 in ANU 49259, the slightly larger specimen. We also note other differences in morphology, such as the deeper lower jaw anterior end in ANU 49259 and attribute these differences to either ontogenetic or intraspecific variations. In all other fine points of morphology the specimens are identical and we do not consider it likely that these specimens represent more than one species.

Ethmosphenoid Unit

This is unusually high, its height being ca. 52–

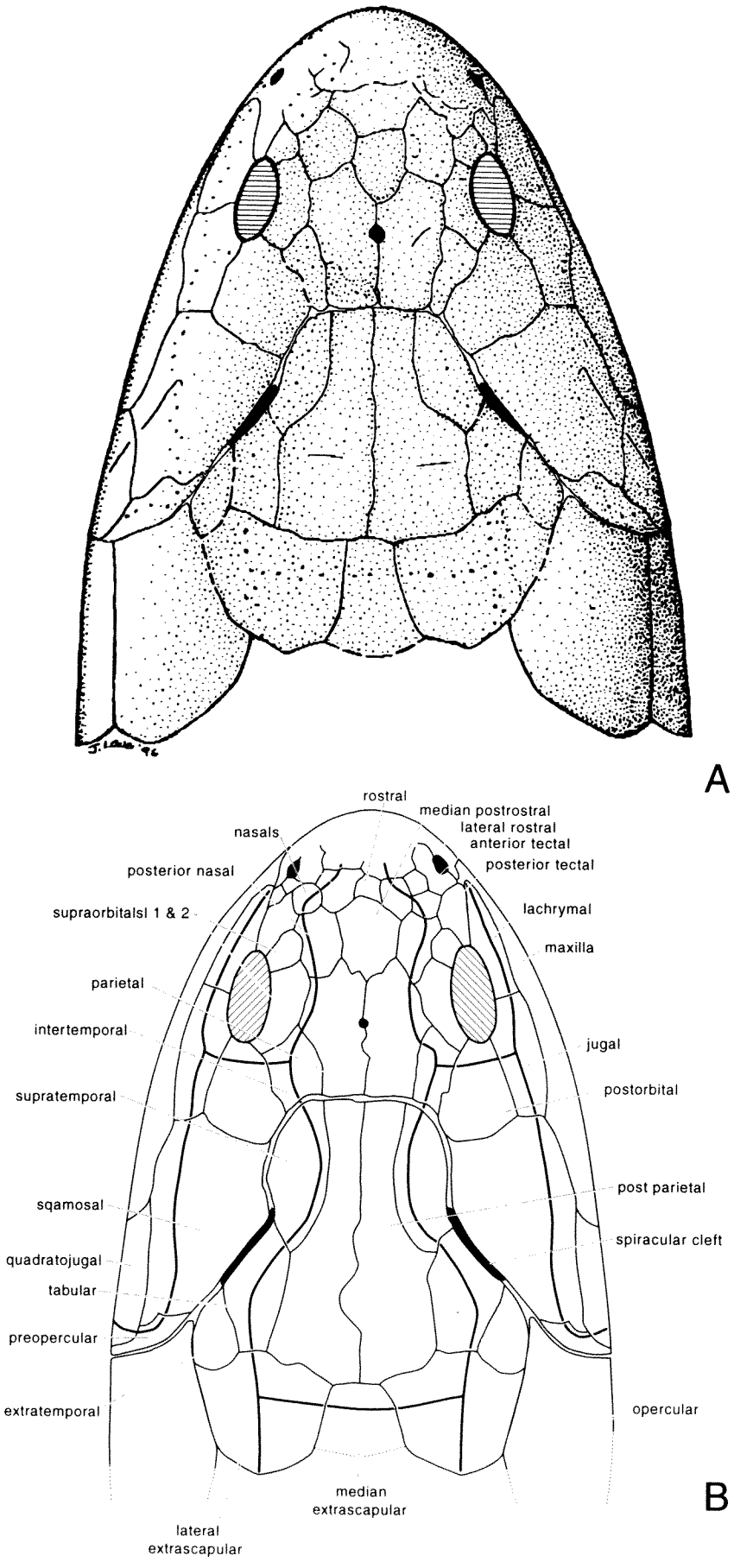


Figure 3 Composite reconstructions of the head of the species in dorsal views based on both complete specimens. A, WAM 86.9.661. B, ANU 49259.

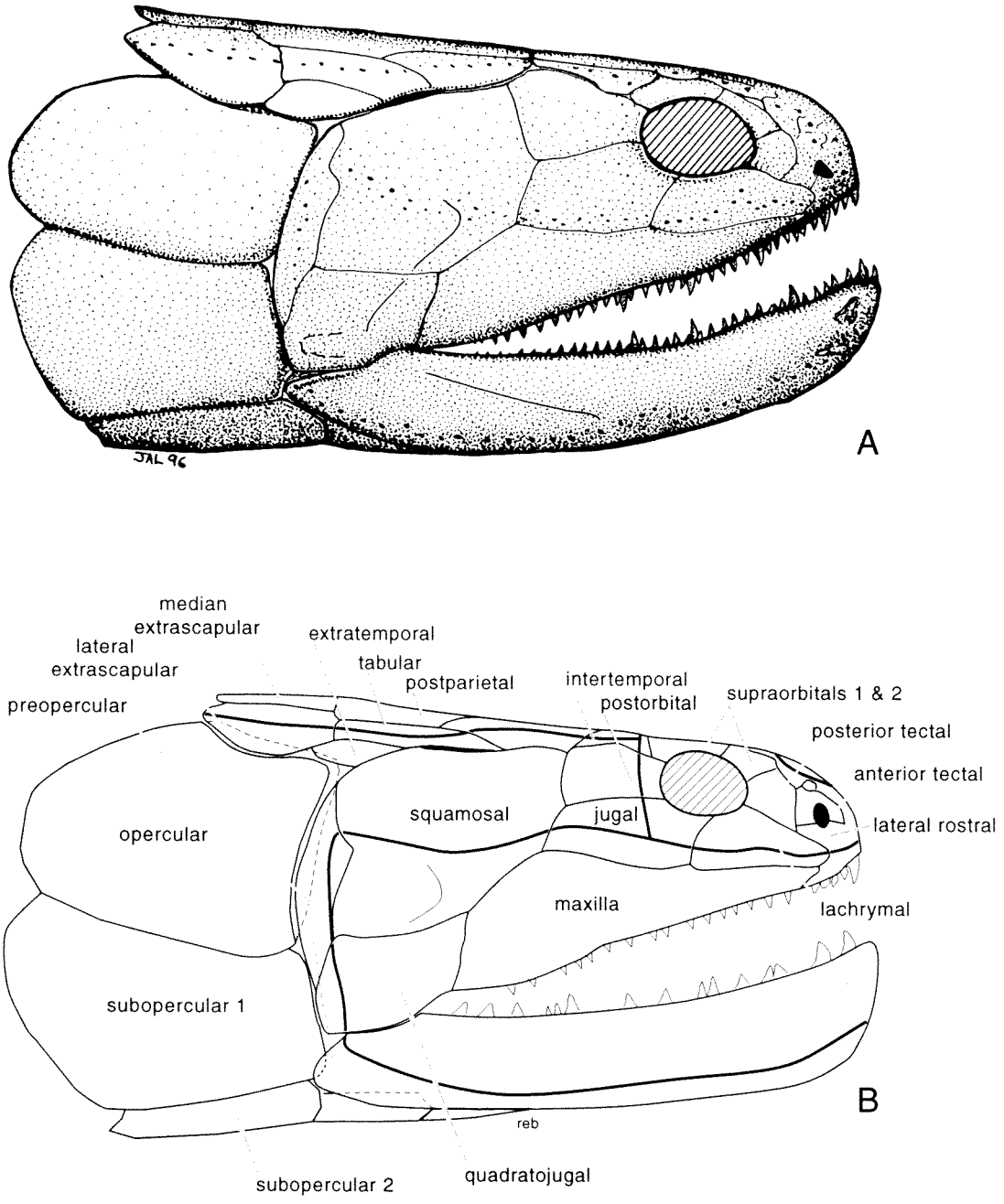
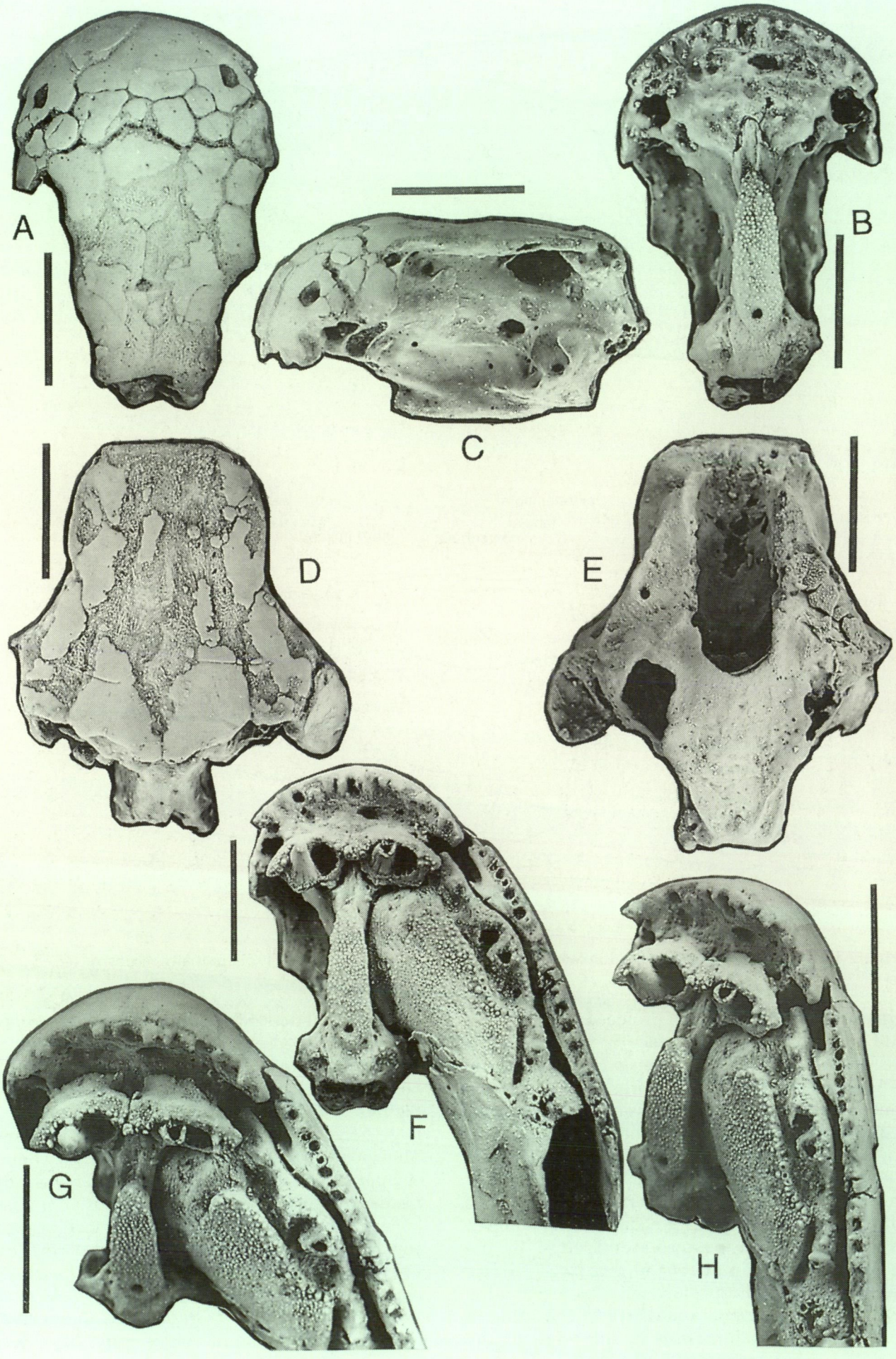


Figure 4 Reconstruction of the head in lateral view. A, WAM 86.9.661. B, ANU 49259 partially reconstructed.

54% of its length. In lateral profile (Figures 5C; 6E; 10D; 11A,B) the anterior face is vertical, never recurved ventrally. The parietals (Figures 5A; 6B; 7A; 8) are narrower posteriorly than anteriorly, and have a slight lateral expansion at the posterior edge of the supraorbitals. The intertemporal is present on the right side of WAM 86.9.661 where it is complete (Figures 7A; 8B,D). In that specimen at least, it has an acute anterior termination, is widest at the posterior point of the suborbital 2, and has a deeply embayed posterolateral edge in the cosmine-covered part, but also a large surface overlapped by the postorbital. The articulation with the otico-occipital unit is weak, consisting of only a slight indentation in the edge of the intertemporal dorsal to a slight posterior projection of the overlapped part (Figures 7A; 8B,D; 10A).

The completely or partially exposed dermal bones of the ethmosphenoid unit are shown in Figures 5–9. The median postrostral is a single large bone, its anterior margin variable in shape. The posterior nasals are also large, being comparable in size with, or even larger than, the median postrostral. A single large posterior nasal bone occupies the space occupied by two or more smaller bones in most other osteolepiforms, e.g. *Osteolepis* and *Gyroptychius* (Jarvik 1948, figure 15), megalichthyids (Jarvik 1966, figure 11; Fox *et al.*, 1995, figures 7,8), and *Eusthenopteron* (Jarvik 1980, figure 121). Two supraorbitals must have been


A
B
C
D
E
F
G
H

present on both sides of WAM 86.9.661, the anterior being half to two-thirds the size of the posterior one (Figures 7A; 8B,D). Their anterior edge lies just behind the anterior edge of the posterior nasal, and their posterior edge is about one-third to one-half the length of the parietal from its anterior edge. On the right side of ANU 49259 both supraorbitals are preserved also (Figures 2C; 5A; 8C), but the posterior one is not so large relative to the anterior one, and it is different in shape from those on WAM 86.9.661. This places the orbit somewhat further forwards relative to the parietals and the pineal foramen than it is in either *Osteolepis* or *Thursius* but not *Gyroptychius* (Jarvik 1948). The posterior supraorbital slightly overlaps the postorbital. The nasals are small and irregular in shape. Rostrals are not always clear, but very variable in size and shape. The posterior tectal is usually large, comparable in size with the adjacent posterior nasal, though on the right side of the holotype two bones occupy this space. The left side of ANU 49259 (Figure 5A) appears to have several bones in this position, but the apparent boundaries are fractures in what is probably a single bone. The lateral edge of the posterior tectal has a distinct overlapped surface for the articulation of the lachrymal (Figures 5C; 10A).

The bones around the external naris are not clear as their sutures are largely covered with cosmine. However, on ANU 49259 a suture runs laterally from the naris indicating a bone posterodorsal to, and another one posteroventral to, the naris (Figure 5A). These would be the anterior tectal and lateral rostral respectively as in megalichthyids. The matter is confused by the absence of clear sutures in the other two specimens, where there is a thicker cosmine cover. Jarvik (1950) refers to the bone bordering the anterior margin of the orbit and immediately posterior to the anterior tectal as the supraorbital-tectal in *Glyptopomus*, yet the bone occupying the same position in *Eusthenopteron* is termed the posterior tectal (Jarvik 1980, figure 122). We follow Jarvik's most recent nomenclature and call this bone in *Gogonasus* the posterior tectal.

The structures inside the naris are interesting. WAM 86.9.661 shows the dermintermedius process (Figures 7D; 9D,C; 10D) covered with small denticles, meeting the tectalis process anterodorsally which also has a cover of posteriorly facing denticles, these being slightly larger than those of the dermintermedius process. In all specimens there is a kink visible at the anterior end of the dermintermedius process, clearly denoting two grooves for water flow direction communicating with the open nasal capsule. Figure 13 shows a detailed sketch of these structures from the left naris of WAM 86.9.661.

The outline of the premaxilla is unknown because of cosmine cover, but laterally it has a deep notch for the articulation of the lachrymal (Figures 7B–D; 10A, D; 11A,B). The maxilla either abuts the ventral end of the premaxilla below the notch or leaves a small gap into which the lachrymal fits. Internally the outline of the premaxilla, where it joins the endocranium, has a well-developed flange with a distinct notch which is well displayed on the holotype and WAM 86.9.661 (Figures 6G). This notch lies anteromesial to the inner edge of the ventral opening of the nasal capsule. Such a notch is not present in *Medoevia*, and though present in *Eusthenopteron* it is much weaker than in *Gogonasus*. In the holotype, a number of perforations penetrate the inner flange of the premaxilla and the suture between the premaxilla and the endocranium (Figure 6G). These are thought to open into the lateral line canal commissure as in *Cladarosymblema* (Fox *et al.* 1995, figure 20), but this cannot be confirmed at present because we do not have sufficient specimens to sacrifice one to an excavation. Jarvik (1942, figure 60; 1980, figure 82C) has illustrated foramina in a similar position in *Eusthenopteron* and (1966, figures 17A;19D) in *Megalichthys*; he interpreted them as foramina for terminal twigs of an anastomosis of the ramus palatinus and ramus palatonasalis nerves (Jarvik 1942:480). This matter is discussed under Functional Morphology below.

The lateral line is exposed on all specimens where it enters the parietal from a posterolateral direction from the intertemporal (Figures 5A; 6F;7A;9), but its anterior course is usually obscured. Its course in the intertemporal is directly forwards from a point close to the suture with the parietal, swinging into the parietal anteriorly just posterior to the junction with the supraorbital. The infraorbital canal leaves the intertemporal bone, which can be observed only on WAM 86.9.661, where its lateral margin swings inwards. In the holotype the surface of the bones forming the snout were eroded before preparation began, and so it is impossible to determine the precise position of the canals in relation to specific bones. On ANU 49259

◀ **Figure 5** All figures are of ANU 49259. A–C, dorsal, ventral and lateral views of the ethmosphenoid unit. D–E, dorsal and ventral views of the otico-occipital unit. The denticulated plates on the left side of E were placed there during preservation, along with some other more fragmentary plates that have been removed. F, posteroventral view of the ethmosphenoid unit with the left palatoquadrate complex and the two vomers in position. Scales =10 mm.

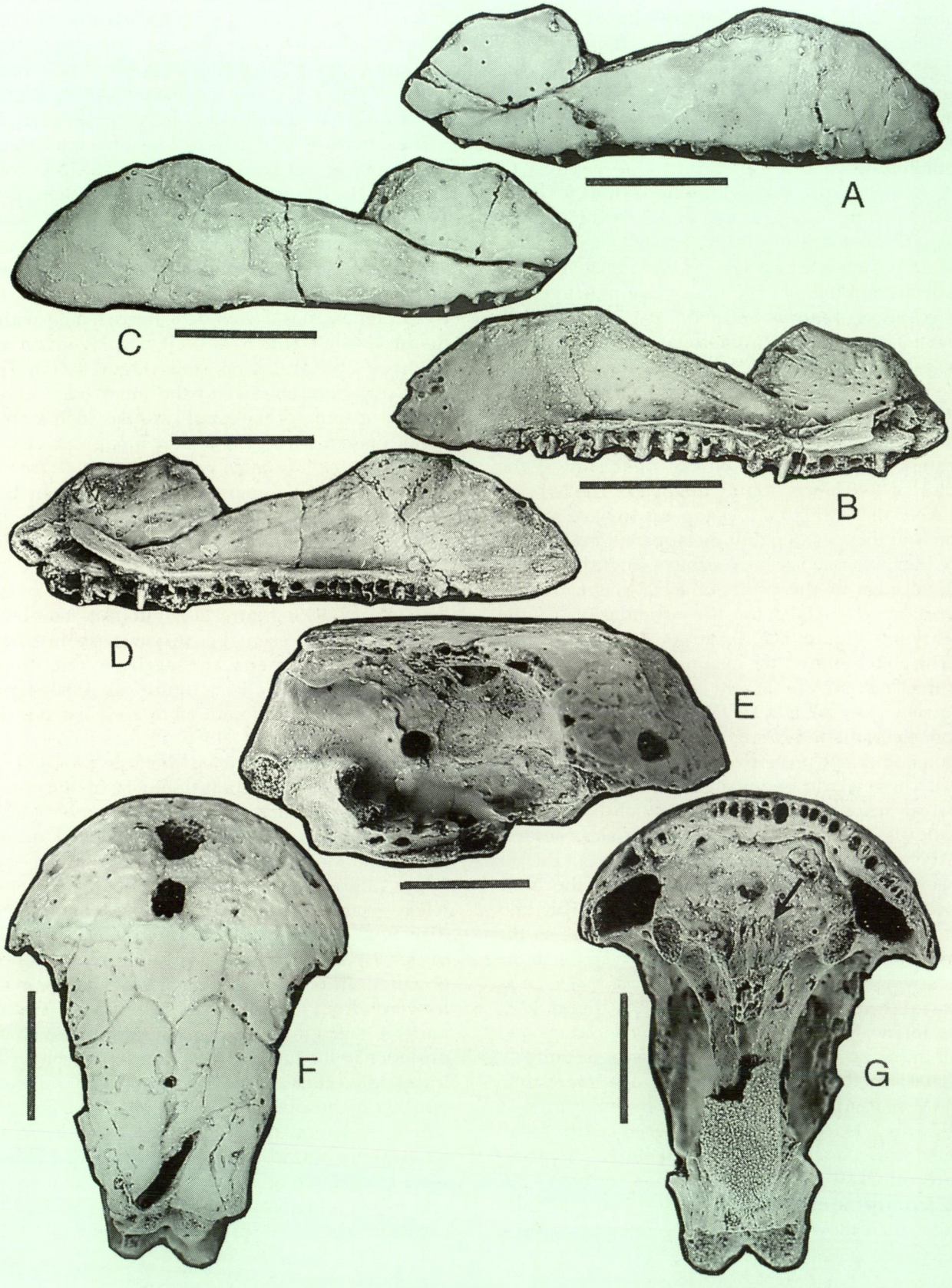


Figure 6 A–D are ANU 49259, and E–G are the holotype. A,B, external and internal views of the left maxilla and lachyrmal. C, D, external and internal views of the right maxilla and lachrymal. E, lateral; F, dorsal; and G, ventral views of the ethmosphenoid unit. This specimen shows particularly well the boundary between the posterior edge of the premaxilla and the palatal lamina with its deep emarginations, the deep notch in the inner margin of the ventral opening into the nasal capsule, the row of foramina in the premaxilla especially on the left side, the foramina in the palatal lamina, and the suture forming the anterior edge of the parasphenoid. Scales =10 mm.

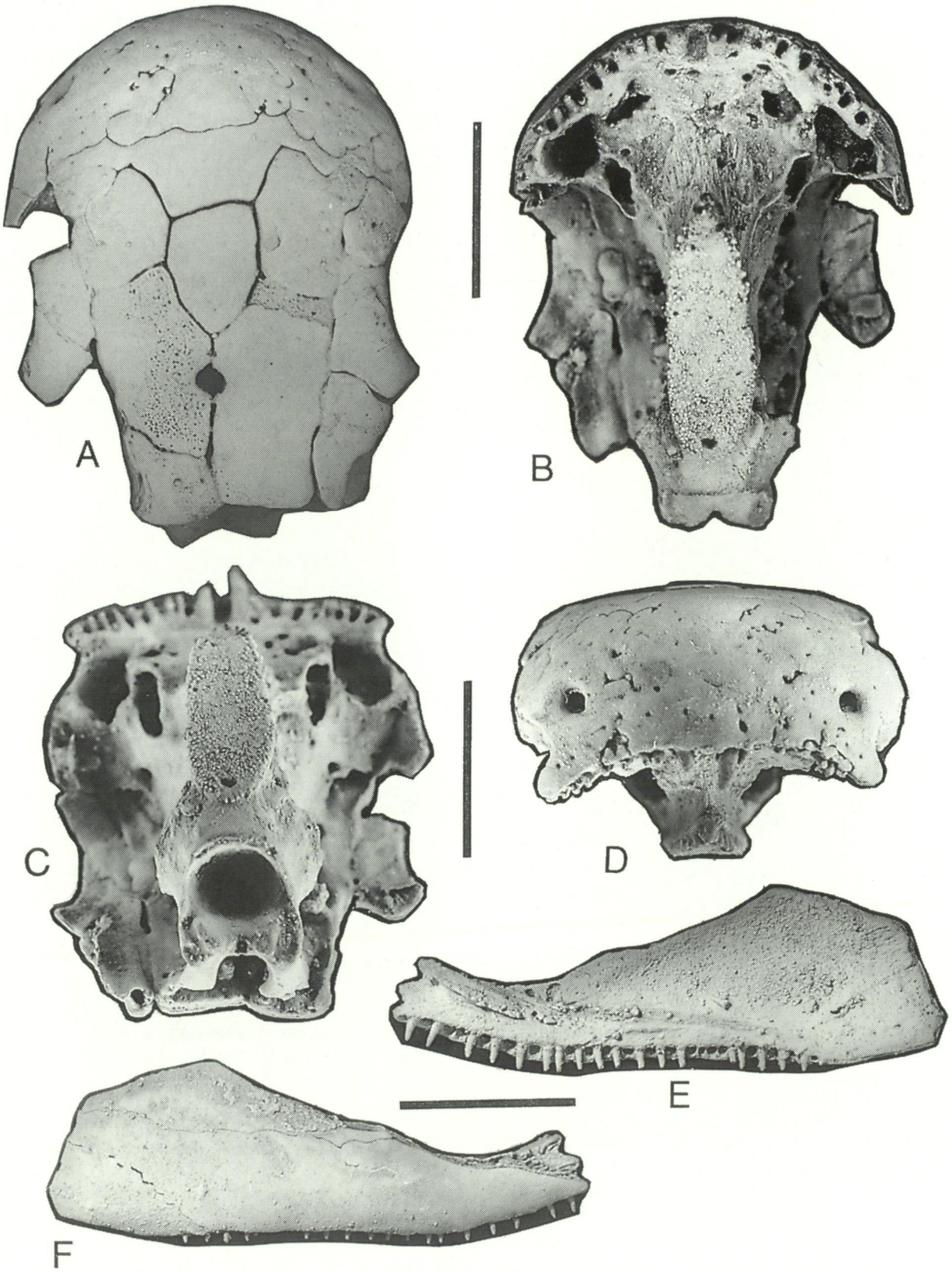


Figure 7 All photographs of WAM 86.9.661. A, dorsal; B, ventral; C, posteroventral; and D, anterior views of the ethmosphenoid unit. In Figures C and D note how ventrally placed the denticulated surface of the parasphenoid is, and in B note the two edges of the parasphenoid on the palatal lamina. E–F, right maxilla in lateral and internal view. Note that the truncation of the posteroventral end is natural and not due to breakage. Scales = 10 mm.

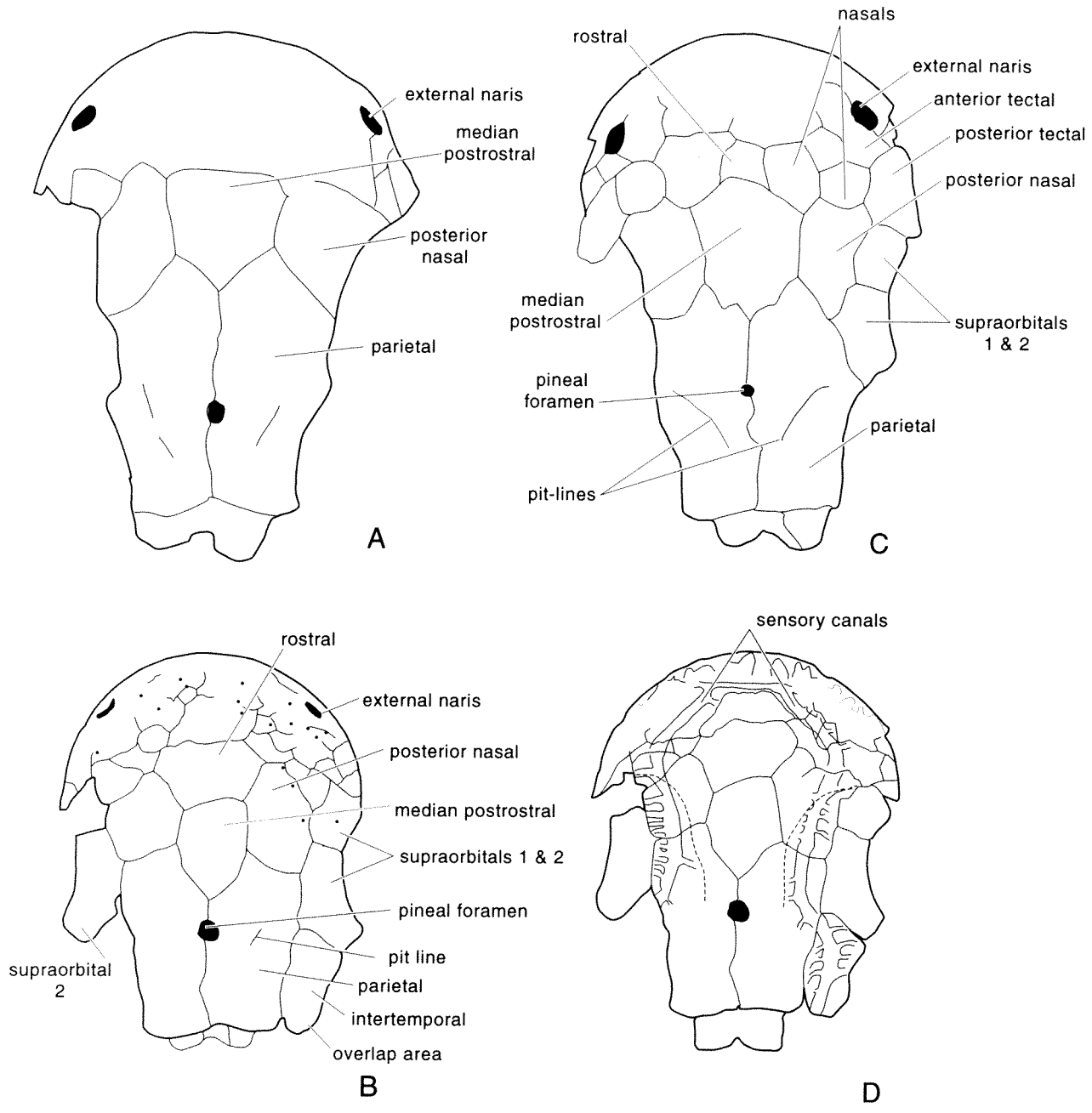


Figure 8 Outline drawings of the roofing bones of the ethmosphenoid unit. A, the holotype; B, WAM 86.9.661; C, ANU 49259. Where the bone boundaries have been observed either on the external surface or on X-radiographs, they are shown as a solid line. Interpolations are dashed. D, drawing of the skull roof of the ethmosphenoid showing the arrangement of the lateral line canals, holotype.

its approximate position can be determined by the lateral line pores (Figure 5A), but as has been shown by Fox *et al.* (1995), these do not always provide a reliable guide. X-radiographs of this specimen and WAM 86.9.661 show the pathway of the main lateral line canal clearly (Figure 9). This shows the normal pattern for an osteolepiform, but a peculiar preorbital lateral line commissure extending from the posterior nasal through the posterior tectal to the lachrymal. This commissure can be observed on the holotype where its exit from the posterior tectal is clearly visible on both sides of the specimen. Such a commissure was illustrated by Jarvik (1980, figure 127) on *Eusthenopteron*, but so far as we are aware it has not been recorded elsewhere. It is possible, however, that *Cladarosymblema* had a commissure of this kind, but no specimen showing the infraorbital canal was available for X-ray. Fox *et al.* (1995, figures 7E,G) show large branching canals in positions where a commissure could take origin. The infraorbital canal in *Gogonasus* can be seen deep in the notch in the premaxilla, but pores opening into the canal are few in number. Large

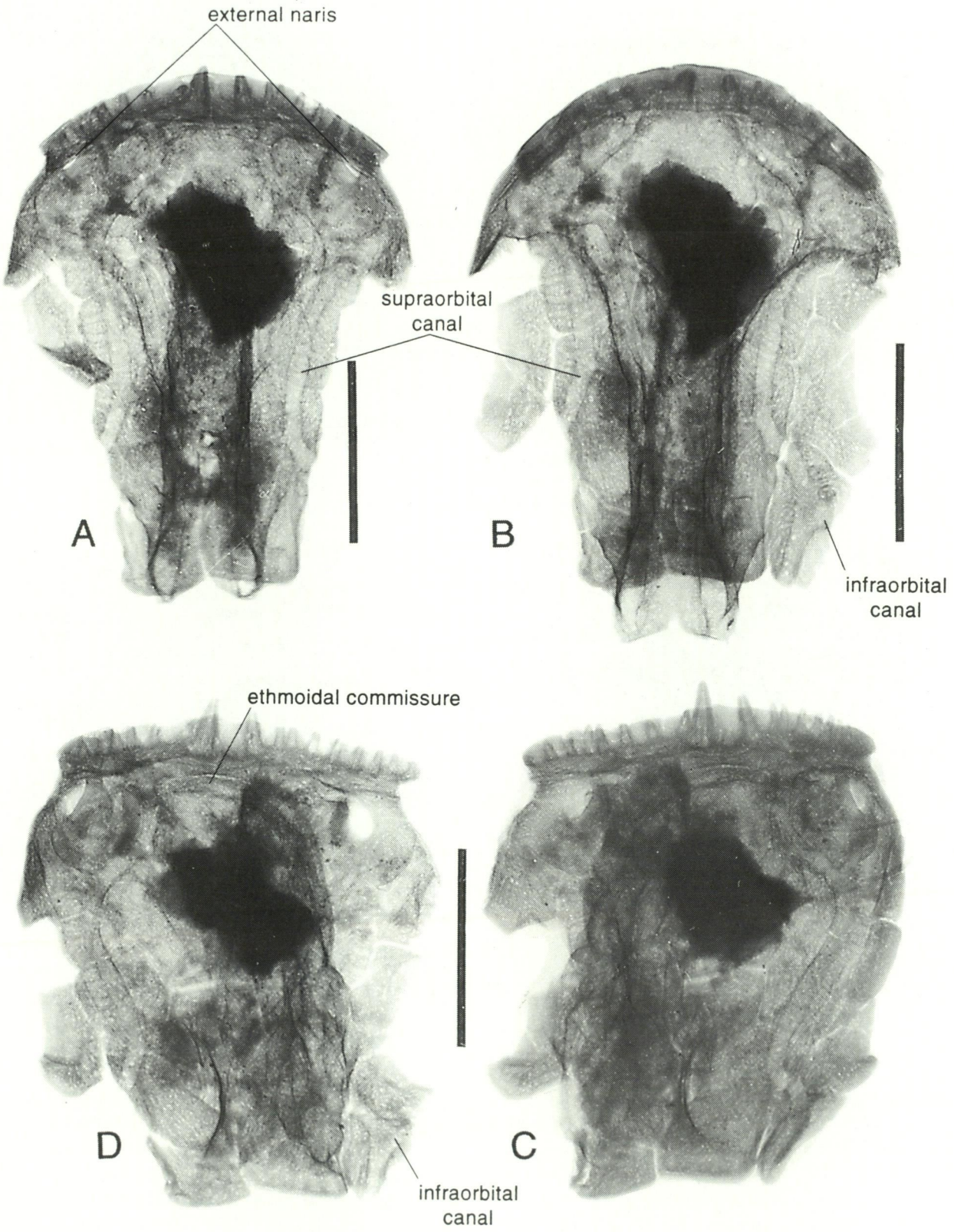


Figure 9 X-radiographs of the ethmosphenoid of WAM 86.9.661. A,B, ventral views, A, with some of the lateral skull roof bones not returned to the normal position, but B. has all the skull roof bones known in their correct position. B. Specimen is tilted more backwards than A. C,D, two views of the same specimen tilted to the right and left to show the arrangement of the lateral line canals and the position of the vaguely defined bones around the external naris. These two illustrations have the bones in their correct positions. Scales = 10 mm.

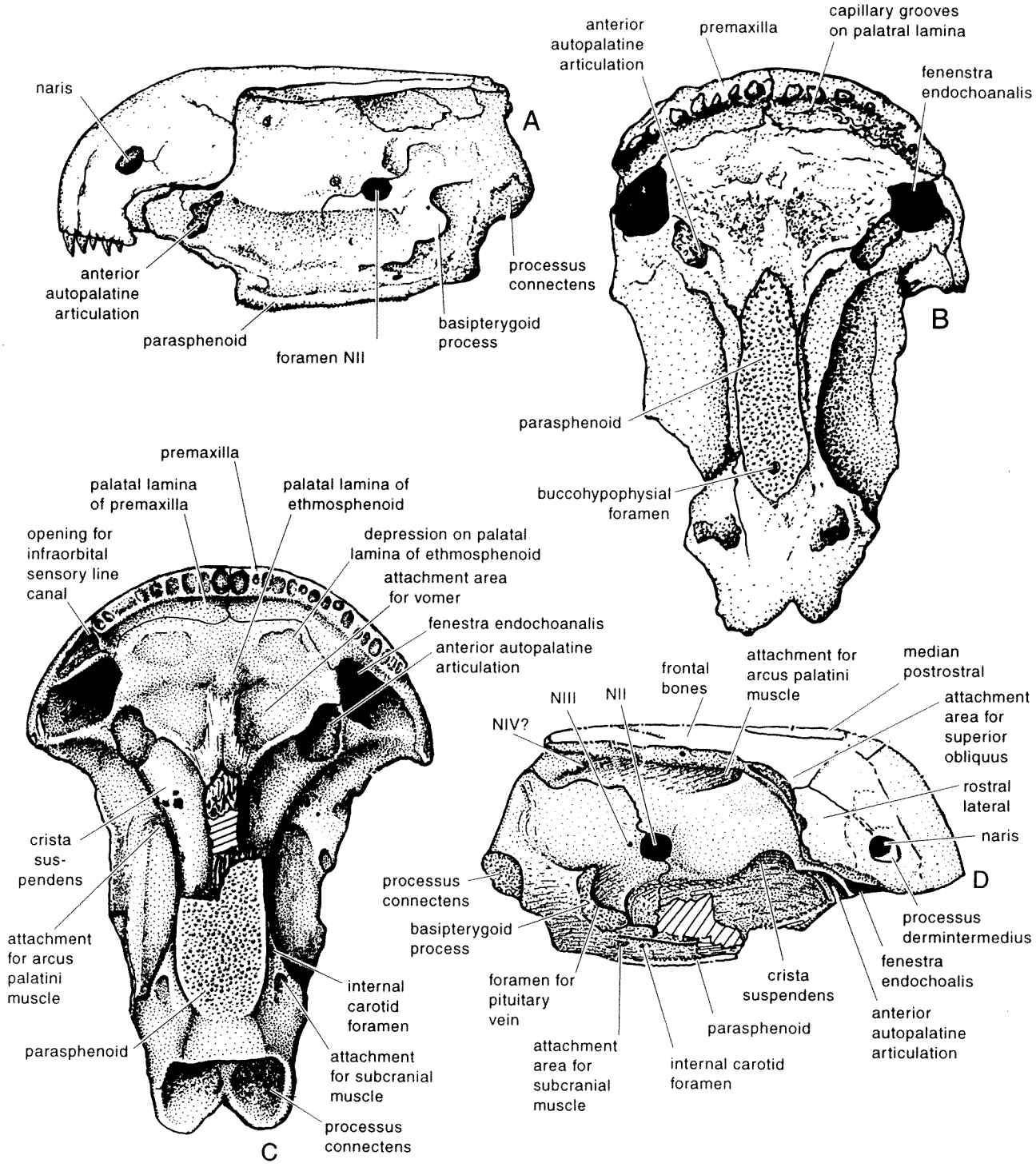


Figure 10 A, B, left and ventral aspects of the ethmosphenoid unit of WAM 86.9.661 with the supraorbital bones removed. C, D, ventral and right aspects of the holotype, slightly modified from Long (1985a). Compare with Figures 6G and 8B.

branches from near the bend in the main canal in the parietal also extend inwards towards the parietal foramen. This arrangement is also represented in *Eusthenopteron*.

The pineal foramen (Figures 2C; 3; 5A; 6F; 7A; 8; 9A) is large and open, situated forward of the mid-point of the inter-parietal suture.

The length of the orbit is ca. 30% the total length of the ethmosphenoid unit, its mid-point being in the same vertical plane as the anterior edge of the parietals. This is quite different from the situation in *Medoevia* in which the eye is only ca. 25% of the length of the ethmosphenoid and is situated in a more posterior position, the line joining the centres of the eyes passing through the pineal foramen.

Otico-occipital unit

The dermal roof of the otico-occipital unit is

known in detail only from ANU 49259 (Figures 5D; 14), and even this specimen has had much of its cosmine resorbed, making the definition of the individual bones difficult. WAM 86.9.661 (Figures 11F,G; 15) has the lateral part of the roof preserved in part, and it has been X-rayed (Figure 16B) to show some details, including parts of the lateral line canals.

The following points have been elucidated. The median suture on the external surface has a large posterior flexure on ANU 49259; it is almost straight on the external surface of WAM 86.9.661, but slightly flexed on the internal surface. On ANU 49259 the postparietals are only about half as wide anteriorly as posteriorly, most of the narrowing taking place adjacent to the supratemporals, but the position is less clear on WAM 86.9.661. Their posterior margin is transverse to slightly projecting, the extent of the projection being partly controlled by the shelf each bone carries to provide a platform for the extrascapulars. The supratemporal is about half as long as the postparietal, and has a pointed posterior end. The tabular increases slightly in width from the rear to approximately its mid-length where it abruptly narrows. Anterior to this point the bone is turned down to make a tight junction with the endocranium (Figures 5D; 22A, D). This downturn forms the smooth inner edge of the spiracular slit. On ANU 49259 the posterior edge of the tabular lies anterior to the edge of the postparietals, making a distinct embayment for the lateral extrascapular, but on WAM 86.9.661 this edge is more posteriorly placed. The lateral extrascapular is supported on a small flange of bone which is entirely on the postparietals (Figures 5D; 14A; 15). The extratemporal is a large bone, approximately half the size of the tabular (Figures 2C; 3; 5D; 14A; 16A). On ANU 49259, the only example we have, it is slightly displaced, but there is no doubt that it extends back behind the temporal making a deep embayment for the lateral extrascapular.

The articulation between the otico-occipital and the ethmosphenoid units should be effected by a process on the supratemporal at the point where the lateral line canal passes across the junction between the two units. It appears that only in megalichthyids is this process and socket junction is well developed (Bjerring 1972; Fox *et al.* 1995). Although this surface is well preserved in *Gogonasus*, there is no sign of a distinct process in the stated position. All that is present is an inflection of the hard external surface of the bone mesial to the opening for the lateral line canal (Figures 11F; 15). This inflection projects slightly forwards, but could scarcely be termed a process. It seems more likely that in this genus the articulation was achieved by a ligamentary attachment.

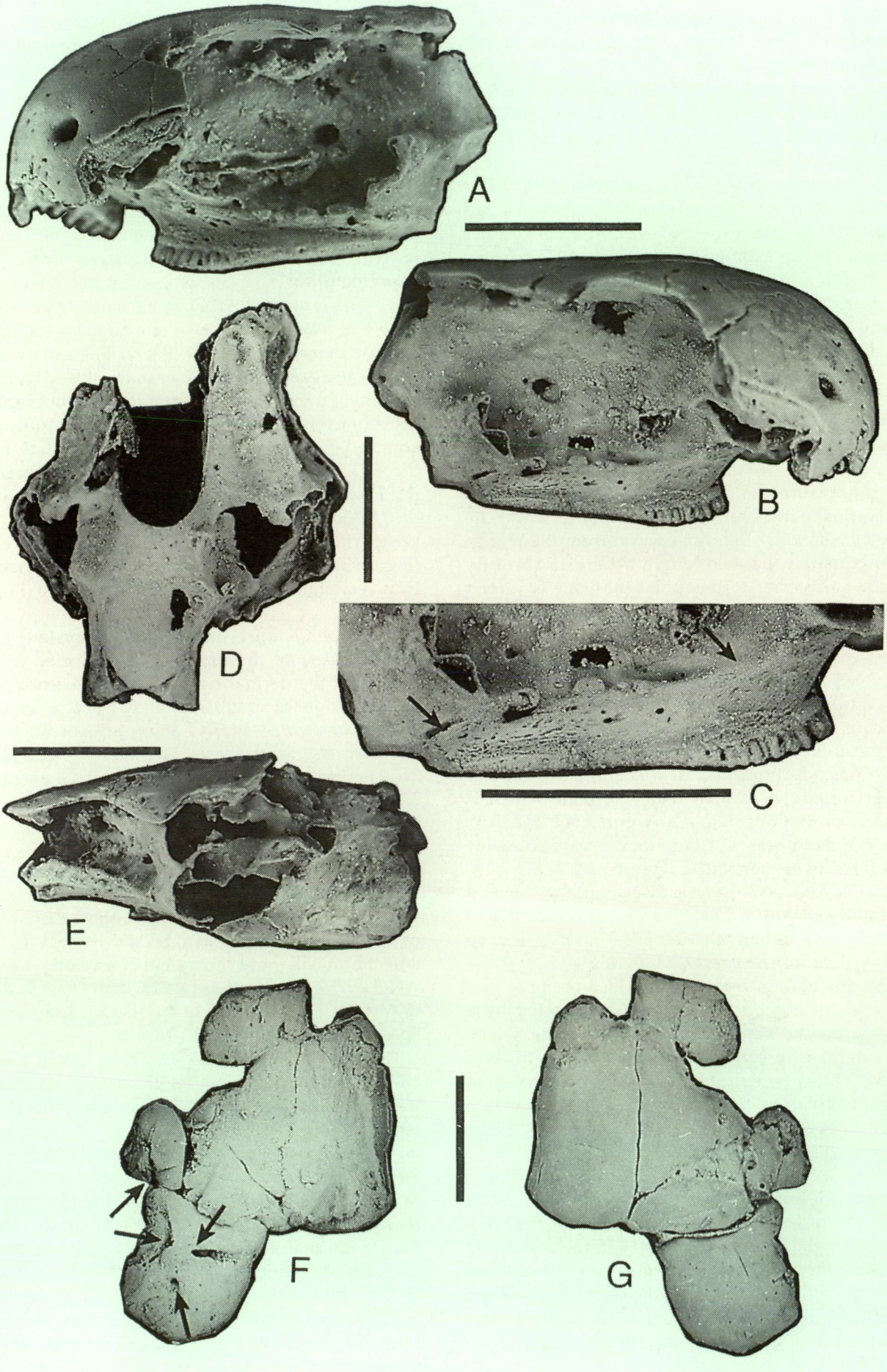
The position of the lateral line canal can be traced by a small number of large pores, by the entry and exit points in the tabular and the supratemporal respectively, and by the X-radiographs of WAM 86.9.661 (Figure 16B). These latter openings are well exposed. In addition, although the endocranium is partly in position in all our material, we have been able to secure X-radiographs that give a great deal of information on the position of the canals. As shown on Figures 5D and 14A, the canal enters the tabular at its mid-width, runs forwards to pass into the supratemporal near its posteromesial edge, and then passes through that bone close to its inner edge, curving laterally near the front of the bone. No pores opening into the lateral line canals have been observed on the postparietals of either specimen, nor are they seen on the X-radiograph of the bones in WAM 86.9.661 (Figure 16B). We conclude that no branches of the canal pass through that bone as was reported by Bjerring (1972) in *Megalichthys laticeps*. A posterior pit-line on ANU 49259 extends laterally from the postparietal to the tabular without any division (Figure 5D), but on WAM 86.9.661 it is represented by a very short line on the postparietal only (Figure 11G).

One other feature of the sensory system is of interest. Despite the excellent preservation of the surface of the dermal bones, we have been unable to find evidence of clusters of sensory pores such are found on many osteolepiforms (e.g. *Gyroptychius groenlandicus*, Jarvik 1980, figure 141). This matter is considered below under Functional Morphology.

Cheek

The cheek without the maxilla and quadratojugal is known from the left side, and the maxilla, squamosal, jugal and lachrymal from the right side of WAM 86.9.661 (Figures 17C,D; 18; 19A–C; 20); and the maxilla and lachrymal from both sides of ANU 49259 (Figures 6A–D; 21). Both cheeks of the WAM specimen have been X-rayed with spectacular results (Figures 18, 19)

The maxilla (Figures 6A–D; 7E–F; 12A,B; 17C–E; 18A–C; 19A–C; 21; 25A; 26; 32) is high relative to its length, has a subrounded acute anterior end and terminates in a slightly rounded or truncated 60–70° angle posteriorly. The posterodorsal edge varies considerably in outline, some individuals being gently curved and others definitely angular. Its highest point is at the jugal/squamosal suture. On its internal surface a long low ridge diverges from the tooth line at a low angle. This lies adjacent to the lateral edge of the dermopalatine and the ectopterygoid; there is no attachment between these bones and the maxilla, the slight gap between them presumably being occupied by connective


A
B
C
D
E
F
G

tissue which allowed some small degree of movement while providing stability (Figures 2B; 25A–D) during the bite. At the anterior extremity of this ridge there is an anterodorsally directed process on a forwardly concave flange; this served two purposes – it formed the posterior margin of the choana, and it provided a buttress against the dermopalatine (Figures 6B,D; 7E; 21). This flange has been described by Fox *et al.* (1995) in *Cladarosymblema*, and by Lebedev (1995) in *Medoevia*, is possibly a feature of all osteolepiforms. The maxilla carries 22–28 major teeth with a small but indefinite number of tiny ones, which show up best in X-rays (Figure 18B,C), scattered between the more posterior teeth. No teeth are present on the posterior quarter of the bone, which is turned upwards slightly.

The lachrymal (Figures 6A–D; 12A,B; 17C–E; 18A,C; 19; 20) has a long orbital margin and, as a result, its posterior edge is steep like that in *Osteolepis* rather than inclined as in *Medoevia*. Its anterior end is bluntly rounded to fit into the notch in the premaxilla. The infraorbital canal lies below the mid-line. In mesial view the lachrymal has an anterodorsal flange which received the posteroventral margin of the ethmosphenoid unit, and a short anteroventral notch that accommodated the anterodorsal process of the maxilla.

The jugal (Figures 4; 17C–E; 18A,C; 19; 20) is distinctly larger in area than the lachrymal, and forms the orbital margin to about the same extent as that bone. The trace of the lateral line canal can be seen on the internal surface of the bone in the position shown on Figures 18–19. There is a strong upward kink in the lateral line where it joins the postorbital branch.

The postorbital (Figures 4; 17C–E; 18A–C; 19; 20) has a more equidimensional outline than the jugal, and forms about the same proportion of the orbital edge as that bone. As in *Osteolepis*, but not *Medoevia*, the postorbital extends back as far as the anterior end of the spiracular slit, the implication being that the squamosal is a relatively longer bone to occupy the space ventral to the slit.

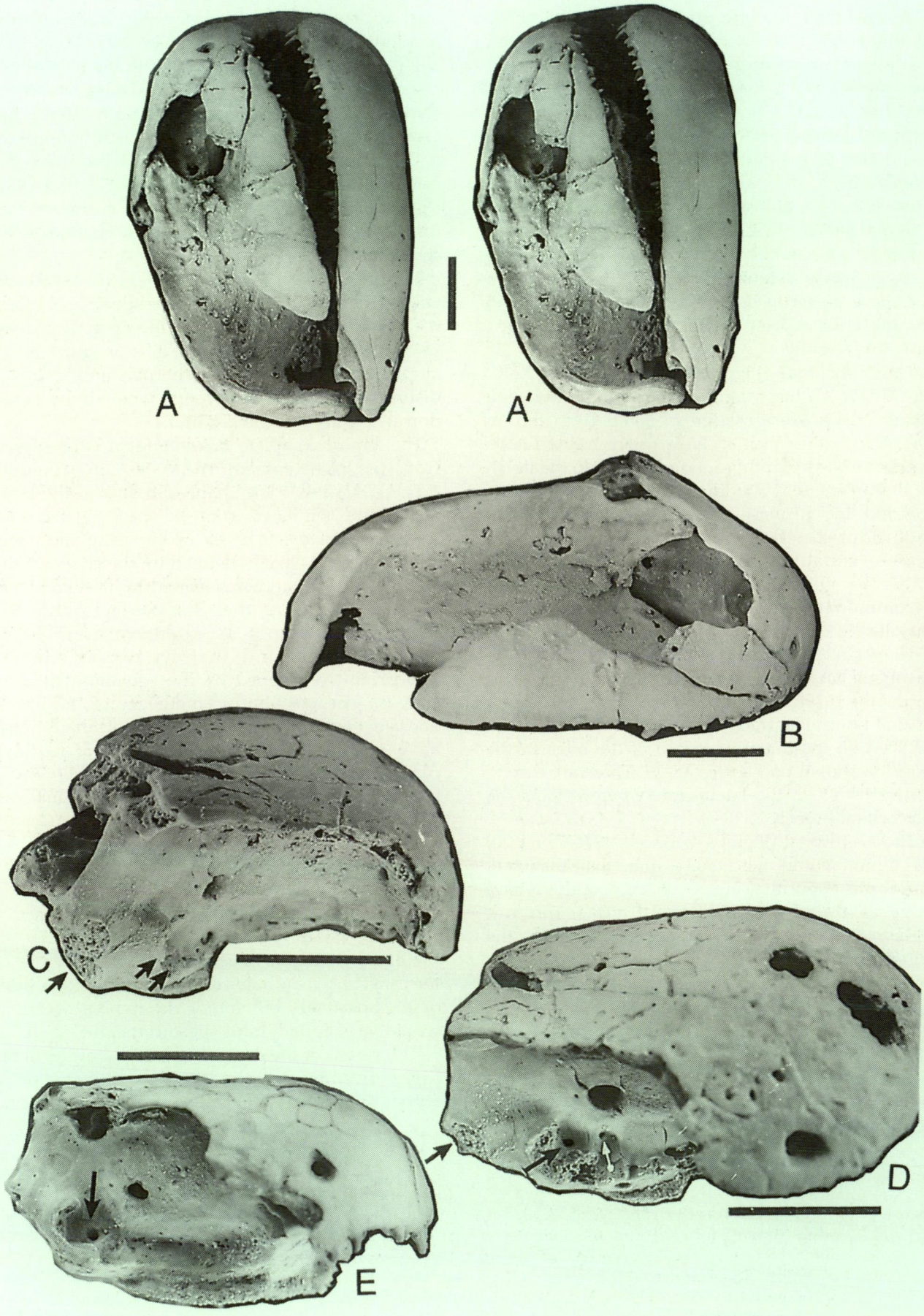
The squamosal and the preopercular are distinctive (Figures 4; 17C–E; 18A,C; 19; 20). The squamosal has a sinuous edge against the preopercular posterodorsally. Its dorsal and ventral edges are only slightly flexed and are parallel; its contacts with the jugal and postorbital are approximately equal. The overlapping relationships of the squamosal are interesting. The anterior edge is overlapped by both the postorbital and the jugal; and the anteroventral edge by a short contact with the maxilla. The posteroventral edge extensively overlaps the quadratojugal, more than it contacts the maxilla, an unusual condition for osteolepiforms such as *Osteolepis* and *Thursius*, but similar to that in *Gyroptychius*. The surface on its dorsal third on both sides lacks cosmine; the significance of this is not understood.

The preopercular (Figures 4; 17C; 18A; 19A,B; 20) is extensively overlapped by the squamosal along its anterior edge and overlaps the opercular along its posterior edge. Its long axis is inclined at an angle of ca. 80° to the tooth row, and it has a distinctly narrow dorsal process where it meets the dorsal margin of the cheek unit.

The almost complete quadratojugal is preserved from the right side of WAM 86.9.661 (Figures 17D,E; 18C; 19C). The shape and size of the bone can also be estimated from the space left for it on the reassembled left cheek of the same specimen, and its ventral edge is defined by the shape of the surface on the mandible covered by it at complete closure. We note that its contact with the preopercular is not as extensive as in other osteolepiforms, and that its dorsal edge is extensively overlapped by the squamosal (Figure 17D, E). The position of emergence of the lateral line canal from the preopercular shows that it must have passed inside the quadratojugal to have carried the lateral line to the mandible. As is normal for osteolepiforms, no sign of a canal can be seen within the quadratojugal. A deep, steeply inclined pit-line occurs on the anterior half of the bone, its position being best shown on the X-radiograph (Figure 18C).

The lateral line in the cheek has some distinctive features, its detail being best studied by X-radiographs (Figure 18, 19C). The arrangement of the canal and its tubules is similar on the two sides of the specimen, but minor differences occur, as would be expected. In the postorbital, the canal lies well forward of the geometrical centre of the bone. Eight or nine slightly irregular tubules open anteriorly towards the eye; one or two longer and

◀ **Figure 11** All photographs of WAM 86.9.661. A, B, left and right aspects of the ethmosphenoid unit. In A the paired ridges running forward from the optic nerve foramen are artefacts of preparation. Both A and B show the notch to receive the lachrymal and the maxilla very well. C, enlargement of the lateral part of the parasphenoid as shown in B (arrows show dorsal limits of parasphenoid). D, E, ventral and lateral views of the partly crushed otico-occipital unit; F, G, internal and external views of part of the dorsal layers of the detached roof of the specimen showing the only preserved lateral extrascapular with its lateral line canals in position (arrowed). Scales =10 mm.


A
A'
B
C
D
E

much more irregular branching tubules run backwards from the canal to open at the numerous pores on the posterior two-thirds of the bone. As is apparently normal for osteolepiforms, the canal lies in the ventral half of the lachrymal. There are about 15 mostly straight, but slightly irregular tubules runing ventrally to open through pores near the edge of the lachrymal, and these tubules also occur in similar patterns on the jugal (ca. 10 tubules) and squamosal (ca. 18 tubules), also having pores derived from minor branches across the whole ventral surface. We observe from the x-radiograph (Figure 18A, C) that in each of these ventrally directed canals one to three of them open along its length, and each canal seems to have another pore at its terminus. We believe that tubules cross the suture to open along the dorsal edge of the maxilla as Jarvik shows for *Eusthenopteron* (Jarvik 1980, figure 127), but unlike that genus this phenomenon is restricted to the anteriormost part of the maxilla. In the dorsal two thirds of the lachrymal bone the large tubules are restricted to the anterior part of the bone, those posterior are small and indistinct. These tubules open through pores along their length, and occasionally have small branchlets which also terminate in pores.

In the squamosal, the canal has a subangular flexure forward of its mid-length, the posterior part being upturned. It also has most of its tubules on the ventral side, clustered together and extending down towards the suture of the maxilla and quadratojugal. Those on the anterior half of the bone are more regular in form than those on the posterior half. Dorsal to the canal, tubules are restricted to the part behind the inflection; they are difficult to distinguish, and are anastomosing. This pattern differs from *Eusthenopteron* in which Jarvik (1980, figure 127) has figured groups of tubules on the dorsal side of the canal at both the anterior and posterior ends. Before reaching the posterior edge of the squamosal the canal passes through the inner surface of the bone, and does not have a bony connection with the canal in the preopercular. On the inside of the preopercular is a prominent vertical ridge within which the canal is placed. At its dorsal end the canal in the preopercular opens through a foramen which is directed upwards and, as indicated above, makes no connection in the bone with the canal in the squamosal. Presumably this means that the canal lay in soft tissue underlying the bone, and it accounts for the fact that the course of the canal in this region is not visible on the X-radiograph (Figure 18). Within the preopercular the canal lies towards the anterior edge of the bone, and its tubules all run posteriorly and almost normal to the main tube. There are no tubules in the dorsal third of the bone, showing that the canal embedded in the soft tissue did not open to the surface. The position of the emergence of the lateral line canal from the preopercular indicates that it must have crossed the middle of the quadratojugal unlike *Osteolepis* and *Eusthenopteron* in which it passes behind the bone (Jarvik 1948, 1980, figure 122). Our isolated specimen of quadratojugal has no canal and no tubules (Figure 18C). Consequently the canal must have passed in the soft tissue inside the bone in the manner described above for the posterior bone of the squamosal and dorsal part of the preopercular. On the other hand, the quadratojugal carries no lateral line pores and the X-radiographs show clearly that no canal penetrates the bone. Hence the canal must have passed in soft tissue across the inner face of the bone as it did between the squamosal and the preopercular. By noting the position of the entry of the canal into the mandible, it is possible to demonstrate the course of the canal across the inner face of the quadratojugal. We note in passing, that this arrangement of canals may be a feature of many osteolepiforms in which the laterosensory system is often treated very superficially by indicating that the mandibular canal passed posterior to the quadratojugal, simply because no pores have been found in its surface.

Extrascapulars

Neither of the specimens which have parts of the otico-occipital unit preserved have the

◀ **Figure 12** A–A′, stereo lateral view of the ethmosphenoid unit with the maxilla, palatoquadrate, and mandible in position of ANU 49259. Note the space in the posterodorsal corner of the mandible for the overlap of the quadratojugal when the mouth is completely shut, and note the large overlap of the palatoquadrate into the ethmoid region. B, same specimen but with the mandible removed and showing the arrangement of the internal structures more clearly. C, posterolateral view of the same specimen showing the large scar for the right processus connectens (black arrow), and the partly eroded basipterygoid process (double black arrow). D, antero-dorso-lateral view of the holotype photographed to show the endocranial wall, the suture through the optic foramen, the partly eroded basipterygoid process enclosing the large foramen for the pituitary foramen (arrowed), and the smaller foramen for the opthalmica magna artery (white arrow) anterior to it. E, anterolateral view of ANU 49259 showing the more complete basipterygoid process enclosing only one foramen (arrowed). Presumably it contained both the pituitary vein and ophthalmica magna artery. Scales = 10 mm.

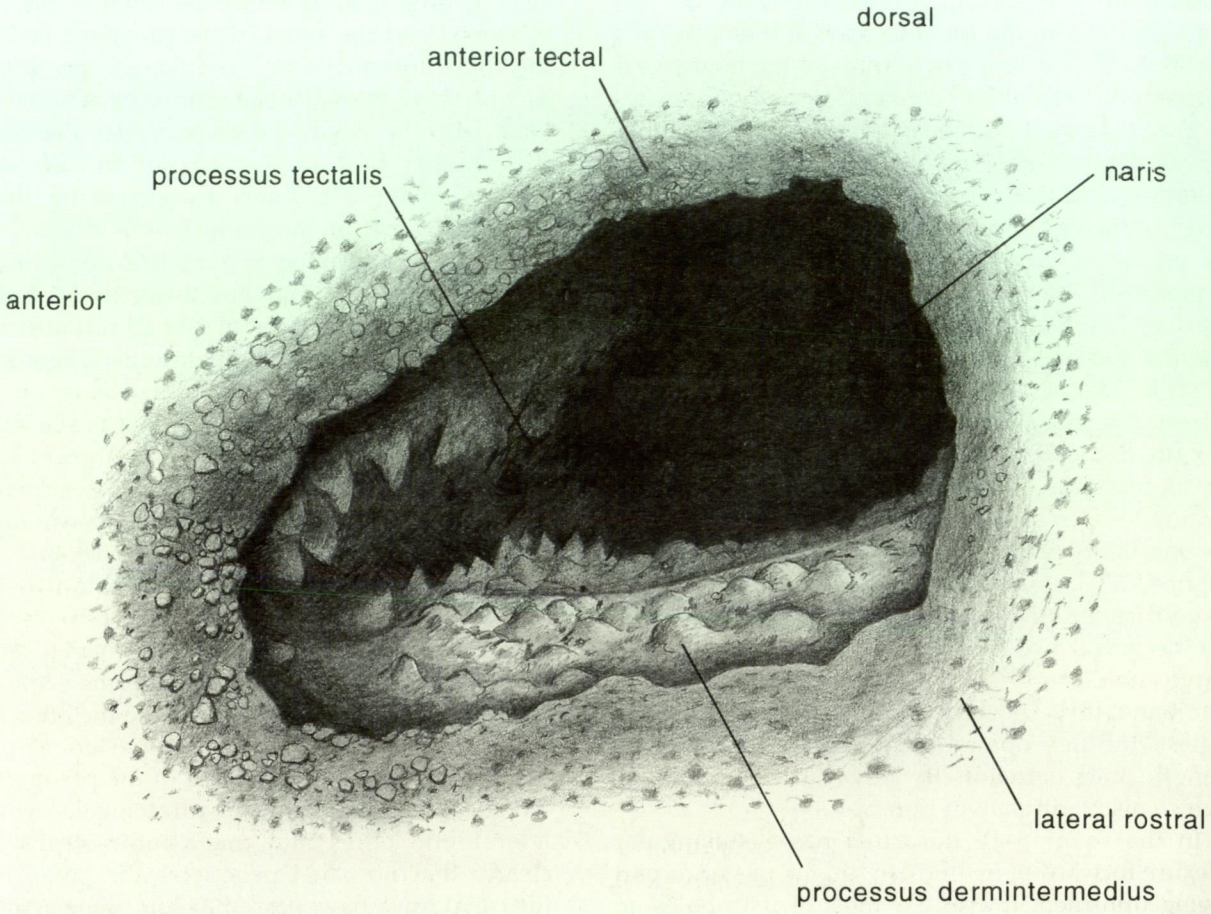


Figure 13 Drawing of the internal view of the left naris of WAM 86.9.661 showing the processus dermintermedius and the processus tectalis.

extrascapulars in position, but part of one of the lateral extrascapulars of WAM 86.9.661 is preserved isolated; it can be restored to its natural position as shown in Figures 11F,G; 15; 16B Both this and the ANU specimen have projections on the postparietals indicating the limits of the median extrascapular (Figures 5D, 14A). From this information it is possible to make a tentative reconstruction of the complete series (Figure 3).

The lateral extrascapular is about 60% the length of the postparietals. It has been identified and oriented by the T-junction and direction of its lateral line canals (Figures 10F, G; 15). Its lateral margin is not preserved, but its mesial and posterior margins are entire, the posterior having a slight angle. The slightly curved mesial margin shows that it overlapped the median extrascapular, a primitive character for crossopterygians (Young *et al.* 1992). Although the lateral margin of the lateral extrascapular is incomplete, the shape of the posterior edge of the extratemporal shows how far laterally the extrascapular extended. The space left for the median extrascapular is very narrow at the front and only twice that at the rear, indicating a narrower anterior margin on the median extrascapular than is found on other osteolepidids (e.g. *Osteolepis, Thursius, Gyroptychius,* Jarvik 1948). Its posterior outline remains unknown, but the posteromesial corner of the lateral extrascapular has a slight angle, indicating the limit of contact with the posterolateral corner of the median extrascapular. From this we have inserted the approximate outline of the bone.

The lateral line canal enters the lateral extrascapular from the tabular at a point well shown in ANU 49259 (Figures 22C; 24), but the tabular on WAM 86.9.661 is poorly preserved, and the fragment cemented into position on the specimen is not precisely placed. Hence the X-radiograph of that specimen is of little use in this respect. Its value lies in the information it gives on the canal within the lateral extrascapular and the arrangement of the tubules extending from it (Figure 16B), as well as the information it provides on the ossification centres of the postparietals and the absence of any lateral lines within them. This information is not available from ANU 49259 because the presence of the endocranium precludes clear X-radiographs of the roof. Surprisingly, given the random distribution of pores on its surface, the tubules are almost all directed posteriorly from the transverse canal, and laterally from the

provided passage for the ganglion for the maxillaris and mandibularis nerves $V_{2,3}$; this notch is adjacent to the large opening for these nerves in the otico-occipital unit. Behind the notch is the short slightly flattened surface which Jarvik termed the paratemporal process. It passes back into a blade-like vertical ridge, the dorsal edge of which curves over in the posterior third to form a thickened, laterally directed flange which curves downwards as a progresively thickened flange to the mandibular articulation. The dorsal edge of this flange carries a number of grooves (Figures 29–30) which give the impression of permitting the passage of vessels or nerves in life. These are vaguely connected ventrally to a long furrow which gradually deepens posteriorly from a point ventral to the paratemporal process and the notch for $V_{2,3}$, from whence it runs parallel with the dorsal edge of the palatoquadrate complex, turning ventrally to the quadrate articulation. Posteriorly, this shallow groove lies in a much broader and deeper notch which in *Eusthenopteron* and in *Medoevia* is referred to by Jarvik (1954, figure 16C) and Lebedev (1995) as a spiraculo-hyomandibular recess. On reconstruction of the best of our specimens it is clear that this is the correct interpretation for *Gogonasus*, and its shape is easily interpreted as corresponding with the high angled bend in the hyomandibular.

Quite clearly the shallow groove in *Gogonasus* lies in the deeper part of this notch and would have carried either a nerve or a vessel that was buried in soft tissue dorsal to the roof of the buccal cavity. It would have supplied tissues between the palatoquadrate and the cheek, as well as the mandible. Its most probable interpretation is that the long groove carried the mandibularis nerve V_3, because it its anterior end lies ventral to the notch for $V_{2,3}$ and it continues down into the mandible across the articulation. In addition there is ample space for the mandibularis V_3 to pass between the palatoquadrate edge behind the notch and the endocranial wall of the otico-occipital unit. This interpretation would also provide an explanation for the grooves running over the top of the palatoquadrate into the adductor mandibulae chamber, because V_3 commonly innervates those muscles. If this is correct, Jarvik's view of the position of the ramus mandibularis in *Eusthenopteron* (1980, figure 129), which shows the nerve passing on the lateral side of the palatoquadrate, is unlikely to be correct. The data on which he based this interpretation is not stated.

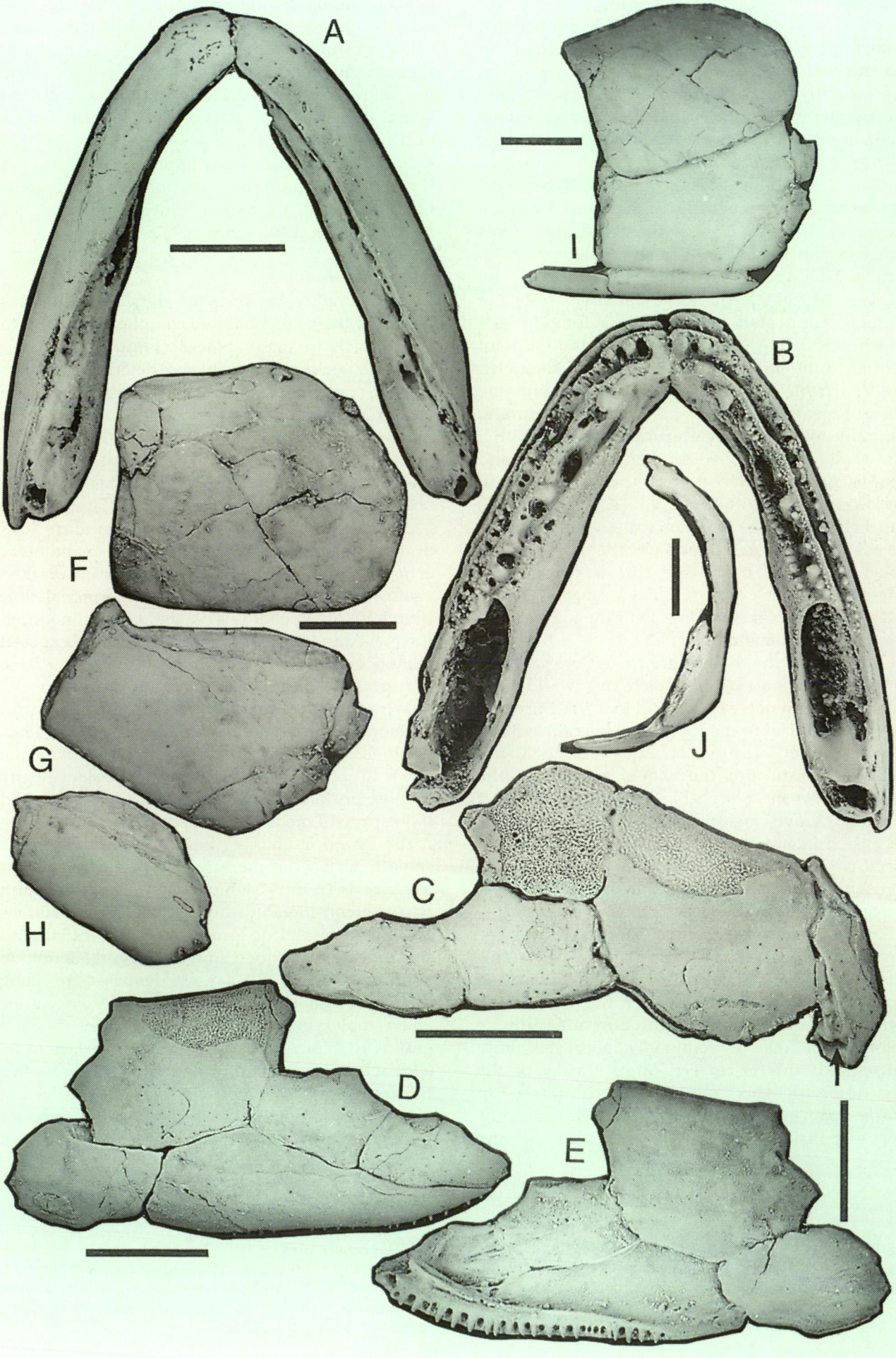
The position of the maxillaris V_2 is obscure. Presumably it passes from the ganglion just outside the foramen in the braincase wall down across the lateral surface of the palatoquadrate, but it does not leave an unambiguously clear mark on that surface. This would be an appropriate course for the nerve judging from its position in modern teleosts and Jarvik's interpretation of *Eusthenopteron* (1980, figure 129).

Entopterygoid

The boundary between the dorsal edge of this bone and the palatoquadrate complex is difficult to distinguish in many places (Figures 29, 30A). However, enough is visible to determine that its anterior extremity lies just ventral to the autopalatine articulation, from whence it runs back horizontally, to the subangular ridge (Figures 30A, 31) which lies just ventral to the dorsal edge of the buccal cavity. Immediately below this ridge the boundary has a distinct indentation (Figures 30A; 31; 32). From this structure the boundary arcs down to a point just anterior to the mandibular articulation. Its ventral edge is sharply marked against the ectopterygoid and the dermopalatine, from both of which it is separated by a pronounced furrow. Although we do not have a clearly exposed section on which to determine if a flange of the entopterygoid extends laterally between the palatoquadrate and the ectopterygoid and dermopalatine as in *Eusthenopteron* (Jarvik 1980, figure 108), enough is exposed at the ends of the bones to show that the flange is not present clearly in those positions in our specimens (Figure 30), and if it is present medially it must be very small.

The anterior end of the entopterygoid has a smooth surface no more than 4–5 mm long at its anterior extremity, which curves upwards and narrows considerably towards the mesial surface of the autopalatine process. The denticulated surface extends farthest forwards anterolaterally to a rounded point. The largest denticles are along the edge of the bone adjacent to the dermopalatine and ectopterygoid (Figures 25B,C). They decrease gradually in size mesially across the surface to an edge where the surface turns upwards. Across this flexure the denticles not only become smaller but also more scattered. From the edge of the adductor gape the denticles decrease posteriorly and

◀ **Figure 16** A, X-radiograph of the otico-occipital of ANU 49259. B, X-radiograph of the posterior roof of the otico-occipital of WAM 86.9.661 showing especially the lateral lines in the lateral extrascapular. C, X-radiograph of the mandible of WAM 86.9.661. Note that the posterior part of the jaw has been destroyed so that it does not show any details of the articular bone. D-E, X-radiographs of the lateral, dorsolateral and ventral views of mandible of ANU 49259. Scales = 10 mm.


A
I
B
F
J
G
H
C
D
E

dorsally, and the area ventral to the sharp flexure has only scattered small denticles.

The entopterygoid of *Gogonasus* is similar in outline to that of *Medoevia*, but that genus lacks the the ridge near the dorsal edge of the buccal cavity, and it has a much more extensive smooth surface anteriorly, and a more strongly denticulated surface on the vertical blade.

Dermopalatine and Ectopterygoid

In palatal view the dermopalatine (Figures 25A–D; 26; 28–32) is clearly sutured against both the ectopterygoid and the entopterygoid. It has a smooth anterior process which protrudes into the open space at the base of the nasal capsule, forming part of the inner edge of the choana (Figures 25A; 26). Laterally it bears a shallow depression into which the flange on the anteromesial face of the maxilla fits, to form the posterior edge of the choana. In transverse section the bone has a high outer ridge and a depressed somewhat concave mesial platform bounded on its inner edge by a faint discontinuous rim. Along the outer ridge there is a series of denticles of various sizes. The largest of these denticles lie along the inner edge of the ridge; these are more in the nature of small teeth because in places an individual tooth has been shed leaving sockets with evidence of radial attachment bone in their bases. Small denticles occur along the remainder of the ridge, the largest patch being between the tusk and the anterior process. In this patch there are denticles of various sizes all mixed up together. The mesial platform of the dermopalatine carries the tusks and adjacent replacement pit which occupy almost the entire surface. So far as we can see no small denticles are present between the tusks.

These are well preserved on the two new specimens (Figures 25A–D, 26, 28–32). As discussed in the previous paragraph, these bones lie in an angle formed on the margin of the palatoquadrate. Their relationships can be observed in lateral view of the palatal complex with the maxilla removed. A high lateral wall is exposed in this aspect, with a longitudinal groove parallel with the upper and lower edges (Figure 25D). Such a groove also occurs in *Eusthenopteron* where it has been identified as the ramus maxillaris V by Jarvik 1980, figure 109). The most dorsal part of the wall is formed of the palatoquadrate which is thick (Figures 25D, 30, 31), and represents a marginal thickening of the pars autopalatina of the palatoquadrate. It is separated from the dermopalatine and the ectopterygoid by a suture that opens up during preparation and must have been weak in the living animal. The most ventral part of this lateral wall is formed of either the dermopalatine or the ectopterygoid, both of which are as thick as the palatoquadrate on this face. They are separated on this face by a zigzag suture (Figure 25D). We are convinced that no part of the entopterygoid is exposed on this face although on ANU49295 (Figure 29B) there is line apparently representing a suture isolating a lenticular bone in the position one might expect to see the endopterygoid if the arrangement is similar to *Eusthenopteron* as figured by Jarvik. However, we consider that the line in question is not a suture because the vertical boundary between the ectopterygoid and the dermopalatine runs across it.

The ectopterygoid is approximately as long as the dermopalatine (Figures 25A–D; 26; 28; 30). In palatal view it tapers to a rounded posterior end, and in transverse section it is almost identical to the dermopalatine. The large denticles on the inner edge of the outer ridge, and the largest patch of denticles is situated posteriorly. The tusks and pits are placed anteriorly on the bone, and on the ANU specimen the left ectopterygoid has a pair of tusks instead of a tusk and adjacent pit (Figures 25A, B).

Opercular series

ANU 49259 has an excellent group of opercular and subopercular bones from the left side in addition to some submandibular plates. We have adopted the view that two suboperculars are present, a view espoused and defended by Fox *et al.* (1995), and we will not reiterate the arguments again here. Our subopercular 2 is referred to by Jarvik (1948; 1980) as the submandibulo-branchiostegal plate.

The opercular (Figures 17F, I; 33) is almost as high as long, its ventral edge almost straight and its posterior edge strongly convex. Its anterior edge in anterior view (Figure 17J) is flexed inwards

◀ **Figure 17** A, B, ventral and dorsal views of the isolated mandible of WAM 86.9.661. C, lateral view of the left cheek of WAM 86.9.661 without the maxilla and the quadratojugal. Note particularly the shape of the preopercular, and the lateral line canal opening through its base (arrowed). D–E, lateral and internal views of the left cheek of WAM 86.9.661 with the maxilla and quadratojugal in place. F–H, opercular, subopercular 1, and subopercular 2 of ANU 49259, oriented in series. I, opercular series and the posterior submandibular to show the extent to which the submandibular 2 is bent beneath the body of the animal. J. Same specimen in anterior view. I and J from ANU 49259. Scales =10 mm.

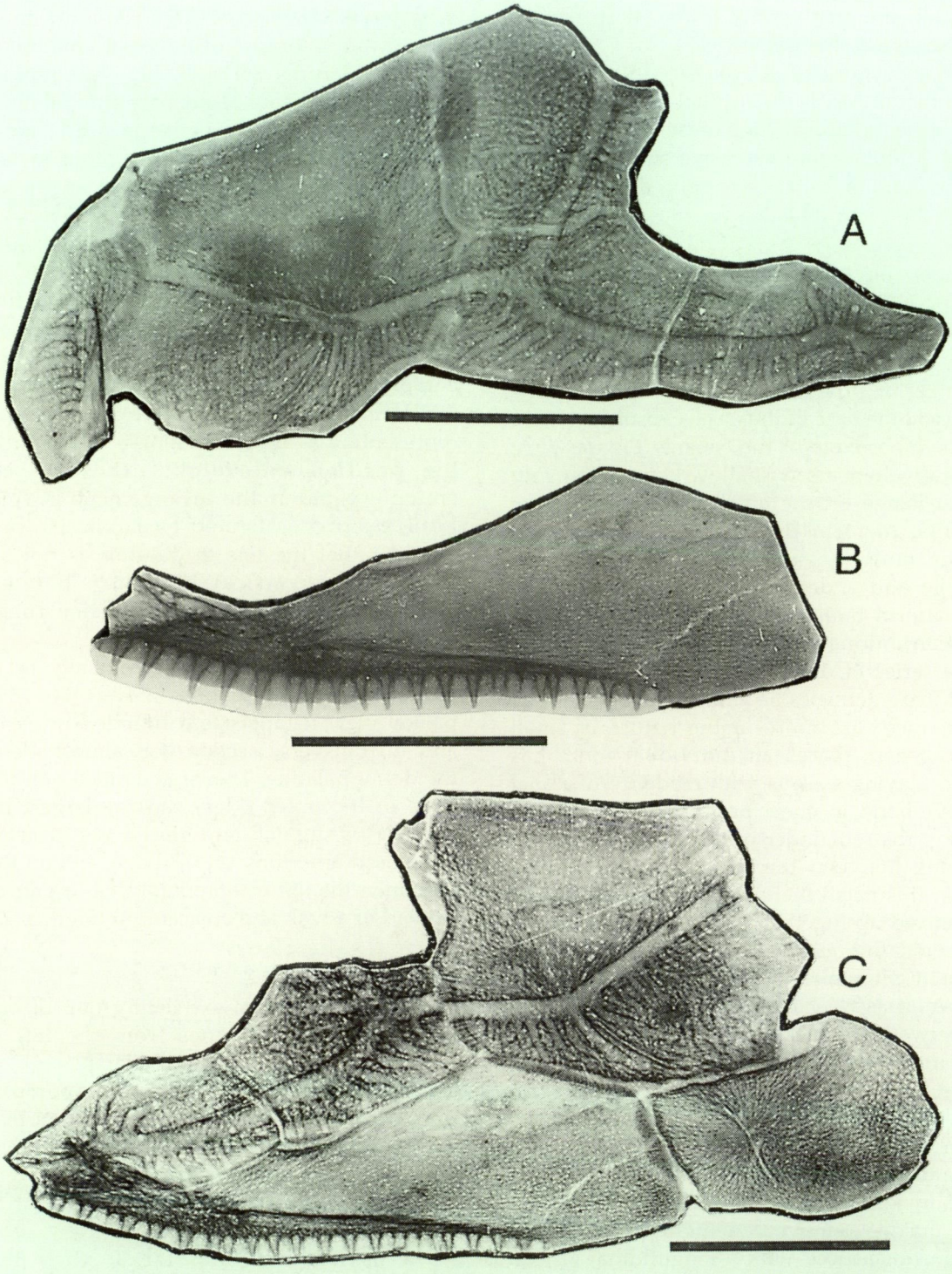


Figure 18 All specimens from WAM 886.9.661. A, radiograph of the left cheek showing the lateral line canals. Note particularly the absence of a connection between the canals in the squamosal and preopercular, and the strong vertical canal in the preopercular. Note also the irregularity of the tubules in the ventral edge of the squamosal. B,C, maxilla and right cheek . This individual has the the maxilla and quadratojugal in place. The squamosal is broken posteriorly. B is shown separately to indicate the process behind the choana. Scales = 10 mm.

dorsally and carries a lenticular overlapped surface ventral to the reflexion. The dorsal edge has an overlapped surface largely occupied by the lateral extrascapular, which is deepest anteriorly and disappears at about half the length of the bone. The anterior end of the internal surface shows a poorly defined circular scar, possibly for insertion of the adductor operculi muscles (Lauder 1980a). A dilator operculi muscle also exists in this region in *Polypterus* (Lauder 1980a, figure 1a). We prefer to interpret the *Gogonasus* scar as an adductor as it lies adjacent to a scar on the hyomandibular to

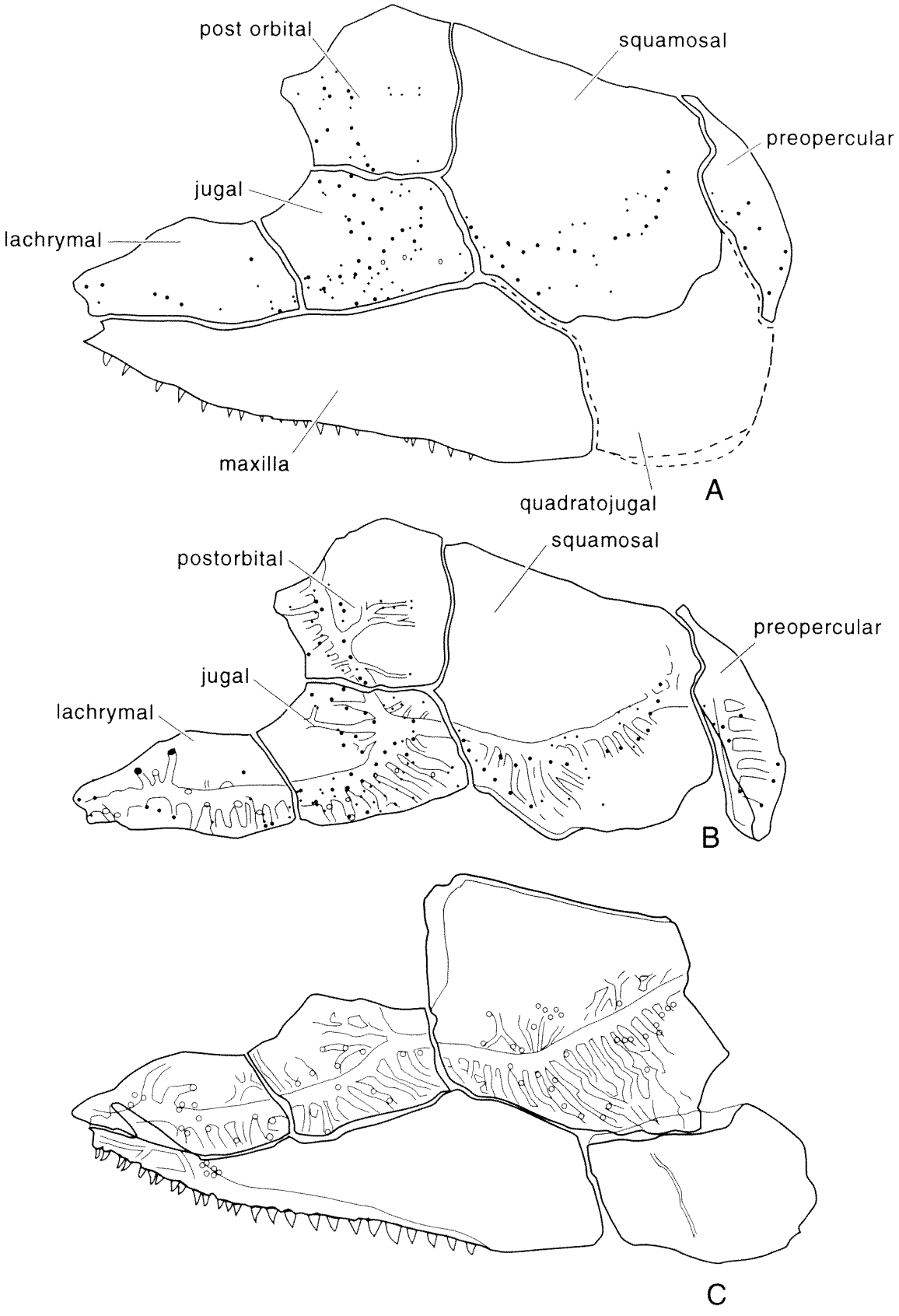


Figure 19 Drawings of the cheek showing the arrangement of the lateral lines and the pores in the cheeks. A, drawing of the cheek plate made up from both sides of WAM 86.9.661. As seen from Figures 17C–E, neither cheek has a full representation of all the bones, and hence Figure 19A is a composite. B, cheek without maxilla and the quadratojugal, drawn from Figure 18A reversed. The lateral lines are drawn from X-radiographs. C, cheek without postorbital and preopercular. Overlaps are shown and the lateral lines are drawn from X-radiographs.

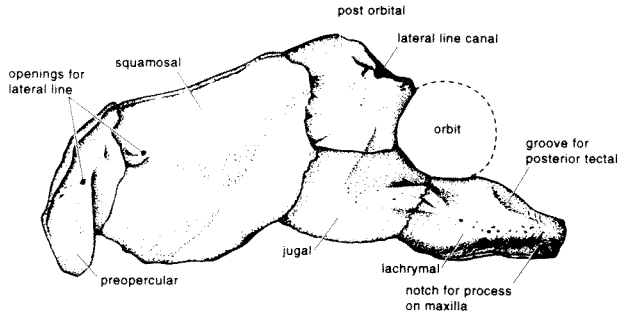


Figure 20 Drawing of the interior view of the left cheek of WAM 86.9.661. Note particularly the strong internal ridge on the preopercular in which the lateral line canal runs (see Figure 18A).

which to which the other end would be attached. Although none of our specimens permits a complete reassembly, it is possible to reconstruct the operculars in relation to the cheek and the roofing bones. This process is helped by the fact that we have the posterior edge of the palatoquadrate down to the mandibular articulation, to provide a guide to the orientation of the edges of the operculars and subopercularis. This reconstruction gives some interesting results. For example, the inwards flexure of the upper part of the opercular lies at about the downward flexure of the palatoquadrate, and this puts the lower edge of subopercular 1 at approximately the level of the jaw articulation. This is very different from the position of that bone in *Medoevia* as reconstructed by Lebedev (1995).

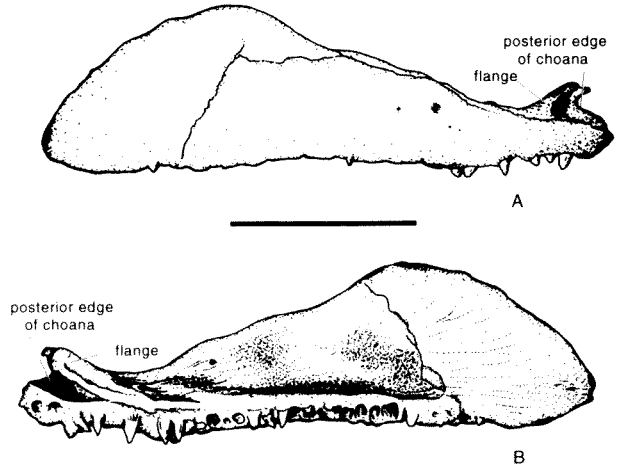


Figure 21 External and internal views of the right maxilla of WAM 86.9.661 showing the anterior process and the teeth. Scale = 10 mm.

Subopercular 1 (Figures 17G; 33) is about three-quarters the area of the opercular. Overall it is much flatter than the opercular, but it does have a slight longitudinal flexure in its posterior third, below which the ventral edge is slightly inturned. It has a straight anterior and an arcuate posterior edge. Its greatest height is posteriorly, where it is about 1.5 times as high as anteriorly. Anterodorsally it has a strong dorsal process, which carries both dorsal and anterior overlapped surfaces; this process is bent up around the edge of the opercular. The dorsal overlap extends the entire length of the bone, decreasing gradually anteriorly and rather more rapidly posteriorly from its highest point. The anterior overlap is narrower and is slightly inturned, and shows no evidence of being overlapped by the preopercular and the lower jaw as does *Osteolepis lepidotus* (Jarvik 1948, figure 24); it extends the entire height of the bone. *Medoevia* has a relatively much longer subopercular 1 as it is represented in Lebedev's (1995, figure 1B). The internal surface has a small ovate scar anterodorsally in about the same position as Lebedev has labelled the pit for contact with the lateral process of ceratohyal 2 in *Medoevia* (Lebedev 1995, figure 12).

Subopercular 2 (Figures 17H, J; 33) is a much smaller bone than the other operculars in all dimensions. Its cosmine-covered surface has parallel dorsal and ventral edges, a straight anterior edge and an arcuate posterior edge. Along the length of the bone just below the dorsal edge of the cosmine, the bone has a slight flexure, its ventral surface turned mesially. The dorsal overlapped surface is relatively larger than the other opercular bones, highest at mid-length, and tapering away completely both anteriorly and posteriorly. The anterior overlapped area, which is covered by the most posterior submandibular, is much smaller, longest dorsally and fading away before reaching the ventral edge of the bone. This surface has a short anteriorly directed process at its dorsal end. Internally the bone has no muscle markings.

The bones of the subopercular series in some other genera have sensory pore groups in their anterodorsal corners (Fox *et al.* 1995). No such clusters have been found on *Gogonasus*.

Gulars

The right principal gular of WAM 86.9.661 (Figures 34 A–B) is preserved complete. As is normal for osteolepiforms, it tapers gradually anteriorly from its widest point at about three quarters of its length from the front, and tapers more rapidly posteriorly. The lateral and posterolateral edges show overlapped surfaces, indicating that they tucked under the edges of the submandibulars and the subopercular 2

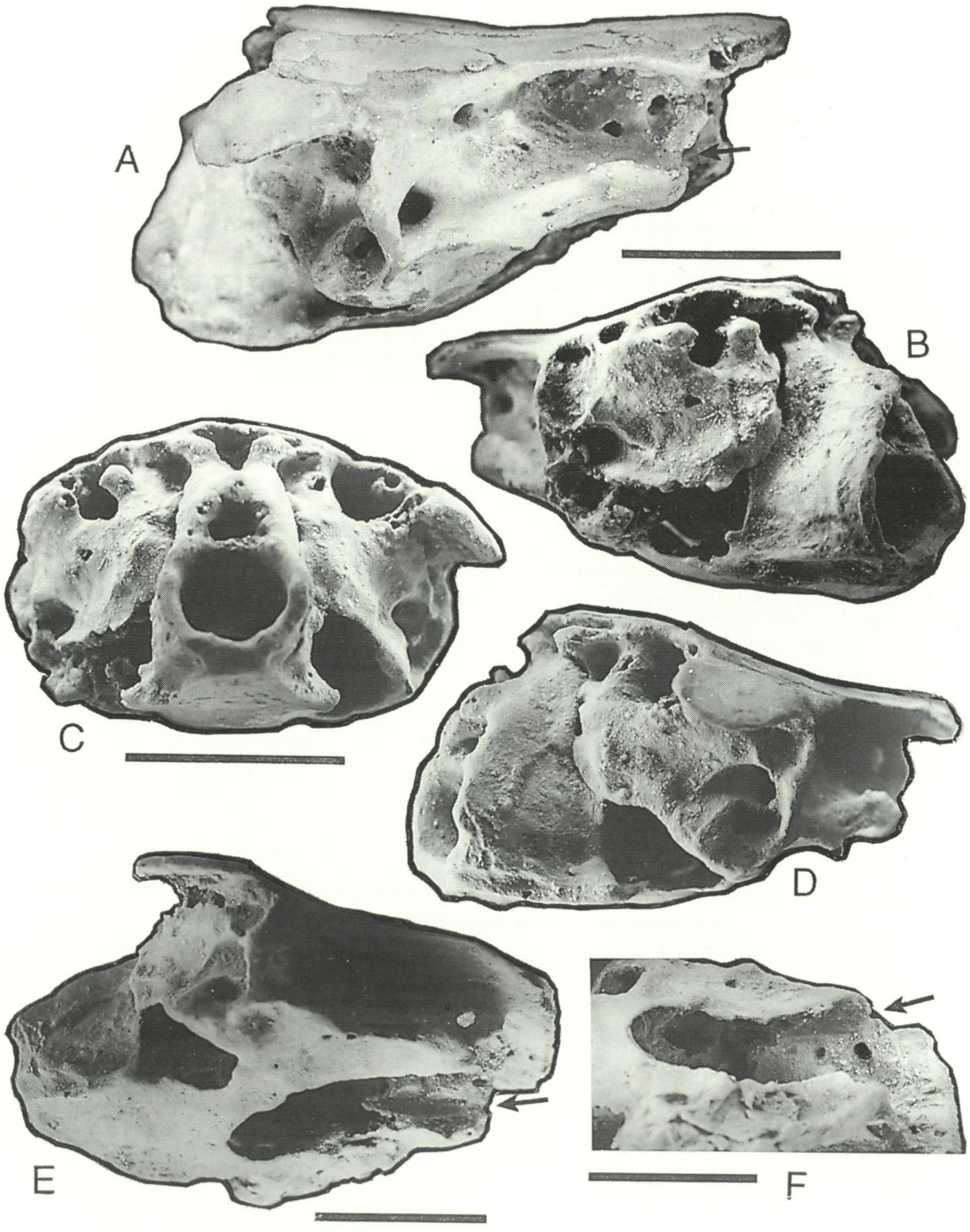


Figure 22 All photographs of the otico-occipital unit of ANU 49259. A, full lateral view (see also Figure 23B). B, left posterior view. C, posterior view (see Figures 23A; 24). D, right posterior view. E, right ventrolateral view. F, ventrolateral view with the specimen turned over, and looking up obliquely into the braincase from the left ventral side. Note particularly the foramen in the wall of the braincase shown in Figures E, F by a black arrow. Scales = 10 mm.

respectively. Anteromedially there is a slightly overlapped edge for the median gular which must have been a small bone, the outline of which we can reconstruct as in Figure 35. The principal gular is covered with a complete sheet of cosmine without Westoll lines. A short pit-line is present laterally about one third of the length of the bone from its anterior end.

Submandibulars

These are not known in position. However, several small plates which are members of this series occur in the etchings. Almost all of them are somewhat longer than wide and occasional ones are three times as long as wide. What we take to be the most anterior plate is tapered anteriorly, indicating that it is not admedial, and that the submandibular series terminated almost in the mid-line, although there is no evidence that they may have met mesially. These bones are not all of uniform length, and one is much larger than the others. We have illustrated some of these bone as photographs and as a reconstruction (Figures 34C,D; 35).

As the part-etched specimen ANU 49259 shows (Figure 34D) a rather larger plate which seems to have the characters of a submandibular, lies towards the back of the specimen. This plate fits well with the subopercular 2 as is shown in (Figure 34D). We consider that it represents the most posterior plate in the submandibular series, implying that the width of the series rapidly increased at that bone. It is similar to the bone in a similar position in *Osteolepis* (Jarvik 1948, figure 24) and in *Medoevia* (Lebedev 1995, figure 7).

Mandible

External Dermal Bones

We have three separate mandibular rami, two from WAM 86.9.661 (length 4.8 mm) and one from ANU 49259 (length 5.3 mm). Those from the WAM specimen are incomplete, but the ANU specimen is probably the best preserved lower jaw of any osteolepiform known. One difficulty with the better WAM specimen is that the dentary became detached from the coronoids during preparation, and it proved difficult to reunite the two parts precisely. This should be taken into account when interpreting the photographs of the specimen (Figures 36G–H). The specimens are remarkably uniform in their characters. The ANU specimen has been figured previously by Fox *et al.* (1995, figure 15A–C).

The height of the ANU specimen (Figure 36 A–E) increases gradually from back to front, but this does not occur on WAM 86.9.661.This is possibly the result of late ontogenetic morphological changes, the ANU specimen being much larger than the WAM specimen. Furthermore, Schultze (1984) suggests in his figures that with increasing growth the shape of the lower jaw's anterior end becomes deeper in *Eusthenopteron*.

The dorsal edge of the surangular (Figure 12A) has a deep embayment in the cosmine cover to accommodate the ventral edge of the quadratojugal on complete closure of the mouth. Immediately forward of that embayment is a much smaller embayment into which the ventral edge of the posterior part of the maxilla fitted on complete closure. A naked blade of surangular surmounts the cosmine in this position. The external dermal bones are covered with cosmine, obliterating the sutures between the bones. The bone pattern does not show up on X-radiographs. Consequently nothing can be said about the dermal bone arrangement. There is, however, an unusual posterior projection on the posterior infradentary that forms a flange inside which the anteroventral corner of the subopercular would have rested.

Neither the horizontal nor the vertical pit-lines are well developed; the ANU specimen shows a discontinuous horizontal line running anteroventrally from about the position where the angular might be expected to terminate posteriorly, and a branch of this line running parallel with the dorsal edge of the cosmine on the surangular. On the same specimen the vertical pit-line is short and slightly convex forwards; in most osteolepiforms it is concave forwards.

The course of the lateral line canal can be traced by the row of small pores that lies close to the ventral edge of the infradentaries, and from X-radiographs of the rami of both new specimens (Figure 16C–F). Anteriorly the line moves away from the ventral edge at a low angle, and it shows a slight flexure approximately in the position of the anterior vertical pit-line; posteriorly it moves upwards towards the entry point behind the glenoid fossa. The ANU specimen shows two large pores along this line, but the WAM specimen shows no sign of these. We do not know how these openings relate to pores inside the mandible. Ahlberg (1991) has illustrated similar pores in Porolepiformes, and Chang (1991) has illustrated pores in *Youngolepis*. Like the posterior pore in *Gogonasus*, those in *Youngolepis* open into a posteroventral groove that extends to the ventral edge of the mandible. Ahlberg (1991, figure 8) has shown specimens of *Holoptychius* and *Powichthys* which also have pores, but those on *Holoptychius* are placed well dorsad to the lateral line canal. He concluded that the infradentary foramina are a synapomorphy of *Youngolepis*, *Powichthys* and Porolepiformes, but that view will have to be considered in the light of the discovery in *Gogonasus*. We are unable to add further to this question for two main reasons – the pores occur in

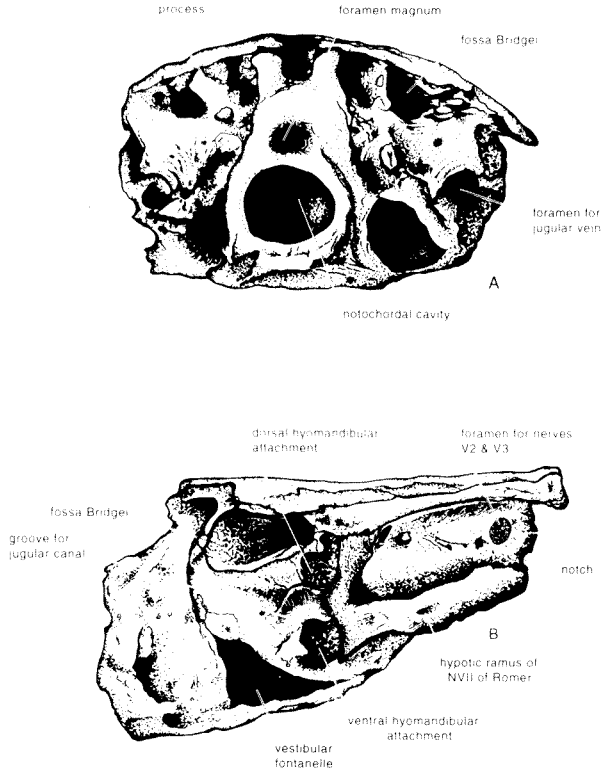


Figure 23 Drawings of the otico-occipital region of ANU 49259. A, posterior view. B, lateral view.

only one of our specimens, and the absence of any knowledge about their internal connections leaves us without any conviction that they are homologous structures in the groups under consideration.

The dentary has teeth reaching posteriorly a short distance behind the anterior edge of the adductor pit (Figure 26), in which region they are very small. Further anteriorly the teeth are larger and of more or less uniform size to a position opposite the anterior coronoid where they increase in size. A very small tooth occurs immediately adjacent to the median symphysis, but the two lateral to that one are the largest in the whole dentary series, being comparable in size with those of coronoid 3.

The closure of the mandible shows the large tusk on coronoid 1 extending up into the space against the anterior end of the pterygoid-dermopalatine complex (Figures 26, 59). It also shows the anterior end of the mandible not reaching the anterior end of the skull.

Internal Dermal Bones

The internal dermal bones are well-known (Figures 36B–E,G,H; 37A,B; 38A,B). The prearticular is highest posteriorly and gradually decreases anteriorly where it is truncated well short of the median symphysis. In WAM 86.9.661, it is 9 mm short of the symphysis, which has a mandibular length of 48 mm. Over its posterior half it carries a shallow longitudinal depression along which the hyoid arch passed. This depression and some of the bone adjacent to it are either smooth, or they carry scattered fine denticles; the remainder of the surface, which must have been exposed in the mouth, is covered with more closely spaced denticles. These are of similar size except at the dorsal margin where there is a row of enlarged denticles which point dorsally or dorsomesially. On WAM 86.9.661 the row of enlarged denticles along the crest of the prearticular is very well developed, and they extend the full length of the bone (Figure 36G,H), unlike in ANU 49259 in which they decrease markedly in size anteriorly. At its anterior extremity, which is blunt and well defined (Figures 36B,D,G,N), the prearticular rests with an abrupt end against Meckelian bone, which will be described in detail below.

In ANU 49259 see nothing comparable with the anterior prearticular process indicated to be present on *Medoevia* by Lebedev (1995, figure 11). The boundary between the prearticular and the Meckelian bone lying in front of it is clearly preserved, and we have no evidence that any part of the prearticular extends forwards on to the Meckelian bone. WAM 86.9.661 has a structure which may be interpreted as a forward extension of the prearticular, but this appearance has not yet been supported. We have also commented on the fact that in *Cladarosymblema* the prearticular did not extend as far forwards as Watson (1926) proposed for *Megalichthys*. The X-radiographs (Figure 16D, E) show clearly that the prearticular has a rather sharp truncated anterior end as we would have expected. It is possible that the prearticular is of variable length anteriorly in different genera, but we suspect that future revisions should take into account the possibility that some bone referred to as prearticular is in fact Meckelian. Dorsally the prearticular is separated from the coronoid series by a sharply defined groove.

Three coronoids are present, separated from each other by zigzag boundaries which are not clear in all positions, and from the dentary by a straight suture that lies at the bottom of a deep smooth-walled groove (Figures 36B,C,G; 37; 38). Each coronoid has a vertical lamina which bears the smaller teeth and denticles. The largest of these are along its mesial margin. Coronoid 3 has a finger-like posterior extension on its inner and outer faces, and these are plastered on to the preaticular and the dentary respectively, within the adductor fossa. Each coronoid has its own tusks and replacement pits. The number of tusks varies from specimen to specimen. For example, coronoid 1 on ANU 49259 has a large tusk in front of the replacement pit and

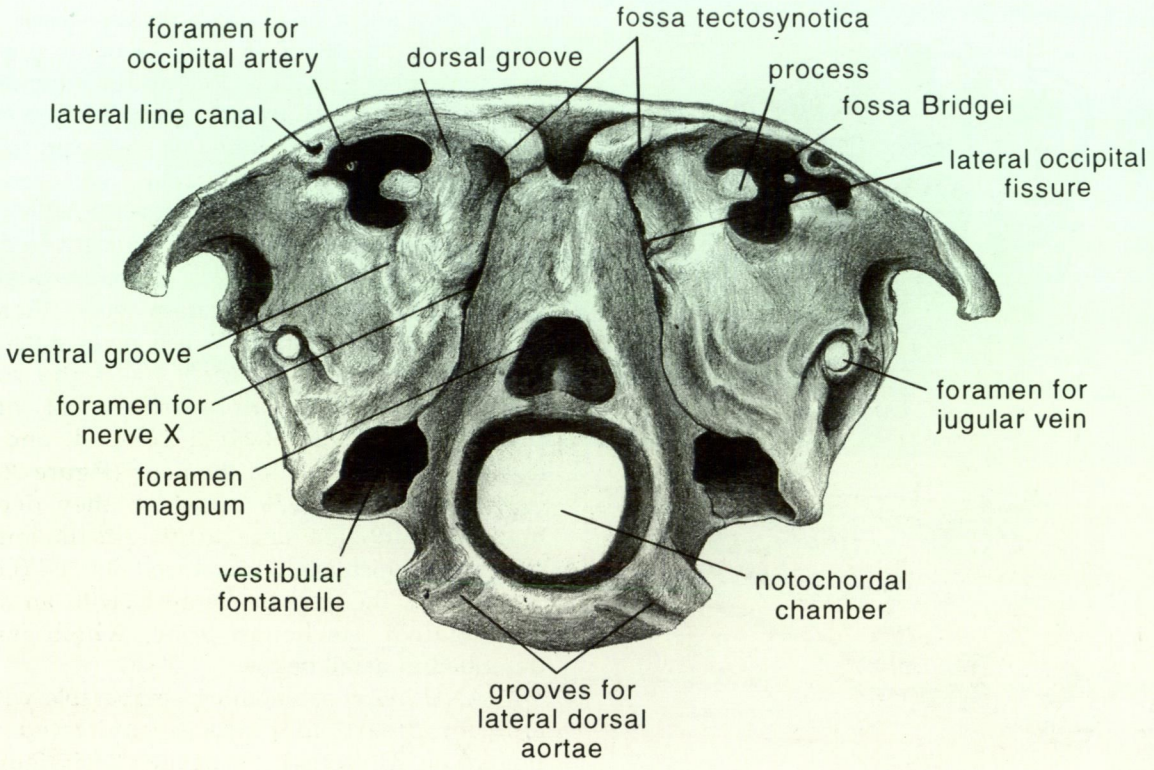


Figure 24 Reconstruction of the posterior view of the otico-occipital unit of ANU 49259.

a smaller one behind the pit, whereas WAM 86.9.661 has only one tusk, and one large and one small replacement pit, on that bone. However, both specimens have a pit and a tusk on coronoid 3, with a group of teeth behind the tusk. This could be a distinctive feature of the species. Along the surface of the coronoids lateral to, and between, the tusks and pits is a mat of denticles. These are largest in the vicinity of the tusks and pits. Those on coronoid 1 form a continuous band with those of the parasymphysial plate. The denticulated surface of the parasymphysial plate extends back almost to the level of the tusk on coronoid 1.

Only the intercoronoid pit between coronoids 1 and 2 is well developed (Figure 36C,D; 37A; 38B). It causes the dorsal edge of the prearticular to be embayed, and its floor exposes a little of the Meckelian bone. The anterior mandibular fossa is not really pit-like.

The parasymphysial plate is defined by a clear suture medially where it lies on the Meckelian bone forming the symphysis (Figures 36B,D; 38B). Laterally its denticulated surface passes into the similar surface of coronoid 1 with only a minor break in ANU 49259, but a slightly more pronounced on in WAM 86.9.661. Posteroventrally a flap of unornamented recessed bone descends against the anterior edge of coronoid 1 from which it is not readily distinguished. As is well seen on the ANU specimen, the denticles on the plate are strongest along the posterolateral edge and are weakest mesially.

Articular and Meckelian Bones

The articular is clearly defined, and has the usual double articulation surface of osteolepiforms. In the adductor fossa the front wall of the articular makes a sloping slightly irregular surface which falls away from the inner surface of the dentary and infradentaries, but is plastered high up on the inner wall of the prearticular. This rugose surface gives indication that it provided the attachment for part of the adductores mandibulae.

The mandible has no unusual development of a retroarticular process as occurs on the articular bone in megalichthyids, instead an almost vertically sloping slight projection extends back from the posterior infradentary for about 1 mm. Its dorsal and posterior surfaces are covered with periosteal bone which shows no sign of being for the articulation of another bone or for the attachment of a ligament or a muscle. On the ventral surface, however, is a thick comma-shaped scar (Figures 36E; 37B; 38A; 39A) formed of vesicular bone surrounded by a thin rim of periosteal bone. The pointed tip of the scar is directed forwards. In general, the scar has a ventromesial aspect, as in *Cladarosymblema* (Fox *et al.* 1995, figures 46D; 47A; 49B,E) where it is labelled "ventral scar". In none of those specimens

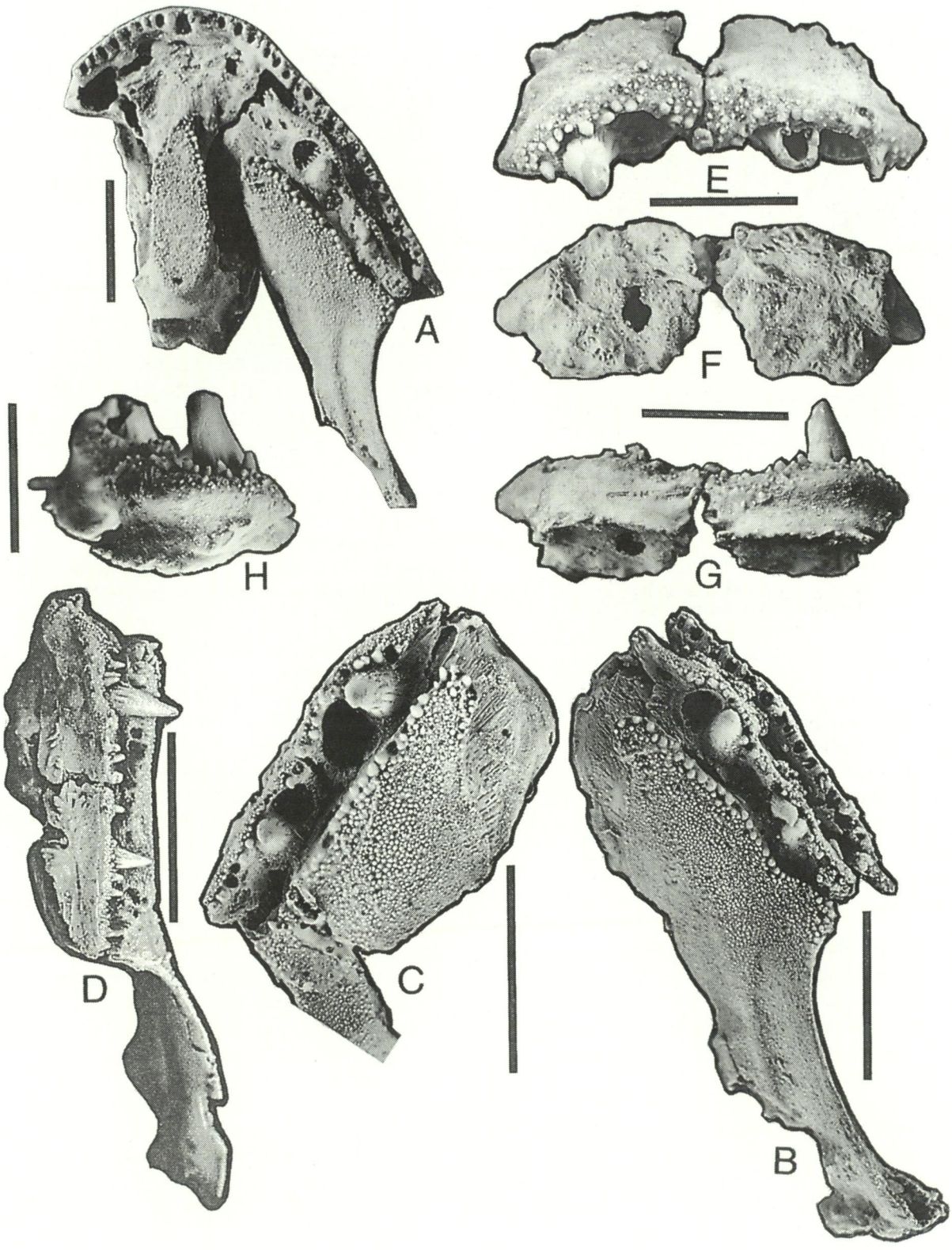


Figure 25 A, ventral view of the palate of WAM 86.9.661 which shows only the left palatoquadrate complex in position. B–C, two partial palatoquadrates, dermopalatine and ectopterygoid of the same specimen, in ventral view. In B part of the maxilla is still attached. D, lateral view of the dermopalatine and ectopterygoid of the right palatoquadrate complex showing details of these two bones. E–H, three views of the paired vomers which have been reunited. E, ventral; F, dorsal; G, anterior; and H, right lateral. Scales = A–D = 10 mm; E–H = 5 mm.

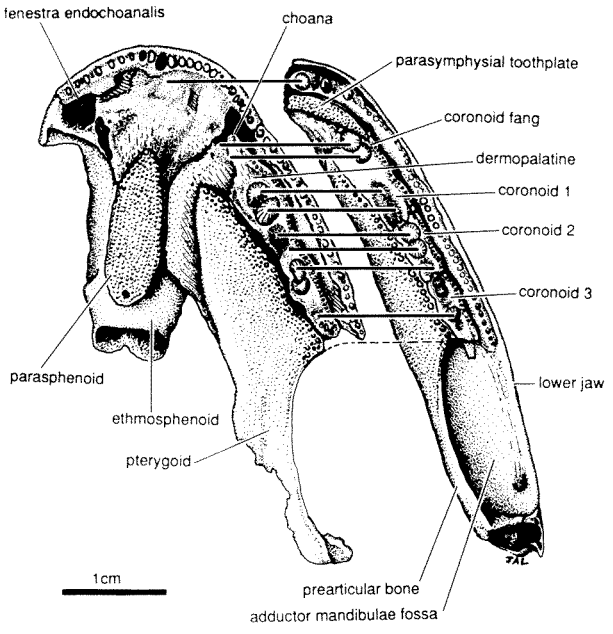


Figure 26 Reconstruction of part of the palatal view of the ethmosphenoid, palatoquadrate complex, and view of the right mandible drawn to show how the various items of the structure should fit together on closure of the jaws. Taken from Long 1988, figure 10.

is it so clearly defined as on *Gogonasus*. Fox *et al.* (1995: 165) concluded that the interpretation of this scar could only be indefinite at this stage of our knowledge, but that it was probably the homologue of the posterior mandibulohyoid ligament in *Latimeria*. In that genus the ligament is attached to the external surface of the mandible. Jarvik (1980) in *Eusthenopteron* and Lebedev (1996) in *Medoevia* both record similar scars, and Lebedev indicates that they may serve as a connection with the tongue-like process on ceratohyal 2. We can make some further suggestions. Its position and orientation indicate that the ligament attached to it was directed ventromesially, which means that its other end must have been attached to an element of the hyobranchial system. Of such elements the ceratohyal is the most likely, although Veran (1981) recorded the presence of a bone between the hyomandibular and the ceratohyal primitively in osteichthyans. Even if it were present in *Gogonasus* it would most probably be too dorsal in position to meet the other end of the ligament in question. Consequently, a mandibulohyoid ligament seems to be the best interpretation. Such a ligament extends from the mandible to either the epihyal or the ceratohyal in primitive actinopterygians and the symplectic in *Latimeria* (Thomson 1967; Lauder 1980b). Its function is considered under Functional Morphology below.

Anteroventral from this comma-shaped scar the surface of the Meckelian bone shows evidence of attachment of muscles as shown on *Cladarosymblema* (Fox *et al.* 1995, figure 46D). In *Gogonasus* it is a much longer scar, and continues along the thin layer of Meckelian bone to the anterior end of the prearticular (Figures 36E; 38A). The lenticular scar in *Cladarosymblema* has been interpreted as attachment for the posterior intermandibularis muscles, but the present species gives no indication of division into anterior and posterior scars, and we conclude that the attachment for the intermandibularis muscles was long and continuous.

Between the front of the prearticular and the median symphysis a wider strip of Meckelian bone is exposed (Figures 36D,H; 38A,B). Dorsally it is bound by the coronoid 1 and the parasymphysial plate. It forms much of the dorsal part of the symphysis. The inner surface of this bone is crossed by a slight ridge which separates off a smooth anterior patch and a dendritically marked posterodorsal patch. These two surfaces and the ridge are comparable with areas defined on *Cladarosymblema* by Fox *et al.* (1995), and interpreted as being for the coracomandibularis and genioglossus muscles respectively (Figure 38B).

We note that the tusks on coronoid 1 are situated much further forward than those on *Cladarosymblema*, and no gap appears between them and the parasymphysial plate. Thus there is no space available for an anterior mandibular (precoronoid) fossa. The tusks on the vomers were not sufficiently long to require special accommodation on occlusion with the mandible.

Vascularisation and Innervation of the Mandible

The mandible shows a clear set of foramina (Figures 36B,D,E; 38; 39). The entry point of the lateral line canal is at the posterodorsal extremity of the ramus, apparently at the junction between the surangular and the articular. The canal runs anteroventrally, parallel with the ventral edge of

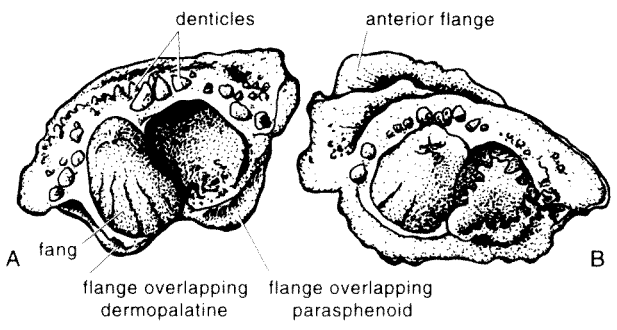


Figure 27 Vomers of ANU 49259, drawn in ventral view.

the jaw. An anterior foramen for the canal is approximately half way up the median symphysis.

Between the surangular and the articular, immediately in front of the glenoid fossa, is a large foramen which opens into a short tube that exits near the posterodorsal end of the adductor fossa. This was for the dorsal mandibularis externus VII nerve. As it enters the foramen it sends two short vertical tubes downwards into the boundary between the surangular and the articular. Internally, it enters a short tube that runs anteroventrally and opens into a foramen in the lateral wall of the adductor pit. On the internal moulds, and on the X-radiographs, this groove and the one beneath it (mentioned below) run along the ventral edges of the denticulated surface (Figure 39). So far as we can observe, they seem to be continuous to the anterior extremity of the mandible. There are no other foramina along the dorsal edge of the ramus.

On the ventral side, near the anterior end of the comma-shaped scar mentioned above, are two more foramina – a lateral one between the surangular and the articular, and a mesial one between the prearticular and the articular (Figures 36E; 37B; 38A). The lateral one opens into a tube that runs directly forwards to exit into the adductor fossa against the surangular below the foramen for the mandibularis externus VII mentioned above. We consider that this was for the ventral branch of the mandibularis externus VII. The internal foramen does not open to any foramen on the inside of the adductor fossa in ANU 49259, but in WAM 86.9.661, because the inner surface of the adductor fossa is broken, it is possible to show that it opens into a narrow tube that runs along the inner face of the prearticular and is covered by the inner wall of the adductor fossa. Anteriorly, it opens into a concealed canal that can be traced forwards in the bone on the X-radiographs. It was presumably for the mandibularis internus VII. We note that the mandibularis internus ran along the internal surface of the adductor fossa in *Cladarosymblema*, and it seems that it had the same course in *Gogonasus*. The courses of all these structures are outlined in Figures 16D,E; 37;38A.

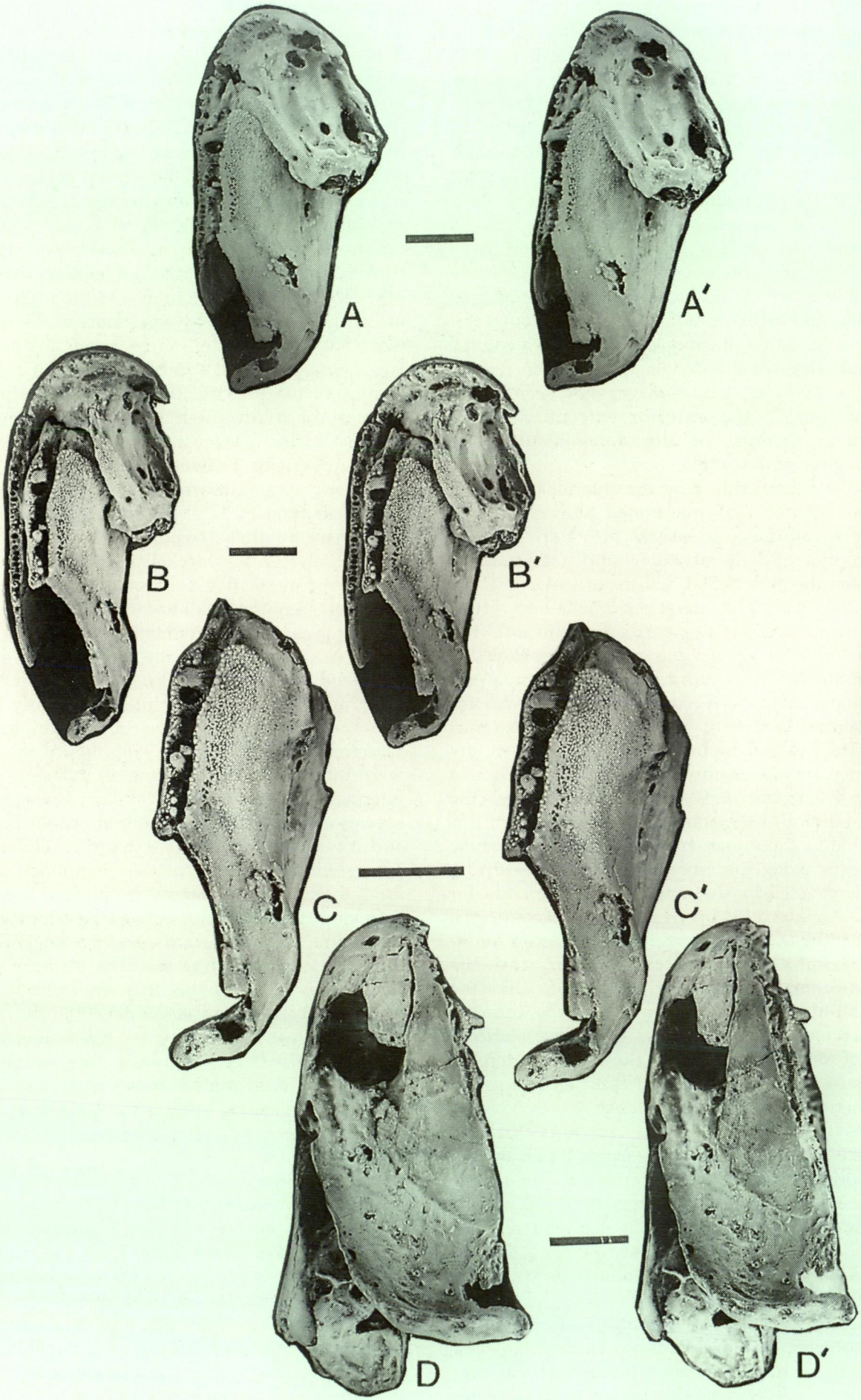
This analysis does not account for the mandibularis V; we can only assume that it entered the adductor fossa dorsally, embedded in muscle tissue. It leaves no mark on the bone.

Along the ventral edge of the mandible of ANU 49259, in the submandibular furrow, several foramina lie along the boundary between the infradentaries and the Meckelian bone, and on the Meckelian bone itself. In the same vertical plane as the anterior end of coronoid 2, there are two foramina in much the same position as the large foramen in *Cladarosymblema*, which was interpreted as carrying a branch of the epibranchial artery and an extension of the intermandibularis nerve V. The X-radiographs show that vertical tubes run vertically from these foramina, and apparently reach the horizontal tube immediately beneath the row of denticles (Figure 16C–E; 39A). Presumably, because this horizontal tube carries the mandibularis VII nerve, the ventral nerves joining it presumably must be for carriage of nerves also. Presumably our estimation that they were the intermandibularis nerves in *Cladarosymblema* was probably correct. The other suggestion that they may also have carried a branch of the epibranchial artery, maybe correct because some of the tubules also show a tendency to branch dorsally, suggesting a ventral source, rather than a dorsal source, of the material they contained. Although we cannot distinguish grooves entering this foramen as in *Cladarosymblema*, we consider that the similarities between the two genera are sufficiently close to warrant a similar interpretation of the foramina.

Anterior to these two large foramina in the groove between the Meckelian and dermal bones, there are four or five very small foramina. These foramina seem too small to carry nerves, but the X-radiographs show a number of unusually large canals extending up into the symphysial region of the mandible (Figure 16D,E). These are complex in their arrangement, branching frequently. They correspond with the tubules in the symphysis of *Cladarosymblema* (Fox *et al.* 1995, figure 58) which were interpreted at that time as branches of the intermandibularis and mandibularis nerves. In that species only a few small foramina could be seen, and it was thought possible that the tubules were extensions of the two nerves mentioned above. From the branching patterns in this new species, it seems most likely that they were developing from the ventral source upwards, and this suggests that they contained blood vessels. The diameter of the foramina is so small that they are unlikely to be nerves, and we now consider that they were branches of an artery – presumably the epibranchial artery. Obviously this cannot be a completely determined answer because of the shortage of material, but it is the best one available at present.

Shoulder girdle

From WAM 86.9.661 we have two well preserved clavicles, the left one of which is almost complete (Figures 40, 41). The bone is long and blade-like with a straight edge against the branchial lamina, two straight posterior edges against the cleithrum, and a straight medial edge, possibly against an interclavicle. The external surface is largely formed of exposed bone without a cosmine cover, but its posteromesial surface is cosmine bearing and


A
A′
B
B′
C
C′
D
D′

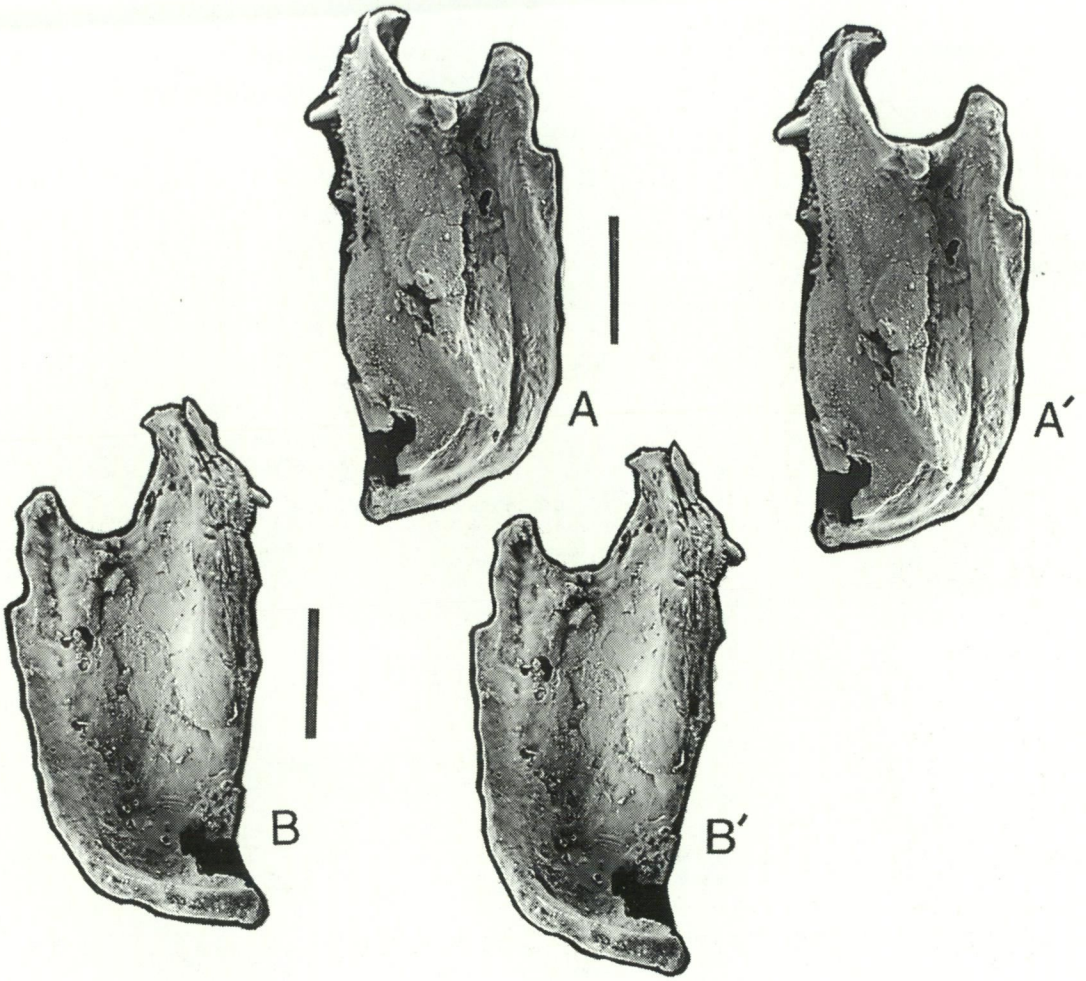


Figure 29 Right palatoquadrate complex of ANU 49259. A–A′, stereopair of inner aspect of palatoquadrate complex. Note particularly the longitudinal groove running along the surface dorsal to the denticulated surface, and bending down to the mandibular articulation. B–B′, external surface of same. The dermopalatine and ectopterygoid are well displayed. For interpretation see Figure 30. Scales = 10 mm.

carries Westoll lines. The exposed bone is sculptured not with superimposed ridges and tubercles, as was the case with *Medoevia* or *Cladarosymblema*, but simply with the highly patterned fibrous texture of the bone after the cosmine has been removed.

The contact with the cleithrum is not simple. Dorsally the cleithrum overlaps it in a narrow band, but ventrally this band is flexed inwards and the overlap relationships are reversed. The lamina marking the inner edge of the overlaps disappears near the point where the two straight edges marking the posteromesial margins of the bone meet, but we suspect that the cleithrum continued beyond this point. Only the base of the ascending process is preserved, so we have no idea of its length. The posterior edge of the clavicle bears a smooth flange for overlap of the ventral scales (Figures 40C,F; 41A).

The anterior edge of the bone is turned inwards over a sharp but rounded zone, to form a narrow branchial lamina. This is deepest where it meets the cleithrum and fades gradually anteriorly.

◀ **Figure 28** Views of ANU 49259. A′–A′, B′–B′, oblique ventral stereo-pairs of the ethmosphenoid unit with the palatoquadrate complex and right maxilla attached. Photographed at slightly different angles, and with different illuminations. C–C′, stereo-pair of the right palatoquadrate complex with the dermopalatine and ectopterygoid still attached. Note particularly the strong ridge that marks both the floor of the groove in which the hyomandibular lay and the curve arching to define the roof of the posterior part of the buccal cavity. D–D′, stereo-pair of skull with maxilla, right palatoquadrate complex, and otico-occipital parts in position. Scales = 10 mm.

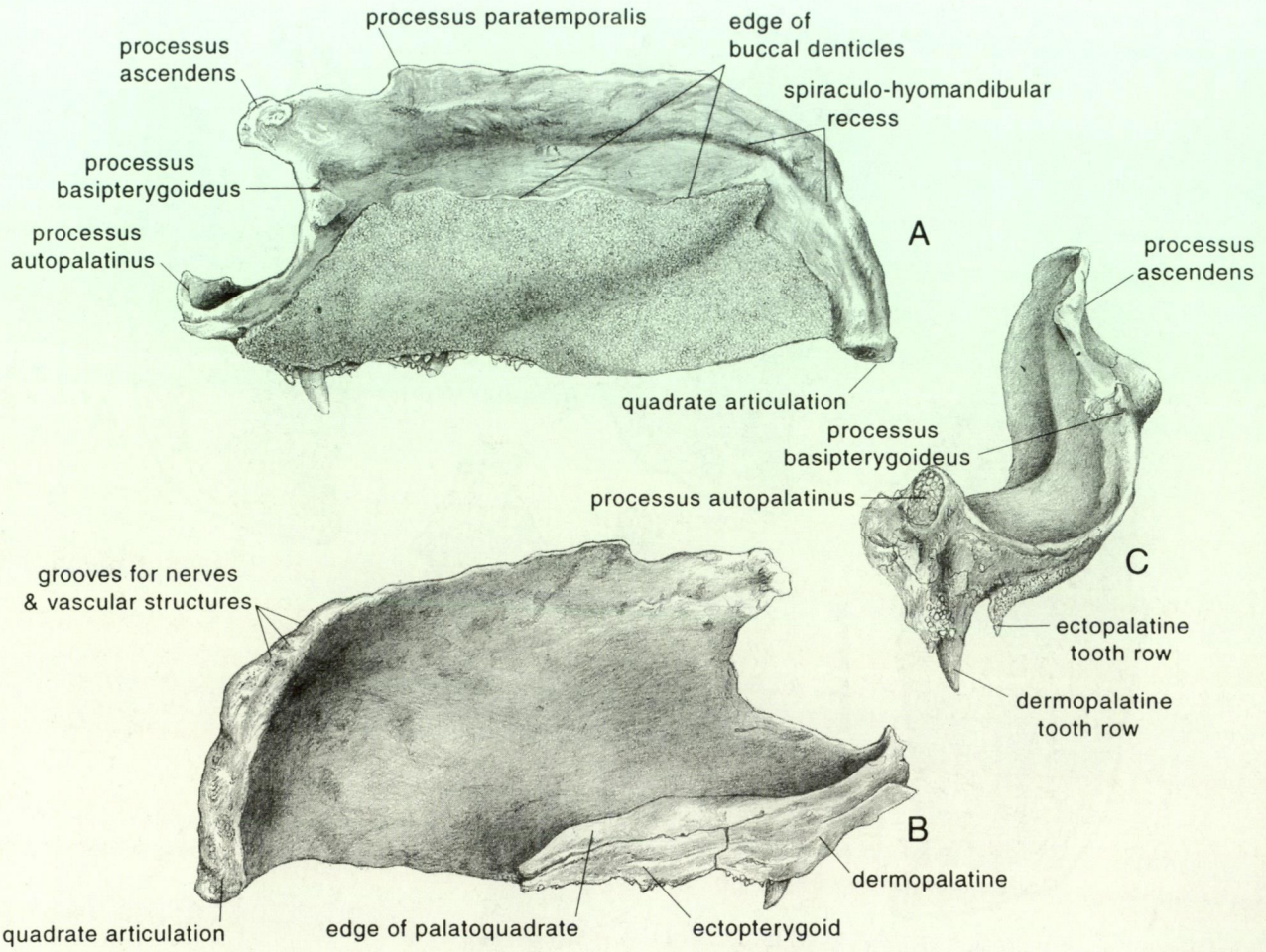


Figure 30 ANU 49259, palatoquadrate complex. A, mesial. B, lateral and C, anterior views. An isolated palatoquadrate complex with the ectopterygoid and dermopalatine attached.

Endocranium of the ethmosphenoid unit

Gross Features

This structure is well-preserved in all three specimens, the holotype having been described by Long (1985a).

The braincase lies close up to the skull roof, the endocranial bone lying against the dermal bone without any intervening septum. Ventrally it is connected to the parasphenoid by a high, thin crista suspendens, except posteriorly where thick bone separates it from the notochordal pit. The lateral walls of the braincase dorsal to the notochordal pit are thickened, and the posterior edge is rounded forming a prominent ridge that is slightly inclined forwards dorsally (Figures 2A; 6E; 10A, B). The ventral extremity of this ridge is occupied by the processus connectens; this is a large rounded surface formed of vesicular bone directed posteroventrally and laterally. This is best preserved on the holotype (Figures 6E; 10D), though on the other specimens relics of the vesicular surface are preserved in part (e.g. Figure 7C). Between these, the base of the braincase and the roof of the notochordal pit has a distinct notch (Figure 7C) which was probably for a median ligament. We note that Lebedev (1995, figure 2D) figured a similar pit in *Medoevia*, but he made no comment on its significance. Dorsally the posterior edge of the ridge thickens and joins its counterpart from the other side to form a bar of bone across the top of the braincase. This bar is well preserved only on the holotype. Its dorsal surface slopes forward to provide a platform to which the postparietals of the otico-occipital unit were applied. This bar defines the dorsal edge of the cranial opening, which is an ellipse with the vertical axis about twice as long as the horizontal.

Brain Cavity

The sediment filling the brain cavity has been removed in the holotype and the ANU specimen, but in WAM 86.9.661 it has been replaced by siliceous material that obscures the walls. Looking into the braincase from the posterior it is possible to discover several points of interest. The floor of the braincase rises sharply above the notochordal pit. In front of this it forms a narrow short

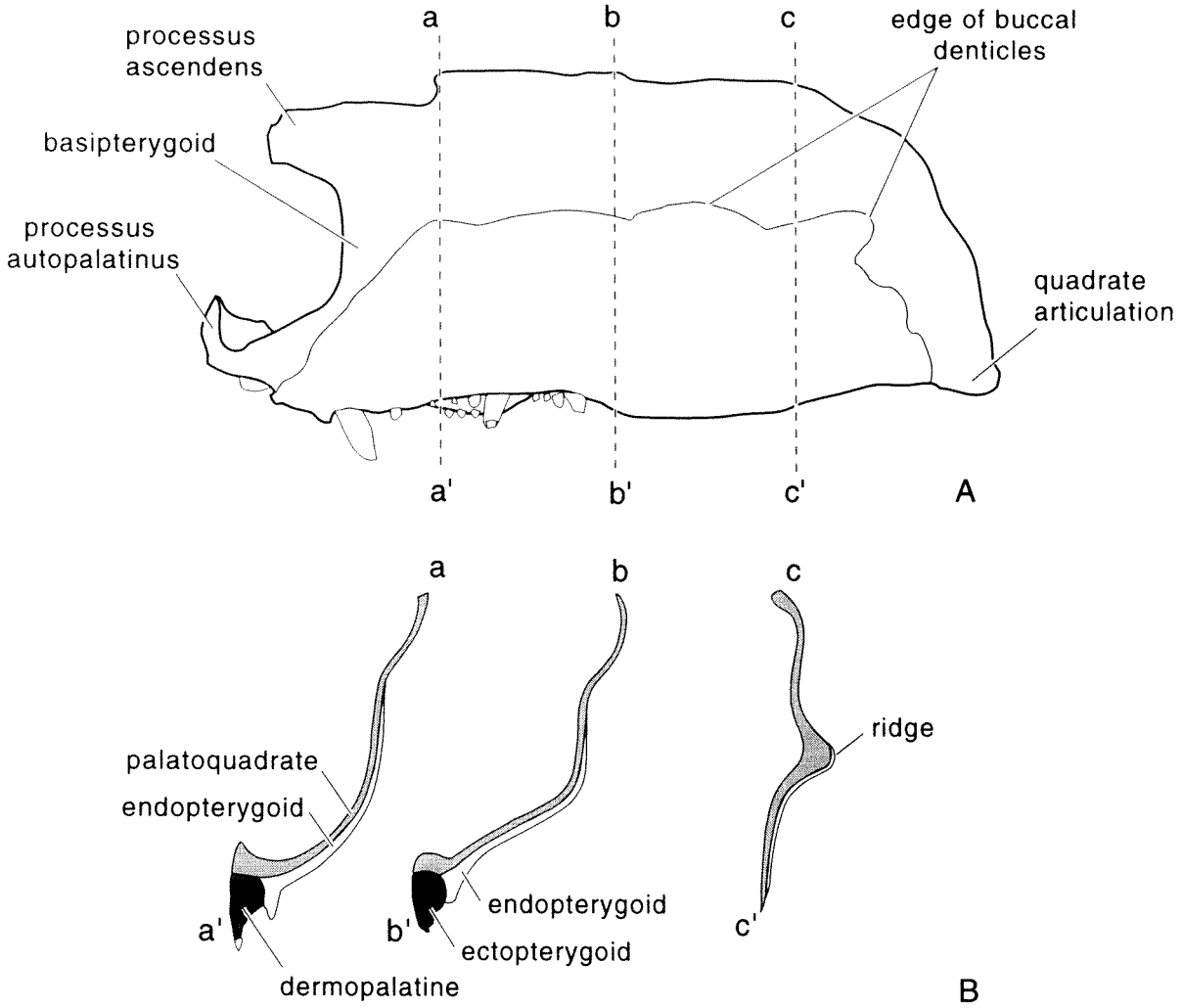


Figure 31 Views of vertical sections across the palatoquadrate complex of ANU 49259 shown in the positions a,b,c on the figure at the top. Note in particular that the cross sections show the change in outline of the large ridge that protrudes across the roof of the mouth.

depression which is the top of the hypophysial fossa. Other details of the walls of the hypophysis are not distinguishable because presumably it widens out at a lower level. However, it is possible to determine that the hypophysial stalk is directed anteroventrally, rather than ventrally as in *Eusthenopteron*, that the pituitary vein passes dorsolaterally from a position low in the hypophysial fossa to open into the cavity demarcated by the inner edge of basipterygoid process as in *Eusthenopteron* (Figures 12C–E); that the small tube for the ophthalmica magna artery opens to the exterior anterior to the pituitary vein; and that the internal corotid artery passes directly laterally to open either through the lateral wall of the parasphenoid, or at the parasphenoid/endocranial suture (Figure 11C). The external openings of these vessels will be discussed below in relation to the basipterygoid process.

The pineal stalk rises out of the roof of the braincase behind the vertical plane containing the nerve II foramina. It seems to be thick at its base and tapers to the dermal roof. This places it more posteriorly than the stalk in *Eusthenopteron*.

As was shown by the X-radiograph of Long (1985a, figure 6) the braincase divides to produce the olfactory tracts at about the mid-length of the ethmosphenoid unit. There is little swelling for the telencephalon.

Lateral Wall of the Braincase

As is normal for osteolepiforms, nerve II exits the braincase laterally immediately forward of the hypophysis. Long (1985a) described a suture running through the optic nerve foramen of the holotype which he suggested divided the unit into discrete ethmoid and sphenoid divisions. This suture can be clearly seen in the new specimens, having exactly the same orientation. Such a suture has not yet been observed in any other sarcopterygian. We suggest that this may possibly be due to the excellent preservation of the Gogo

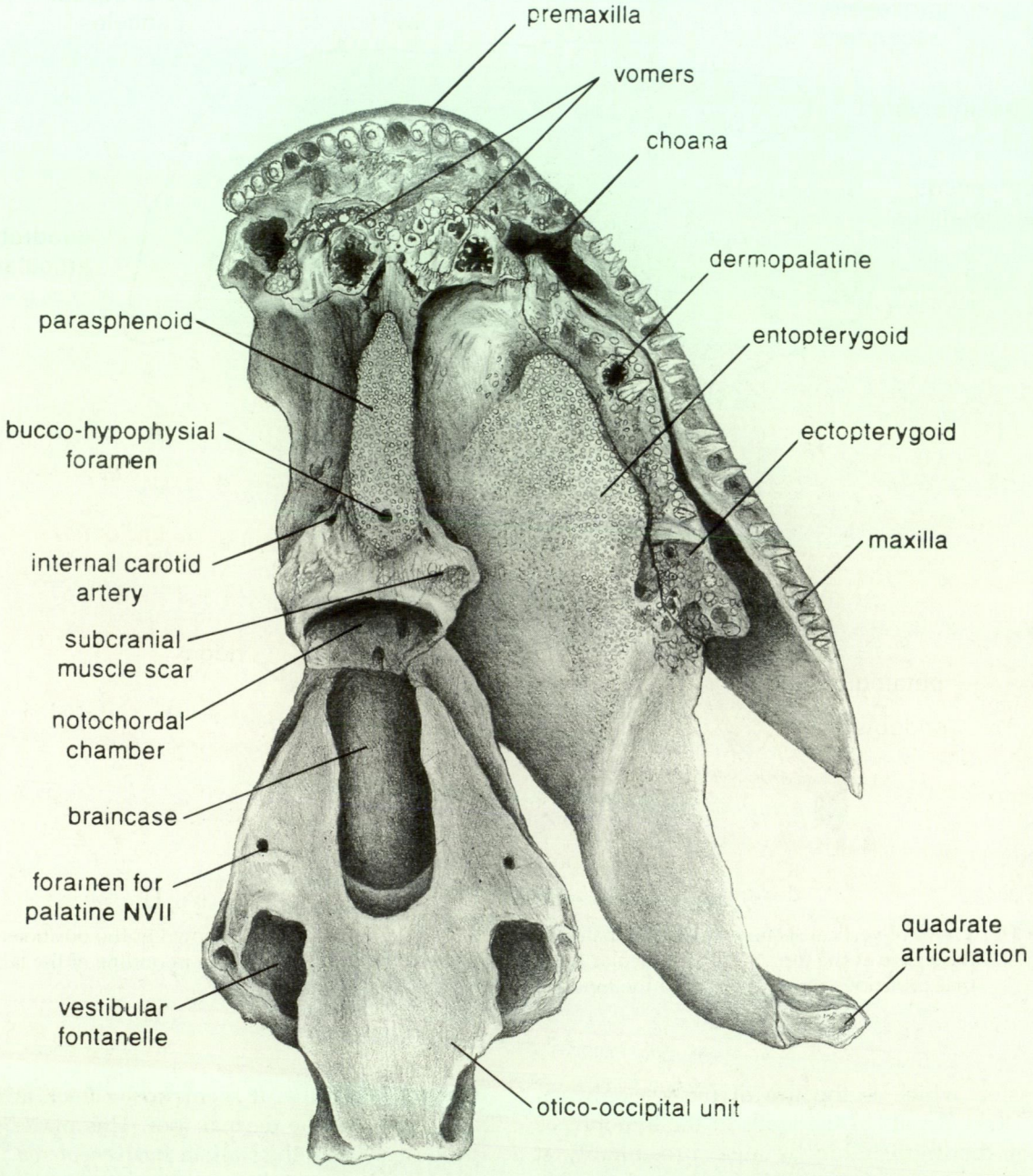


Figure 32 Labelled reconstruction of ANU 49259, reconstructed as an almost complete specimen.

material, and might predict its future discovery in other osteolepiforms. Alternatively, it may be an ontogenetic feature that disappears at a later stage of growth. It possibly follows the anterior margin of the embryonic pila antotica, thus dividing the ethmosphenoid into two entities, one a posterior unit comprising the orbital cartilages and pila antotica, the other an anterior unit comprising the trabeculae and nasal capsules (Schaeffer 1968, figure 4). However, it can be distinguished just behind nerve II foramen on the right side of all three specimens, and the left of ANU 49259 and WAM 86.9.661. Its opening into the braincase is not apparent (Figures 5C; 6E; 10D; 11B). The external foramen for nerve III is small, and requires good preparation to become visible.

The foramen for the internal carotid artery is well represented on all three specimens (Figures 5C; 6E; 11A–C). It is situated near the anteroventral edge of the basioccipital process, and on or near the suture between the parasphenoid and the endocranium. The foramen opens into a tube that runs directly inwards and slightly posteriorly, and must enter the hypophysial pouch anteroventral to the pituitary vein.

High on the external wall of the braincase directly above the nerve II foramen, in a region that is not usually well preserved, are one or two

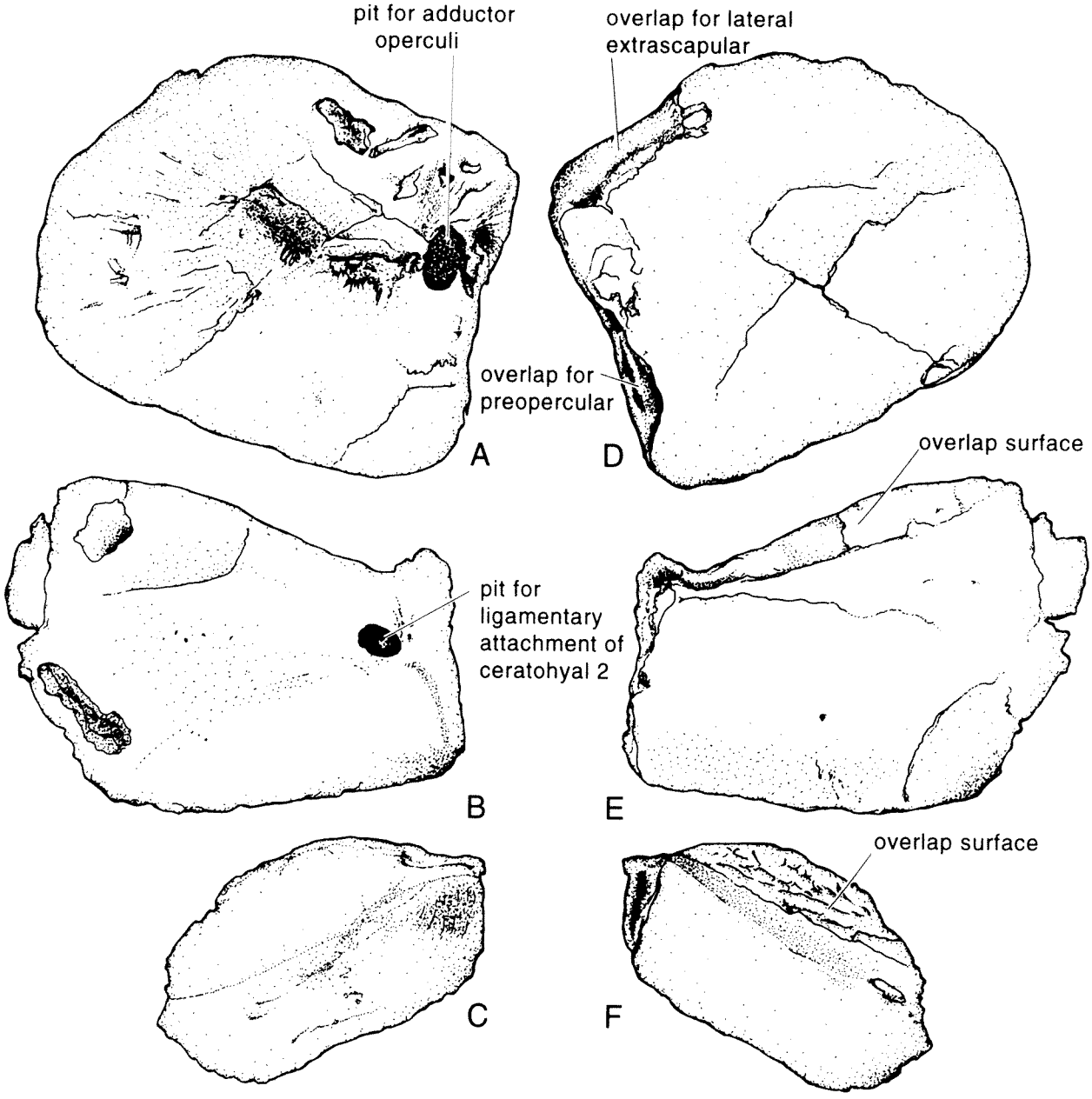


Figure 33 Mesial and lateral view of the opercular series of ANU 49259. The specimens are all drawn as though they were flat. In fact they are all curved as is shown on Figure 17I,J. A,B,C are internal views. D,E,F are external views.

very small foramina which presumably were for nerve IV. In the holotype, in front of this foramen, is a myodome, presumably for the superior rectus muscle (Long 1985, figure 3).

The olfactory tracts show up as swellings half way up the lateral walls of the braincase (Figures 5B,C; 6G; 11B). Naturally they extend forwards to form part of the postnasal wall, which is best preserved in detail on the holotype. Immediately anterior to the large optic nerve foramen there is a small circular ridge of bone which may be for an eyestalk (clearly seen in Figures 5C; 6C, 10A). High on this wall are two foramina. The lower one opens into a short tube that extends into the posterodorsal wall of the nasal capsule. This carried the profundus V. The upper foramen, which lies close to the dermal roofing bones, opens into the space above the nasal capsule, a space that is occupied by numerous bone trabeculae and a number of tubules. This foramen provided passage for the ophthalmicus superficialis VII.

Ventral Endocranium

We now describe the ventral part of the endocranium, from posterior to anterior.

The thickened endocranium lateral to the notochordal pit has muscle attachment scars which vary in strength across the three specimens. The

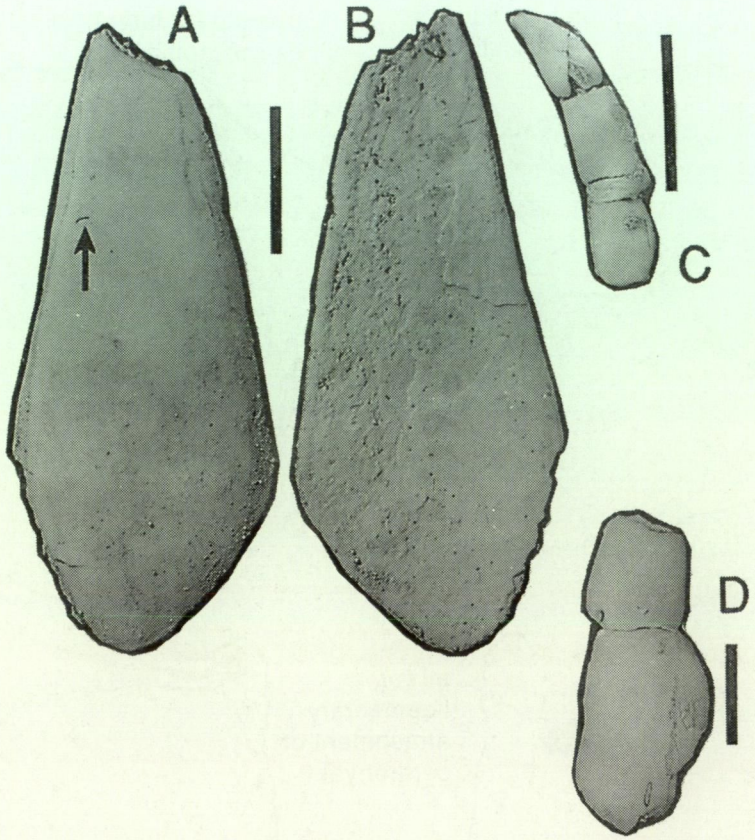


Figure 34 A–B, an isolated gular from WAM 86.9.661 in ventral and internal views. C, part of the anterior set of submandibular plates of ANU 49259 found seperately in the etchings and subsequently reassembled. D, subopercular 2 and the most posterior parts of the submandibular plates of the same specimen in ventral view. Scales =10 mm.

strongest are on ANU 49259 in which they are deeply impressed and expose vesicular bone. They are presumably for the attachment of the subcranial (basicranial) muscle. Long (1985a, figures 4; 5) figured small muscle scars forward of this position as being for the basicranial muscles. Further cleaning of the specimen shows the scars to be much more extensive than he indicated (Figure 7F; 32). Anterior to this is the foramen for the internal carotid artery. This is well-shown on the holotype and ANU 49259.

On the dorsolateral edge of the notochordal pit, where the lateral wall of the braincase meets the pit, lies the processus connectens. This is best preserved on the holotype, but is also clearly visible on WAM 86.9.661. In lateral profile it does not break the line of the posterior edge of the braincase wall, and so the term "process" is something of a misnomer. It really consists of a slight thickening of the wall, the outer surface of s hich lacks a perichondral covering, exposing a patch of vesicular bone. This patch is more extensive on the lateral than on the posterior side of the "process".

The front of this thick region forms the basipterygoid process, which in our opinion is also a misnomer. Really the structure in question is a forward-facing concave attachment surface exposing vesicular bone which was the site for the attachment of ligaments to the basipterygoid process on the palatoquadrate (Figures 5C; 6E; 11A–C;12C–E). Its outer margin is formed of a sharp comma-shaped periosteal layer, and its inner margin by a similar, but much less distinct layer. Functionally, then, it is a concave surface for the articulation of a projection from the basipterygoid, rather than a process. However, we continue with this unsatisfactory usage, simply because it is so entrenched in the literature. In lateral view the "process" is shaped like the smooth arc of a quadrant, with the ventral tip drawn out beyond the limits of the vesicular bone. In anterior view the attachment surface is wide towards the dorsal end, the mesial edge is concave inwards, and ventrally the surface expands again producing an hour-glass effect as shown by Long (1985, figure 2B). In the holotype the ventral margin of the scar has a notch which apparently formed a gap through which a branch of the ophthalmica magna artery passed. As mentioned above, however, in

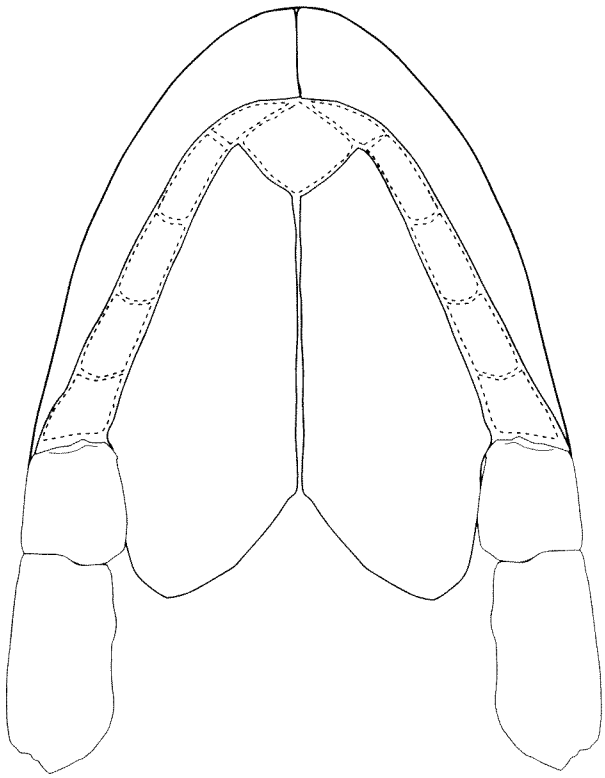


Figure 35 Ventral view of the head to show a reconstruction of the gulars and submandibular plates. Note that in preparing this figure, we have reconstructed the median gular from the edge of the gulars and the shape of the edge of the mandible. The number of the submandibulars is unknown, but we have adjusted them to match what we consider to be the shapes from the few isolated individuals we have.

ANU 49259 there is a groove in the lateral wall of the endocranium leading to the foramen for the ophthalmica magna, and indicating that a branch of that artery ran anterodorsally rather than laterally (Figure 5C). Deep within the mesial concavity the foramen for the pituitary vein is situated, thus allowing the vein access to the orbital chamber along the concave surface on the lateral wall of the endocranium mentioned above.

Near the ventral edge of the basipterygoid "process" is the foramen for the internal carotid artery. It passes directly and a little posteriorly into the hypophysial fossa. On the external surface forwards from this foramen is a shallow groove that runs off the endocranium at a slight notch in the holotype and ANU 49259. In WAM 86.9.661 (Figure 11C), however there are two or three such notches in a series, presumably indicating that the artery branched several times in this position.

Forwards of this basipterygoid "process" the endocranial wall is concave, the roof of the concavity being formed of the weak olfactory ridges, and the base by the parasphenoid posteriorly and the subocular shelf anteriorly. In this genus the subocular shelf is very narrow and it does not widen anteriorly to anything like the same extent as in *Cladarosymblema* or even *Medoevia*.

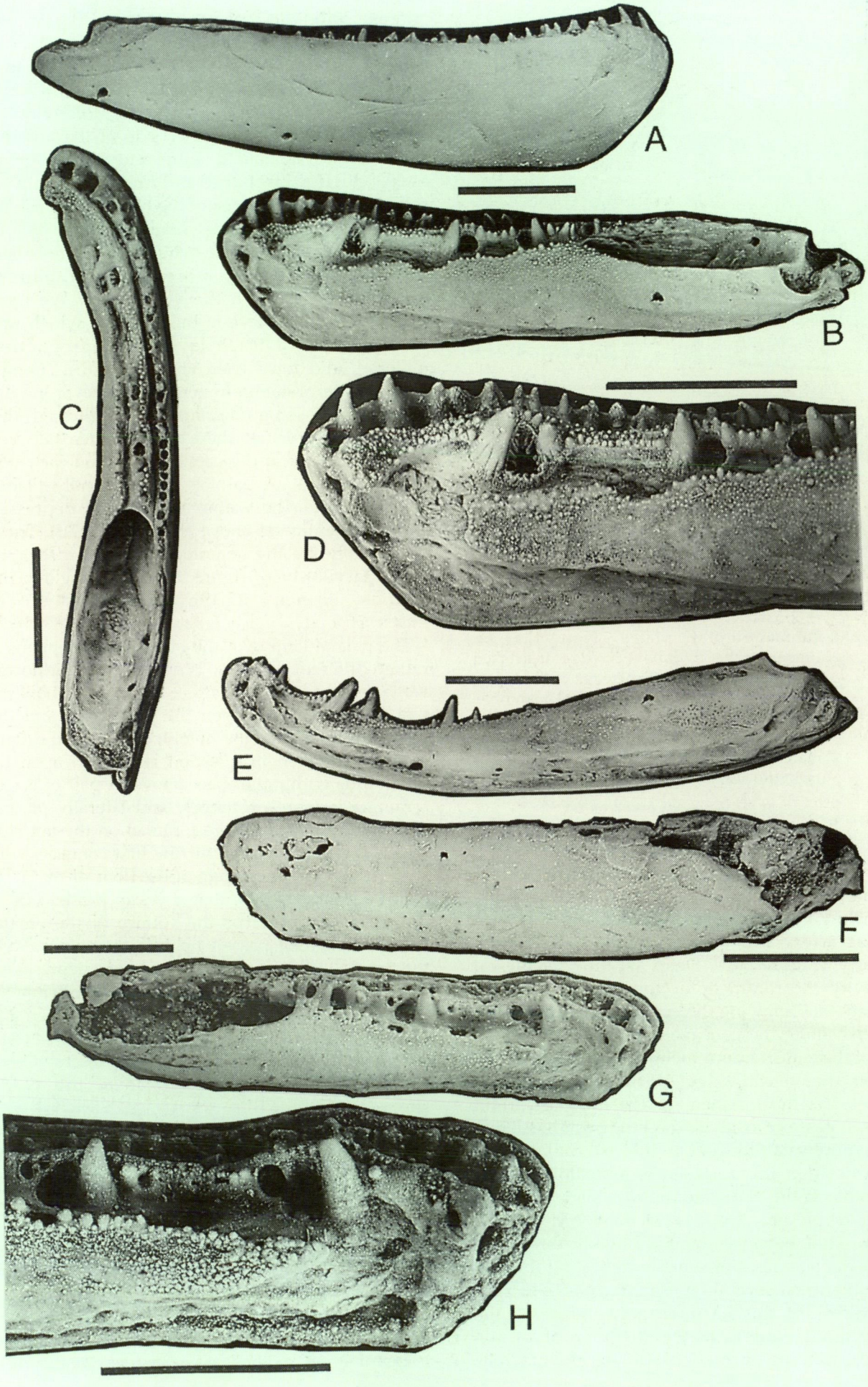
The endocranium on either side of the anterior end of the parasphenoid is thin and tends to break away during preparation. Long (1985a:370) recorded that in this area of the holotype, which he referred to as the palatal lamina, was a pair of shallow depressions just behind the premaxillae, and another slightly more posterior pair of depressions in which the vomers sat. We have cleaned off the surface in the holotype which was covered with a thick layer of impregnating material, and have been able to confirm Long's original interpretation in general. However, he did not recognise some foramina passing through this surface. In particular there is a foramen between the premaxilla and the palatal lamina on each side of the mid-line. A pair of asymmetrically placed small foramina lie within the slightly depressed surfaces mentioned above (Figures 6G; 7B). These presumably are the homologues of those referred to by Jarvik (1966, figure 17B) as being for the median branch of the palatine canal in *Eusthenopteron*.

The palatal lamina in the other two specimens is rather different. That in WAM 86.9.661 is not as well preserved as ANU 49259, but it does show the pair of foramina between the premaxilla and the palatal lamina as in the holotype, and on the right side the foramen in question is seen to open up into a tube within the space above. A pair of larger foramina is more posteriorly and laterally placed. ANU 49259 has one large foramen on the left side which is entered from a furrow that connects with a notch in the mesial edge of the floor of the nasal capsule. This suggests that a vessel passed out of the capsule, ran across the surface of the palatal lamina, and then passed up into the space above the lamina. Although there are deep depressions on the right side of the specimen approximately in the same position as the foramen on the other side (Figure 5B), we have been unable to satisfy ourselves that such a foramen is present. Other small foramina are present as in the WAM specimen (Figure 7B).

A most distinctive feature of ANU 49259 is the rugose surface for the attachment of the vomers (Figure 5B), which is better preserved than on either of the other specimens. Its anterior edge is in front of the parasphenoid and is almost transverse, leaving a large part of the palatal lamina uncovered. It extends posteriorly along the edge of the parasphenoid for only a short distance.

Nasal Capsules

Examination of the nasal capsules on the right


A
B
C
D
E
F
G
H

side of ANU 49259 and the left side of the holotype, which have been cleared of sediment, show that their inner walls have large foramina which also open into the space above the palatal lamina. Our description of *Cladarosymblema* shows foramina in similar positions; the largest one of these was interpreted as being the nasobasal canal, but it passed mesially into the prenasal fossa. We are of the opinion that homologous structures were present in *Gogonasus*, but that the structures transmitted passed medially to join with their antimeres within the enclosed space, and not into the depressions in the palatal lamina. This has important implications for the interpretation of the soft tissues occupying the prenasal fossae, a topic dealt with under Functional Interpretations. Other smaller foramina also open through the mesial wall of the nasal capsule. According to Thomson (1964) these admitted the passage of the ramus medialis narium and the ramus lateralis narium of the profundus nerve. Fox *et al.* (1995:134) gave reasons for not accepting such an interpretation for *Cladarosymblema*. We have no additional information from the current material which could permit an addition to the discussion.

Much of the floor of the nasal capsule, the solum nasi, is covered by the a lateral extension of the palatal lamina (Figures 6G; 7B,C), and posteriorly the autopalatine and a process of the dermopalatine form its margin. As indicated elsewhere, the posterolateral margin is an elongate slit-like opening whose lateral wall is formed from a process on the maxilla, and whose internal wall is made of the dermopalatine. Anteriorly the slit is bordered by the mesial process of the premaxilla (Figure 10C), and mesially by the edge of the vomer (Figure 26). This slit is the choana, its bounding bones being identical with those of primitive amphibians. One of the arguments used by Rosen *et al.* (1981) against the view that the opening in this position in *Eusthenopteron* was a choana was that a processus intermedius partly occluded any passage for a choanal tube (see their figure 14). In *Gogonasus* such an argument is quite inapplicable because the nasal capsule is situated much further forward relative to the choanal opening (Figure 32) and hence the processus intermedius is placed well out of range of any possible choanal tube. In fact, the passage vertically from the opening into the nasal capsule is totally unobstructed.

As is normal for osteolepiforms, a strong flange, the dermintermedius process, extends into the nasal capsule from the bone lying anterior to the external naris (Figure 7D). In the holotype this flange can be viewed through the naris and through the gap in the solum nasi (Figure 13). Although in no specimen is its complete extent visible in any one aspect, the holotype is good enough to enable us to determine its size and extent. Laterally the flange runs up the inner wall of the naris fading away gradually half way up its edge (Figure 13). Mesially it increases in size and moves away from the narial margin, and has a slight notch near its inner margin. In *Eusthenopteron*, Jarvik (1980, figure 81) shows a distinct rise in the surface of the flange in this position, with a semblance of a notch, and a narrow surface he refers to as a superior lamina. This corresponds approximately with what we observe in *Gogonasus*. An interesting point is that in the vicinity of this notch the holotype shows clear evidence of a suture between the dermal component and the endocranial component of the flange as Jarvik shows for *Eusthenopteron* (Jarvik 1980, figure 81C, right side). Denticles occur in the narial opening in WAM 86.9.661 on the dermintermedius process and tectalis process (Figure 13), although the other two specimens lack these, possibly because of increased abrasion. These denticles are not as clear as in *Cladarosymblema*. None of the capsules is sufficiently well preserved to see if the rugose surface lining the dorsal surface of the capsule as described for *Cladarosymblema* by Fox *et al.* (1995, figure 28), is present in this species.

Endocranium of the Otico-occipital unit

Posterior and Ventral Faces

This is well-preserved on only ANU 49259 (Figures 2; 5E; 14; 16A; 22; 23; 24), though some useful information has been obtained from the crushed WAM 86.9.661 (Figure 11D). Even the ANU specimen is not complete. In particular, the denticulated plates that were attached to the various parts of the endoskeleton have been displaced, and the inner wall of the braincase has broken away in places. Nevertheless the specimen provides three-dimensional views of the otico-occipital unit as good as any previously discovered etched osteolepiform.

The posterior face shows the fossa Bridgei clearly, with its margins on the left side almost entire. Dorsomesially and dorsolaterally on the left side, it is interrupted by a large rounded process

◀ **Figure 36** A–E, various views of the right mandible of ANU 49259, to show detail of the whole structure. A–C, E, are the lateral, medial, dorsal and ventral views. D is the enlargement of the anterior end of B, F–G. Lateral and medial views of WAM 86.9.661. Note that H represents the same view as D. Scales = 10 mm.

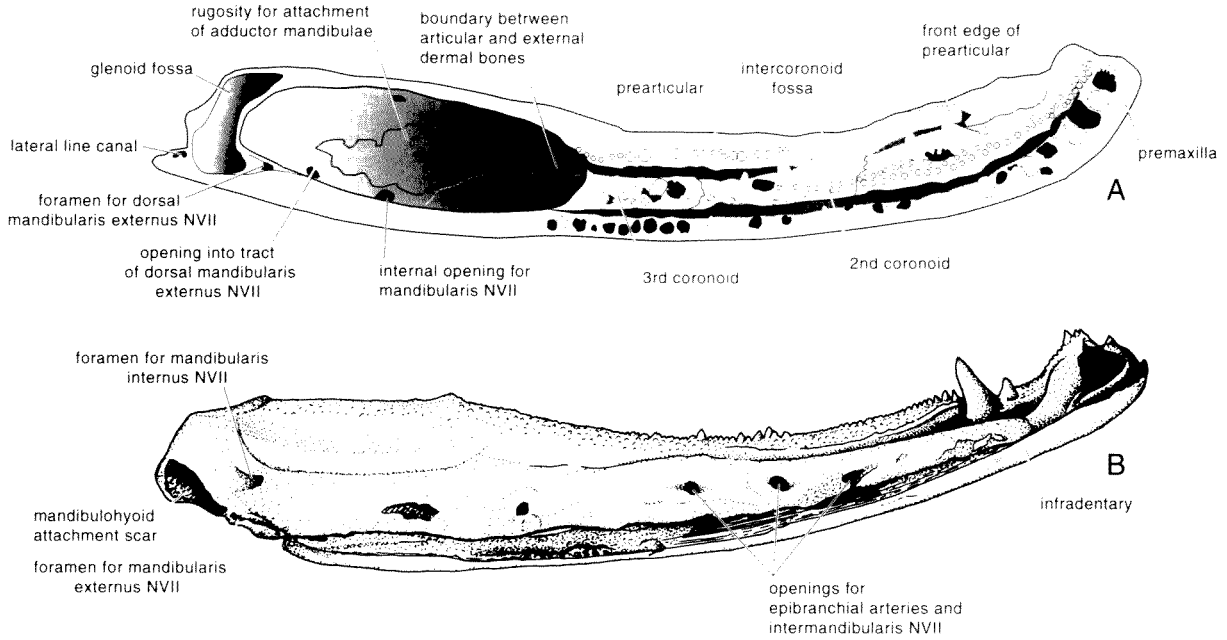


Figure 37 A, dorsal view of ANU 49259. B, ventral view of WAM 86.9.661. B is intended to show that the openings in the ventral surface are different from those in ANU 49259.

(Figures 22C; 24); on the right side the processes have been broken away leaving their bases clearly visible. So far as we are aware, no such structures have been described from any other osteolepiform. At the anterior tip of the fossa is a foramen for a lateral branch of the occipital artery, as in *Cladarosymblema*. This foramen opens through to the trigemino-facialis chamber via a large foramen which is clearly visible on both sides of the specimen (Figures 22A-E; 23; 24).

Ventral to the fossa Bridgei on the left side of ANU 49259, and joining it in the embayment

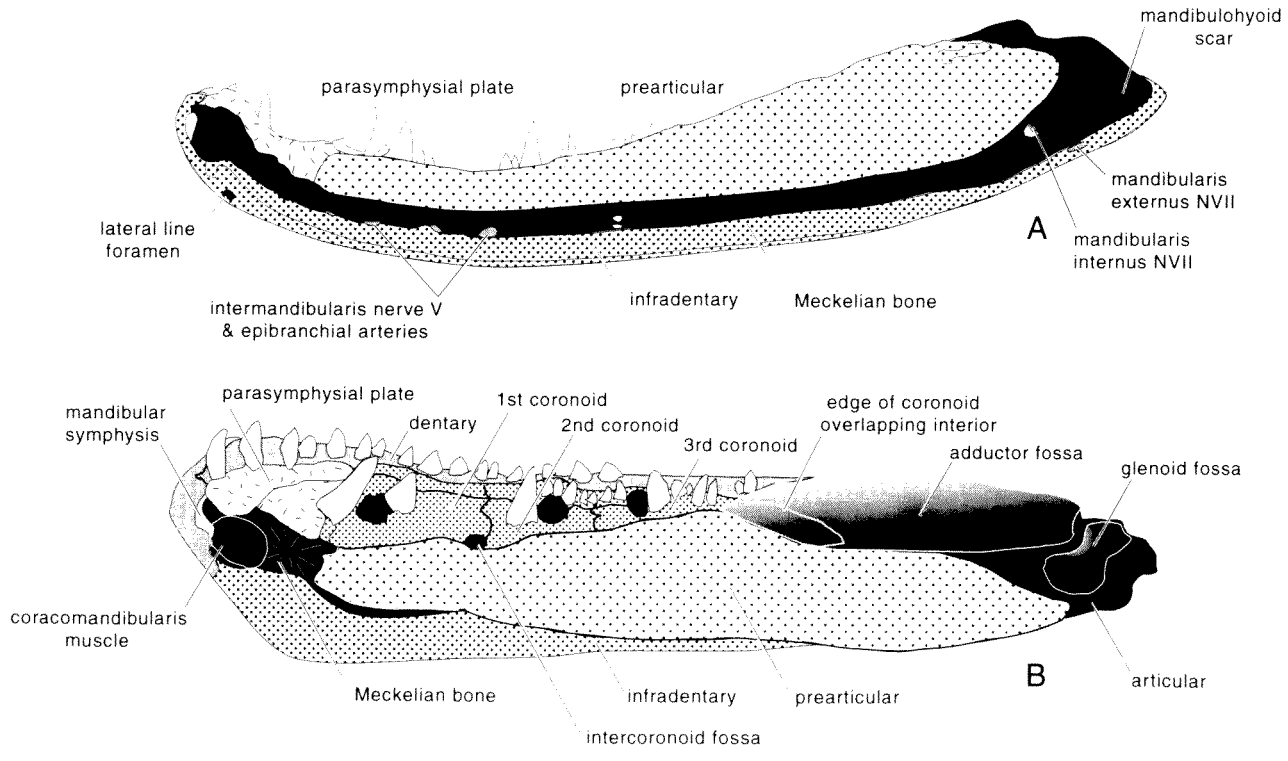


Figure 38 A–B, two reconstructions of the mandible of ANU 49259 in ventromesial, A, and mesial, B, views. This is drawn to show the distribution of the various types of bones, the foramina, and the attachment areas of several muscles and ligaments.

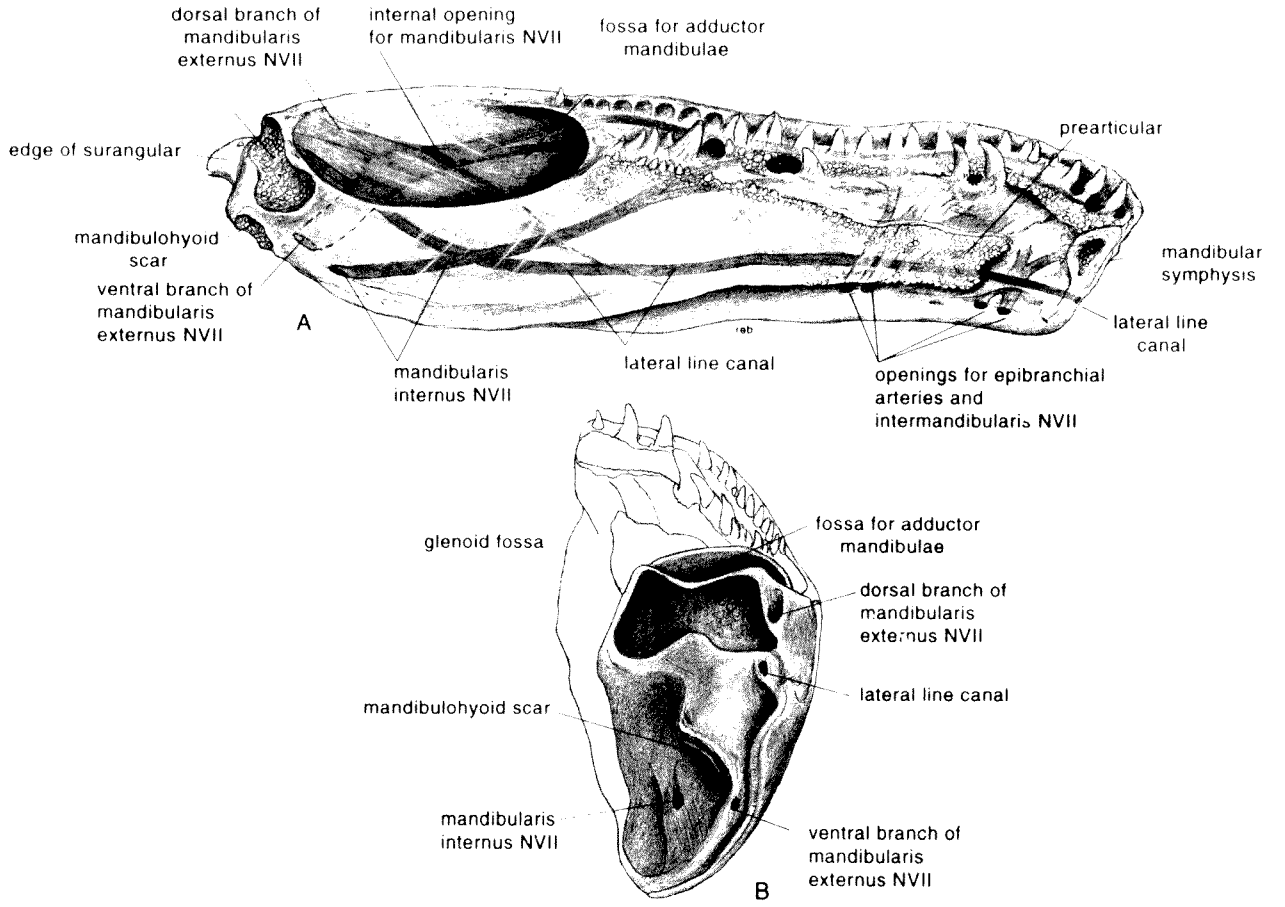


Figure 39 A, Reconstruction of the mandible prepared from X-radiographs of ANU 49259. B, Posterior perspective of the same mandible showing all the foramina and scars of ligaments.

between the two processes, is a slightly impressed groove that descends to the edge of the vestibular fontanelle (Figure 22B). In *Cladarosymblema* we interpreted this as carrying a branch of the occipital artery, and we see no reason to modify that interpretation for this genus. The right side of this specimen has a groove in the ventral edge of the fossa Bridgei, but no groove running ventrally from it (Figures 22C,D; 24); we interpret this as meaning that the artery was present but did not impinge on the bone below the fossa. WAM 86.9.661 has notches in the ventral edge of the fossa Bridgei, but breakage prevents tracing the course of the grooves running ventrally from them. The groove for the occipital artery is present on both sides of the occipital ossification.

A well-developed occipital fissure is present on both specimens, but is most clearly seen on ANU 40259 (Figures 22C, D; 23A). Laterally it extends from the dorsomesial edge of the vestibular fontanelle in a dorsal direction, but with a slightly sinuous course, up to the shelf on which the median extrascapular rested. Ventral to this shelf, the fissure turns mesially to join its counterpart from the other side below the pit for the supraneural ligament. The dorsal part of the fissure is not as open as the lateral part, but it can be clearly distinguished, especially when the specimen is wet. Laterally the fissure contains a slit-like opening which on the right side appears to be single, but on the left encloses a number of small foramina (Figure 22B). In *Eusthenopteron*, Jarvik (1980, figure 86) has interpreted these foramina as containing the lateral line nerve, and nerve X, which is reasonable in view of the fact that they lie within the occipital fissure. On both sides of the ANU specimen a broad groove runs ventrolaterally from this slit, passing off the bone immediately dorsal to the vestibular fontanelle. Such a course would be consistent with nerve X.

A pair of much less impressed grooves run laterally from the upper foramen, and this would be consistent with it being for the lateral line nerve. Thus, although we cannot trace the canals from the foramina into the braincase, and cannot offer direct evidence of the position of exit of these structures from the braincase wall, we accept Jarvik's interpretation in general terms.

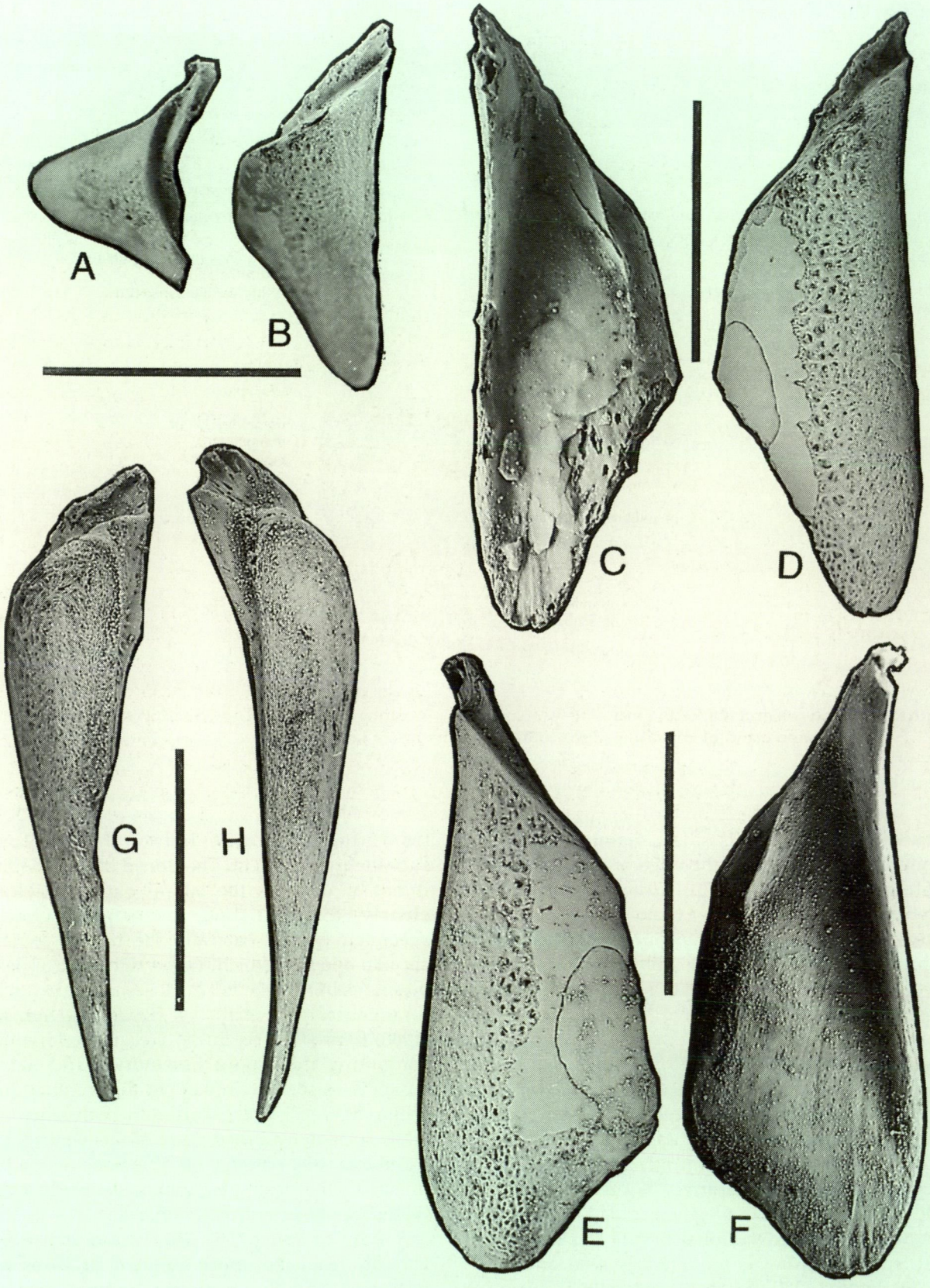


Figure 40 Clavicles of WAM 86.9.661. A, B, posterior views of the two clavicles showing the furrows for articulation with the cleithrum. C, D, internal and external views of the left clavicle. E, F, right clavicle. G, H, two views of the same specimens showing the outer edges. Scales = 10 mm.

However, we point out that at least on the right side of the ANU specimen, both the foramina show some evidence of being paired, and at least the dorsal one has two clear grooves running laterally from it. Does this mean that additional structures definitely exit from these foramina? This is a serious point because we have definite exit points for neither the posterior cerebral vein nor nerve IX. The posterior cerebral vein in fishes normally exits the endocranium with nerve X, and this seems a likely explanation of the doubling of the lower foramen in our specimen. Nerve IX is still not completely understood, but there is a small foramen mesial to the jugular foramen on ANU 49259 (Figure 22C), and a suggestion of a small foramen in the same position on WAM 86.9.661. This is a possible site for the foramen for nerve IX.

Dorsal to the occipital fissure on each side of the pit for the supraneural ligament, lies a prominent rounded process, the posterior surfaces of which are not covered with periosteal bone (Figures 22C; 23B; 24). They do not have the appearance of being surfaces for the articulation of other bones; in any case, the evidence from other osteolepiforms (Andrews and Westoll 1970a,b; Jarvik 1980) is that the neural arches of the first vertebrae of such forms are placed in a position much too posterior for articulation with the back of the skull. Also, as Figures 5E and 11D show, the walls of the notochordal chamber extend even more posteriorly than those of other known osteolepiforms, excluding *Medoevia* with which it is of similar extent (Lebedev 1995, figure 6A); thus making a bone to bone articulation highly unlikely. We can only conclude that the processes in question were for the attachment of ligaments that held the first neural arch in a definite orientation with the back of the skull.

Lateral to this process on each side of the specimen is a deep pit; on WAM 86.9.661 this level is broken down to the level of the pit, and a canal

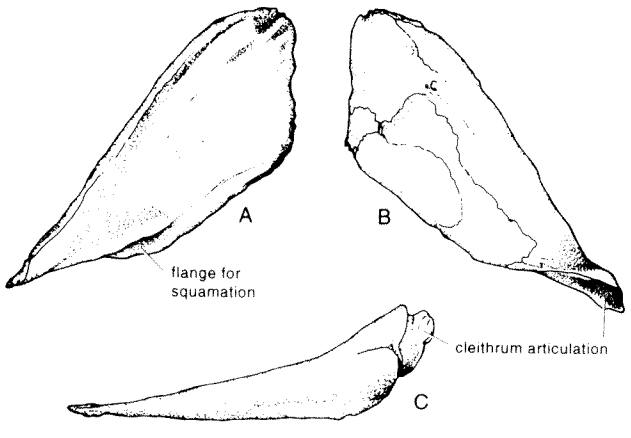


Figure 41 Drawings of the right clavicle of WAM 86.9.661. Compare with Figure 40C.

runs forward into the top of the braincase. Jarvik (1980, figures 12, 36, 212) identifies the fossa tectosynotica in this position on *Amia*, *Eustenopteron* and *Nesides*. In *Amia* these pits house mesial bundles of epaxial trunk musculature. In *Cladarosymblema* there are also paired pits in this position as well as foramina for the occipital arteries. On the left side of the ANU specimen the pit contains a single small foramen, and the pit on the right has three or four even smaller foramina. We conclude that these represent the foramina for the mesial branchings of the the occipital arteries, but the pits are much too large for this to be their only function. In addition, we note that there is a deep ventral groove running out of the fossa tectosynotica (Figures 22C; 24), and another groove of similar dimensions running dorsolaterally from it to the fossa Bridgei. No other osteolepiform seems to show such structures and so we cannot assign a function to these grooves, but suggest that it is possible that epaxial trunk muscles were inserted into the pits and that the grooves mark the sites of surrounding connective tissue.

The broad mass of endocranium lying posteroventral to the pit for the supraneural ligament and anterodorsal to the foramen magnum, has a pronounced but rounded median ridge. In *Cladarosymblema* (Fox *et al.* 1995, figures 38B; 39B), a sharper ridge in this position served to separate broad flat attachment areas for the longitudinal musculature. On ANU 49259, the surfaces adjacent to the median ridge are narrow and angled, and show only weak muscle attachment markings. These surfaces are penetrated by two small foramina, presumably for nerves or for branches of the occipital artery. We incline to the former view because they open directly down through the braincase wall. Anterolateral to each of these surfaces is an apple-seed shaped surface which is slightly sculptured as though for muscle attachment (Figures 22C; 23B; 24). These also have their counterparts in *Cladarosymblema* (Fox *et al.* 1995, figure 38). The specimen shows a median ridge which thickens posteriorly and probably was the buttress dorsal to the site for the attachment of the supradorsal ligament as is figured by Jarvik (1980, figure 86A; 97) for *Eusthenopteron*.

Lateral to the foramen for nerve X is a slight process which has no periosteal covering on it posterior face. It is the postotical process of Jarvik (1980, figure 86c). On WAM 86.9.661 the surface of this process has been removed on both sides, but the bases are well preserved (Figure 11E).

The foramen magnum is subtriangular in section as is normal for these fishes (Figures 22C; 24). Its floor is divided medially by a low ridge which separates two well-defined canals, which presumably are for the basilar artery. This also is

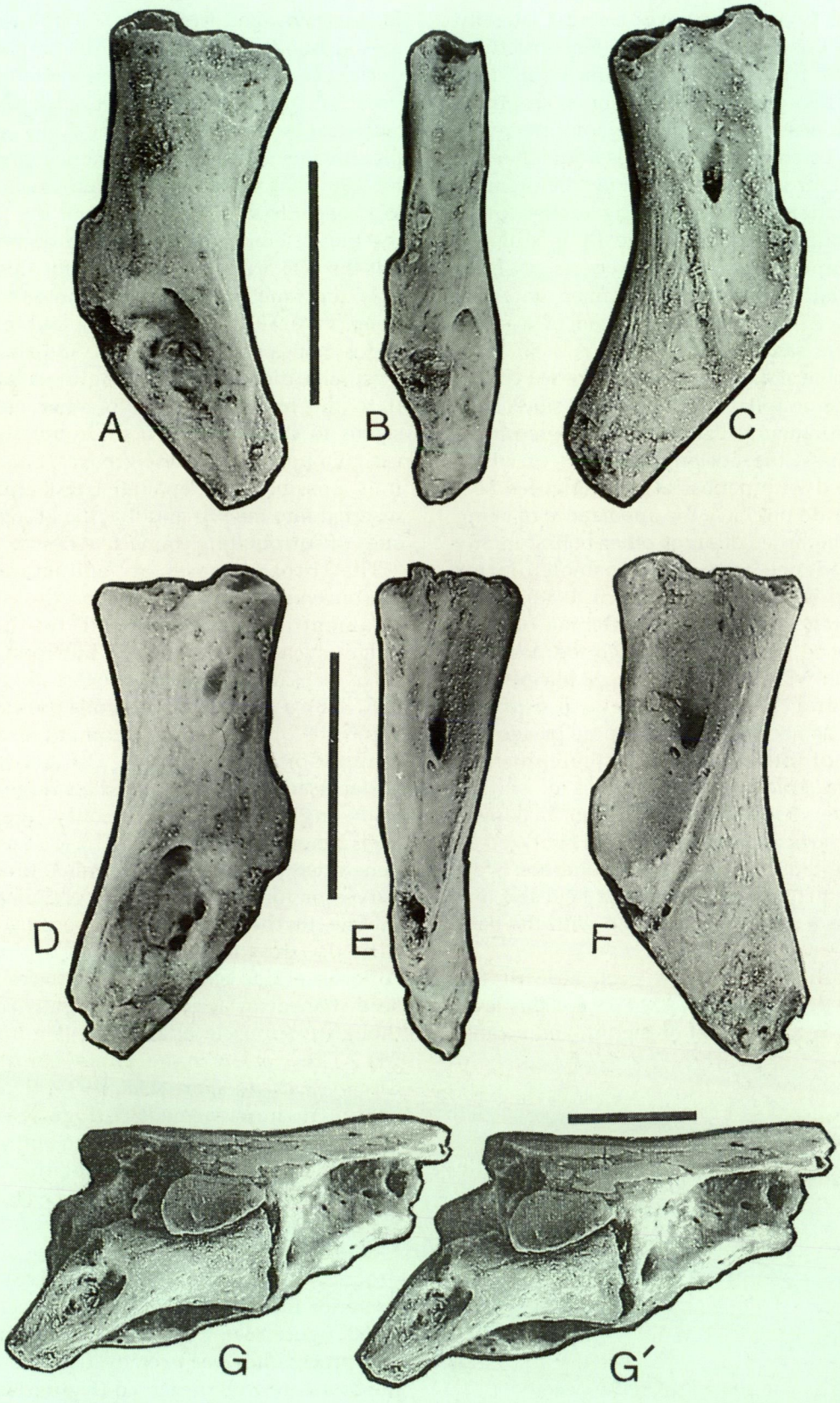


Figure 42 Hyomandibulae of ANU 49259. A–C, three views of the left hyomandibular. D–F, three views of the right hyomandibular. G–G[1], stereo-pairs of the otico-occipital region of ANU 49259, which has the right hyomandibular in position. Scales = 10 mm.

unlike *Eusthenopteron*, which has a single median canal for this artery (Jarvik 1980, figure 86c), but is comparable with *Cladarosymblema* (Fox *et al.* 1995, figure 34). The notochordal foramen is large, almost circular in cross section, and thick-walled as is normal for osteolepiforms.

At the lateral extremity of the posterior wall is the foramen for the jugular vein. It is circular in outline, and is completely enclosed. Laterally a narrow strip of bone is present on both sides of the animal. A wide groove runs posteroventrally from the jugular foramen to the dorsolateral edge of the vestibular fontanelle (Figures 11E; 22A–D; 24), where it disappears. This obviously carried the jugular vein. It was probably joined by the groove for the posterior cerebral vein before reaching the fontanelle, but on the specimen it is not quite clear. The vestibular fontanelle terminates anteriorly at a point about half way along the length of the otico-occipital unit, and in a transverse line with the posterior extent of the basicranial fenestra. In lateral view little of the vestibular fontanelle can be seen (Figures 11E; 22A). The anterior margin of the vestibular fontanelle is square-shaped. Compared with *Eusthenopteron* the fontanelles in *Gogonasus* are of similar size and position, and are placed in a more posterior position to those in *Panderichthys*, noted to have significantly smaller and more anteriorly placed vestibular fontanelle than other osteolepiforms by Ahlberg *et al.* (1996).

Also exiting from the jugular foramen is the hyomandibularis VII (Figures 22E; 23B). That nerve enters the floor of the tube carrying the jugular canal back from the trigeminofacialis chamber via a large foramen. It then runs directly posteriorly along a groove on the inner face of the hyomandibular to enter the hyomandibular foramen in that bone. This does not show up well on the photographs (Figure 22F); it is clearly seen on both specimens inside the jugular canals shown diagramatically on Figure 44.

The attachment areas for the hyomandibular are worth special comment; on neither side of ANU 49259 are they complete (Figure 22B–D), and on the left side of WAM 86.9.661 (Figure 11E) they are preserved as outlines only, lacking the perisoteal articulatory surfaces. The dorsal attachment, best preserved on the left side of ANU 49259 (Figure 22B) and on the right side (Figure 22D,E) is higher than wide, expands dorsally, and faces posterolaterally. The ventral attachment, best preserved on the right of the same specimen (Figure 22C,D) is more equidimensional, has a pear shaped outline, is more basicranial, and faces rather more posteriorly.

Posterior to the basicranial fenestra, the floor of the notochordal chamber is formed of a broad, flat, solid, bony lamina (?the suboccipital plate), which is shield-shaped in ventral view. Laterally it is extended into obtuse angles, and posteriorly it narrows considerably. This seems to be a normal osteolepiform feature seen in both *Medoevia* and *Eusthenopteron*. Posteriorly this plate is flanked on each side by a deep groove for the lateral dorsal aorta that fades towards the lateral angles of the plate. WAM 86.9.661 shows a pair of slit-like foramina on the posteroventral edge of the suboccipital plate (Figures 11D,E). This specimen also has clear grooves for the lateral dorsal aorta, which are joined in front by the vertical groove for the occipital artery. These slits are difficult to interpret because it is not clear if they are real foramina or slots into the bone (cf. Jarvik 1980, figure 88B). Lebedev (1995, figure 1D) shows a roughened area in the same position. These have been interpreted as sites of muscle attachment in these genera. The slits in *Gogonasus* are turned posteriorly, so such an explanation is unlikely in that genus.

Running dorsally from the lateral dorsal aorta groove is an occasional short, irregular, narrow branch. These branches cross the ridge which Jarvik considers to have provided the sites of attachment for the branchial elements. Our specimen shows indefinite patches that could have served that function, but we are unable to comment further.

The attachment surfaces for the basicranial muscles are of the usual osteolepiform type (Figures 5E; 11D; 22E,F). They are formed of thick bone, the ventral surface of which is distinctly concave and bears a sharp anterolateral edge which fades away abruptly posteriorly. The foramen for the palatine nerve VII is situated in a slightly more posterolateral position than normal, and opens into a short tube directed posterodorsally towards the hyomandibularis VII foramen.

Lateral Face

In dorsal view the lateral wall has a short segment parallel with the mid-line, and a much longer segment sweeping back obliquely to the lateral commissure (Figures 11E; 22A; 23A; 44). This latter meets the skull roof along the edge of the tabular where it joins the inner face of the spiracular slit. This arrangement is quite different from that in the megalichthyids in which this part of the endocranial wall is much more transverse (Fox *et al.* 1995, figure 29). At the junction between the two parts of the lateral endocranial wall, immediately under the skull roof, there is a profound depression in the lateral wall which is probably an attachment site for the levator arcus palatini. Such a muscle would insert on the paratemporalis process of the palatoquadrate. Figure 45 shows a restoration of the palatoquadrate attached to the endocranium, showing the

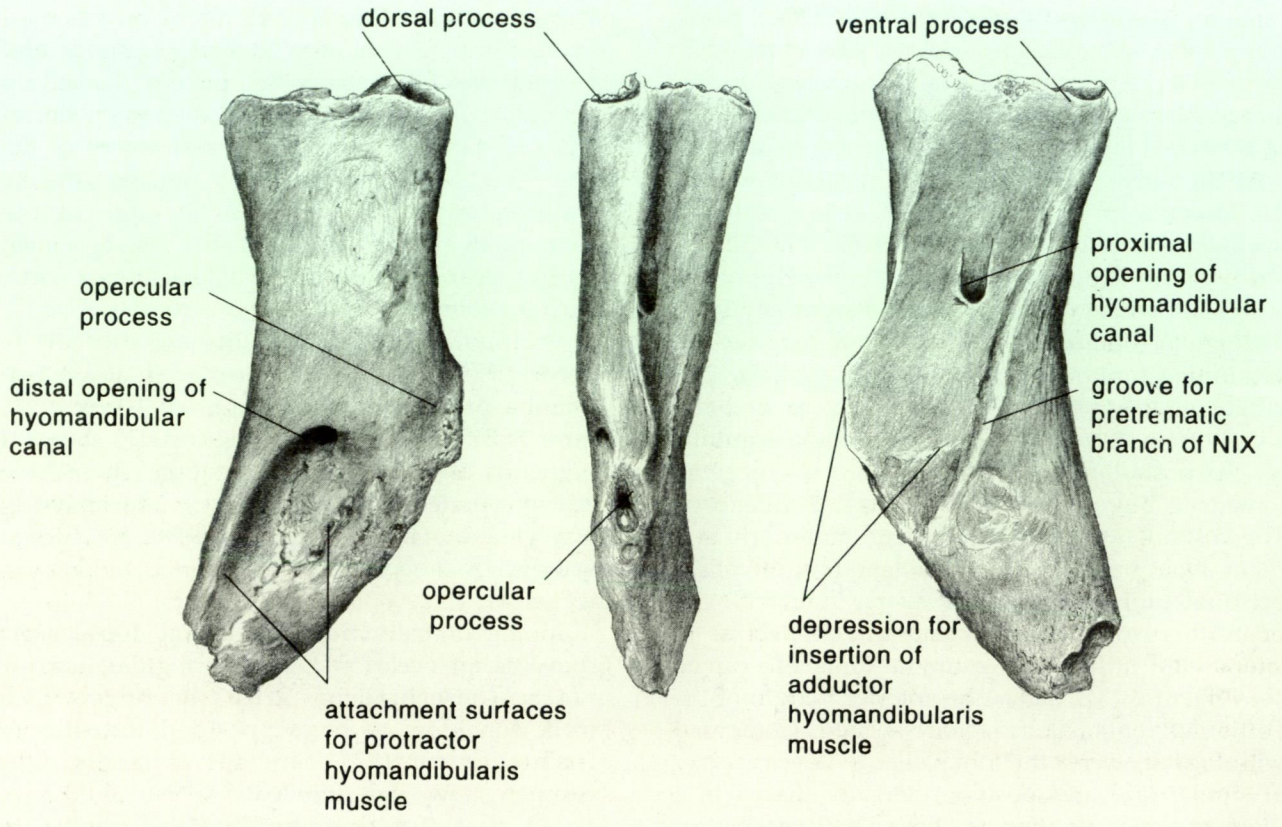


Figure 43 Lateral, dorsal and medial views of the hyomandibular to show the organisation of the various elements.

estimated positions of these surfaces and the overall fit of the palatoquadrate to the braincase. Immediately anterior to the foramen for the occipital artery and lateral to the attachment area for the levator arcus palatini is a well developed small process (Figures 22A, 23A,B; 44), probably for ligamentary attachment to the palatoquadrate complex.

As can be seen from a reassembly of the two cranial units, the processus connectens on the ethmosphenoid unit does not project back into the otico-occipital unit as it does in *Eusthenopteron*. The ventral connection between the two units has to be effected by a ligamentaryattachment which does not involve the direct approximation of the two halves. The posterior end of this ligament is attached to the otico-occipital unit is inserted into a slight depression on the inner surface of the cranial cavity just dorsal to the anteroventral edge of the endocranium (Figures 11E; 22A,E; 44).

Just dorsal to the above attachment surface the leading edge of the lateral wall of the endocranium has a distinct notch which obviously formed the posterior margin of a foramen partly enclosed by soft tissue between the two skull moieties. On both left and right sides of the inner wall of the endocranium (the wall of the braincase) a pronounced groove runs posteriorly disappearing at the edge of the otic capsule, where the bone surface is broken. This seems to be unrepresented in other osteolepiforms so far as we can gather. According to Jarvik (1954, 1980) and Thomson (1965), the profundus branch of nerve V passes out in the space between the two units, and hence the normal interpretation of a nerve in the position described would be that it was this nerve. The course of the groove within the braincase shows that it is not connected with the other branches of nerve V, and its long course along the wall suggests that it originates in too posterior a position for it to be nerve V; its orientation is much more like nerve VII. We are of the opinion that the nerve in question is part of the buccalis branch of nerve VII, and the whole concept of the interpretation of the nerve in other osteolepiforms needs to be reinvestigated. This interpretation leaves the true course of nerve V_1 unresolved.

A large and complete foramen near the anterior edge of this skull moiety (Figures 22A, E–F; 23B; 44) opens directly into the braincase. This is in the normal position and has the same size and orientation with respect to the braincase to be for nerve $V_{2,3}$ as seen in *Eusthenopteron* and megalichthyids.

A short distance posterior to the large foramen for nerve $V_{2,3}$ is a much smaller foramen that opens

into a tube of different length and orientation on the two sides of the specimen. On the left side, this tube runs backwards within the endocranium to open near the edge of the otic capsule. On the right side the tube passes directly through the bone to open through a foramen only slightly behind the external foramen. This position on the external surface is the site of the ramus ophthalmicus lateralis, as shown by Jarvik (1980, figure 86) for *Eusthenopteron*.

Behind this foramen and forming a straight line with it and the foramen for nerve V are one (left side) or two (right side) smaller foramina. In *Eusthenopteron*, Jarvik (1980, figure 86) has identified foramina in this position as transmitting the rami oticus lateralis (Figures 22A; 23B).

The foramen carrying the occipital artery into the trigemino-facialis chamber is well represented on both sides (Figures 22A–E; 44). Forwards from this foramen is a slight groove which divides into a dorsal branch running slightly dorsally immediately under the skull roof, and a broad anteroventrally directed groove which curves in a gentle arc before moving off the endocranial wall. These observations are visible on the internal surface of the braincase and it is difficult to represent them photographically. On the left side the more dorsal groove runs through a bony arch, but on the right side, although a strong process borders the groove ventrally, it does not make a complete arch. We consider that these carried the blood from the occipital artery to the roof of the palate and possibly the orbital chamber.

The hypotic ramus of nerve VII probably separates from the hyomandibularis VII and runs laterally in the bone to open through a small foramen situated on the vertical flange lateral to the surface for the attachment of the basicranial muscle, and about 2 mm anterior to the foramen for the ramus palatinus VII (Figures 22A; 23B; 44).

Otic Apparatus

This is not well shown in either specimen, though WAM 86.9.661 is broken in such a way as to expose the structures if they were preserved. Unfortunately compression has destroyed all the fragile structure. ANU 49259 is more complete, but the internal structure of the otic region is not exposed. X-radiographs show the vertical semicircular canals; these lie as shown on Figure 16A their position is easily determined from the actual specimen in conjunction with the X-radiographs. Posterior to the anterior vertical canal the upturned edges of the supraotic cavity forms a narrow canal on the X-radiographs. On the left side there are two clear openings where the anterior and posterior semicircular canals meet just lateral to the sinus superior. A pair of long thin endolymphatic sacs (Figure 16A) also runs backwards from the same point, but unlike those of *Eusthenopteron* (Jarvik 1980, figure 89) they are separated along their length, leaving a gap of about the same width as the tubes themselves between them. The specimen itself shows these tubes in part, but they are submerged in part deep in the tissue; they do not open to the surface in the usual way.

Hyoid arch elements

Hyomandibular

This structure is almost perfectly preserved from both sides in ANU 49259 (Figures 42; 43), and less well preserved in WAM 86.9.661. As has already been indicated by Fox *et al.* (1995), the similarity to *Cladarosymblema* is quite striking, and the existence of most of the structures described for that genus is confirmed in *Gogonasus*. The differences are ones of proportion. Much the same can be said for similarities with *Medoevia* (Lebedev 1995, figure 16), although some of the features illustrated in that genus are not quite clear. The overall proportions of the hyomandibular are more delicate than those of *Cladarosymblema*; the curvature of the ventral edge is slight, and the the angle made by the intersection of the axes of the distal and proximal sectors is ca. 45°–50°; the proximal opening of the hyomandibular canal is more posteriorly placed, and lies at the end of a deep and wide groove; the groove for the pretrematic branch of nerve IX impinges on the bone in a more posterior position, well behind the point of articulation with the skull, and it passes off the bone directly without a pronounced ventral flexure; the attachment surfaces for the protractor hyomandibularis muscle is of variable depth on the two individuals from ANU 49259, the right bone having a deep excavation within which lie three distinct pits giving the appearance of ligament attachment; the proximal edge of the opercular process is more angular; and the distal tip has a well-defined bony rim around the unossified cartilagenous extremity than in *Cladarosymblema*, in which the bone has a large irregular unossified ending. Many of these features are probably related to the fact that the hyomandibular of *Gogonasus* was attached to the skull with the proximal part almost horizontal and the distal end adjacent to the scar on the inner face of the opercular.

The hyomandibular of *Medoevia* is distinguishable from that of *Gogonasus* by its more curved outline; its less obvious opercular process; its relatively long proximal and short but deep distal portion. We consider that this relates to the fact that *Medoevia* has a relatively large opercular series in relation to *Gogonasus*, as is discussed under Functional Morphology.

As indicated in the next section, the

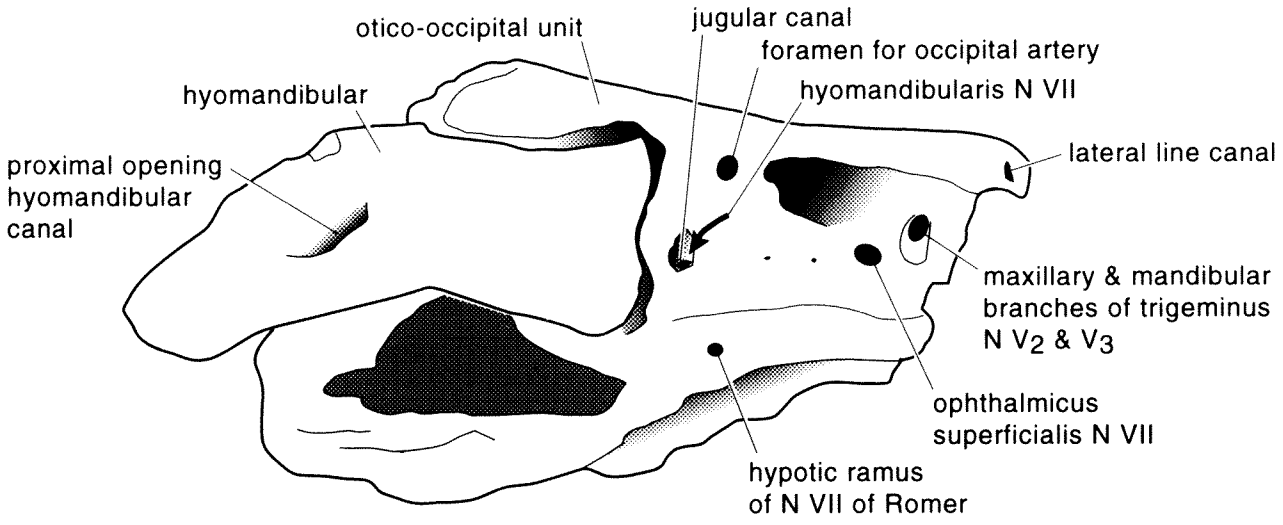


Figure 44 Lateral view of ANU 49259 with the hyomandibular in place, and showing the various named parts of the skeleton.

hyomandibular attachments to the endocranium are such that the proximal portion is placed almost horizontally (Figures 42G; 60). This is in marked contrast to that of *Eusthenopteron* as illustrated by Jarvik (1954, figure 23; here reproduced in Figure 60). It has been suggested to us that we have restored the hyomandibular in too horizontal a position in the Figures, and that space is left in the articulations for soft tissues that would allow considerable vertical movement. We do not accept this view for three main reasons. First, the dorsal and ventral surfaces of the hyomandibular are well preserved and are joined by a strong continuous layer of bone. This fits against the bone on the otico-occipital unit in such a way that it will act as a hinge for the rotation of the hyomandibular, and will not allow its forward movement. Secondly, the edge on the otico-occipital unit is well preserved, and shows that the amount of movement in a ventral direction is very limited. Thirdly, the palatoquadrate ccomplex when placed in position, shows that the unusually high curvature on its posterodorsal surface will not permit a more ventral position of the hyomandibular. Although this may cause difficulties in interpretation in comparison with *Eusthenopteron*, the observations will not allow a position for the hyomandibular similar to that illustrated by Jarvik.

Interhyal

If the hyomandibula is restored to its life position as shown in Figure 42G (see also Figures 60, 62), its ventral tip is well short of where the dorsal end of the ceratohyal would be. There must have been a bone joining these two elements, but we have not recognised it, either because it was poorly ossified or because it was not distinguishable. Veran (1988), after an extensive analysis of osteichthyan hyoid arches, concluded that a bone, which she referred to as an interhyal, occurred primitively in all osteichthyans. Jarvik (1954, 1980) recognised such a bone in *Eusthenopteron*, but he referred to it as a stylohyal. For present purposes its name is of little consequence. Its main significance is that it was covered laterally by the subopercular 1, and that bone has a distinct scar on its internal face which would have been for the attachment of a ligament from the interhyal (Lebedev 1995, figure 12D). Lebedev (1995, figure 12D) shows a scar on the same bone, which he refers to as the subopercular, and interprets it as being for the contact with the lateral process of the ceratohyal 2.

Ceratohyal

We have only one part of a ceratohyal (Figure 46 H–J), with no indication of whether one or two ceratohyal elements were present. The one we have is from the left side of ANU 49259, and if two parts were present in the original, it would have been the anterior one. In dorsal view the bone is gently curved with the convexity outwards. In lateral view it is highest posteriorly and tapers gently towards the front, which is incomplete. It is thickest dorsally and gradually thins out ventrally.

The bone has an articulation surface in the dorsolateral corner indicating that the next posterior bone slightly overlapped it. The identity of the next posterior bone remains unknown. Jarvik (1980) and Lebedev (1995) indicate that it would be a second ceratohyal, but we see little evidence for this. We further note the discrepancy in shape between the ceratohyal 1 as indicated by Lebedev

(1995, figure 17) and the articulatory surface for his ceratohyal 2. We also suggest that the ceratohyals in his figure 18 are too widely spread.

Although the posteroventral edge of our specimen is broken, it is clear that it was broadly rounded rather than having a knob-like lateral crest as does *Eusthenopteron* (Jarvik 1980, figure 110). Along the dorsal edge it has a distinct but narrow groove which is the homologue of the groove on the dorsolateral margin of the ceratohyal of *Eusthenopteron* and *Medoevia*, and referred to by Jarvik (1980:153) as possibly carrying the efferent artery of the first branchial unit. On the outer surface and parallel to the partly broken ventral edge is a less well-impressed groove, the ends of which are not preserved. This also has its counterpart in *Eusthenopteron*. Although no markings reminiscent of muscle attachments can be observed in this groove, it is probable that it marks the ventral edge of the interhyoideus muscles. Dorsal to this shallow groove, and occupying much of the anterior three quarters of the lateral surface of the bone, is a network of markings which have the appearance of muscle attachment (Figure 46I). These are unlike the concentrated muscle scars on the lateral face of dipnoan ceratohyals (Miles 1977; Campbell and Barwick 1988), and do not seem to have been described previously in rhipidistians. The muscle mass attached to scars of this shape must have been rather sheet-like at least at the hyoid end, and since they would not have passed around the ventral edge of the ceratohyal where the interhyals would be in position, they must have been attached distally either to the median raphe in the floor of the throat or around to the ceratohyal on the other side. Muscles in this position would have to be the interhyoid. The mesial face of the ceratohyal is crossed by anastomosing shallow and narrow grooves. The clearest of these runs from the posterodorsal attachment surface. They have the appearance of being the sites of blood vessels and

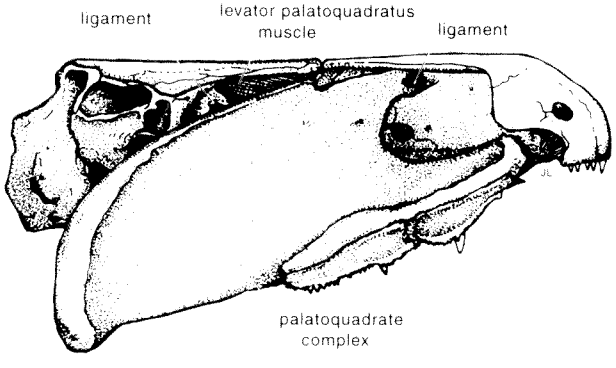


Figure 45 Reconstruction of the whole head without the cheek region to show the attachment of certain ligaments and muscles.

are comparable with those found on the inner surface of the ceratohyal of *Griphognathus* (Campbell and Barwick 1988, figure 16C). We note that the ceratohyal of *Medoevia* has markings in almost exactly the same position.

Hypohyal

From ANU 49259 we have two elements (Figure 49G) which we tentatively identify as hypohyals by comparison with similar elements from *Medoevia* (Lebedev 1995, figures 17G,H; 18) and *Eusthenopteron* (Jarvik 1954, figure 8). They are short deep triangular bones with a broad ventral articulation surface surrounded by periosteal bone for making ventral contact with the basihyal/basibranchial. The dorsal surface has an elongate articulation with the ceratohyal. These bones differ from the hypohyals previously described in *Medoevia* in that they are twice as long as deep. This is a result of their oblique articulations with the ceratohyals. The anterior face has a short scar similar to the one in *Medoevia* (Lebedev 1995, figure 18A); this was probably for the attachment of the interarcual ligament. A weak groove on the lateral face was for the efferent pseudobranchial artery.

Basihyal/Basibranchial

Only one basihyal/basibranchial element is preserved, and that is from ANU 49259 (Figures 46; 48). In many respects it is very similar to what Lebedev (1995, figure 18) refers to as the basibranchial in *Medoevia*; the differences will be discussed below. It is also similar to the single basibranchial of *Glyptolepis groenlandica* as described by Jarvik (1972, figures 28–29). We point out that this bone in both *Medoevia* and *Gogonasus* is more similar to that of *Glyptolepis* than *Eusthenopteron*. In view of the fact that this bone provides the articulation for the hypohyals and the hypobranchials, it must be a composite bone formed of the basihyal and basibranchial. Hence we refer to it as basihyal/basibranchial.

The bone (Figures 46A–E; 48) is a depressed unit that is symmetrically kite-shaped in dorsal view with roughly parallel sides but with scalloped anterolateral and posterolateral margins. The anterior margin is prow-like, carrying a projection referred to by Jarvik (1972) as a lingual process, for the articulation of the sublingual rod. We note that there is no scar for the attachment of a sublingual rod, but it seems that any rod would not be strongly attached; this is not surprising in view of the fact that it in both *Eusthenopteron* and *Medoevia* the sublingual rod is not in direct contact with the basihyal. We have found no sublingual bone in either of our specimens, but we assume that it if it were present it would be short and not well ossified. The posterior margin of the whole unit is

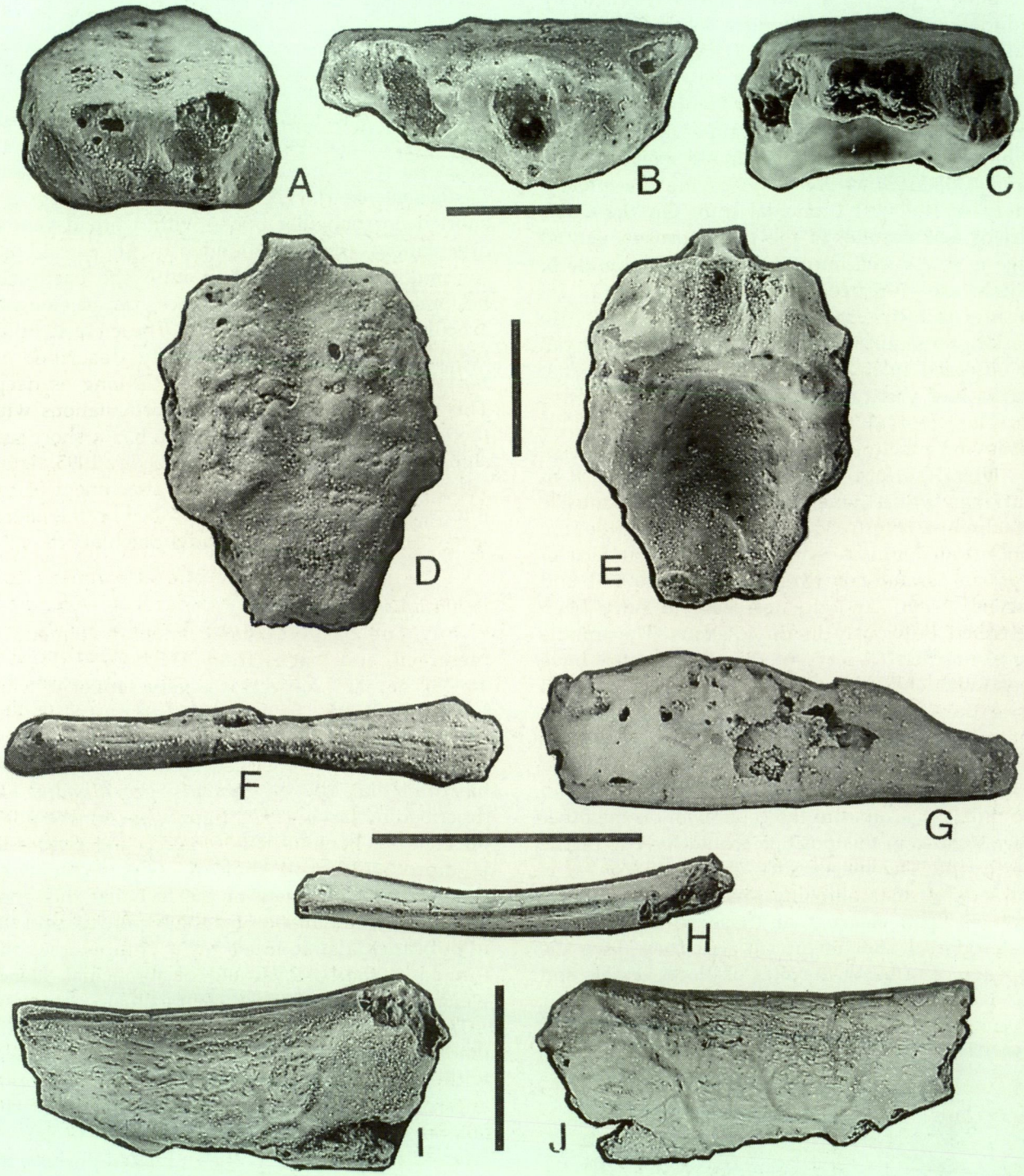


Figure 46 A–E. Views of the basihyal and basibranchial element. A, anterior; B, right lateral; C, posterior; D, dorsal; E, ventral views. F–G, ventral and right lateral views of the urohyal. Note the linear markings on F. H–J. Dorsal, lateral and mesial views of the ceratohyal. Note the strong corrugated area on I showing the attachment for the basihyal muscle scars; the linear scars for the blood vessels on J and to a lesser extent on I; and the linear scar for the efferent artery of the first branchial unit along the top of H, I and J. Scales = 10 mm.

more transverse and about one third as wide as the maximum width of the whole unit.

Its dorsal surface (Figure 48C) has a shallow median furrow flanked on each side by transverse and longitudinal furrows that are quite irregular in depth and shape. In the original preparation there were fragments of a thin denticulated dermal bone on this surface and no doubt they represented paired dental plates beneath which were vessels that occupied the furrows mentioned above. The ventral surface has a deep excavation, the ventral basibranchial fossa of Jarvik, occupying most of its area. This probably served for the attachment of the sternohyoideus muscles, between which lay the main body of the urohyal. This excavation is bordered anteriorly by a strong ridge the crest of which lacks periosteal bone and corresponds with the transverse ridge in the same position in *Medoevia*. In that genus the crest of the ridge also lacks periosteal bone, a fact which led Lebedev to suggest that it possibly marks the fusion line between the basihyal and the basibranchial. Laterally the ridge weakens and posteriorly it is scarcely distinguishable. It is clear that no canal pierced this thick ridge of bone in the manner of the median basal canal figured by Jarvik (1980, figures 112, 130) and interpreted by him as transmitting the hyogenioglossus muscles. In fact *Gogonasus* is more similar to *Glyptolepis* in this respect as in others, though it is not possible to make much of this similarity because *Medoevia* also has the *Gogonasus* arrangement. Hence this pattern may be a primitive feature of both osteolepiforms and porolepiforms.

The anterior face (Figure 48E) carries a transverse teardrop-shaped scar on either side of the median ridge in the anterolateral excavation mentioned above. This scar, like all the other attachment scars on this bone, has a slightly raised perichondral rim around a vesicular surface. It is separated from a more ventrally placed upright scar by a narrow strip of periosteal bone, best preserved on the left side of the specimen. Both these scars are present on *Medoevia*, the dorsal one being interpreted by Lebedev (1995, figure 18) as being for the attachment of the hypohyal, and the ventral one for the articulation of the urohyal (Lebedev's 'auh ar'). These latter scars are apparently too long to be just for the articulation, but the surface on which they lie is at such a low angle to the length of the urohyal that instead of being a simple articulation, it must have been for the attachment of ligaments oblique to the bone surface, thus producing an elongate scar. Between these two scars there is a slight depression floored by periosteal bone. This depression would have contained the dorsal surface of the anterior stalk of the urohyal, the posterior end of the stalk being marked by a slight change in the slope of the dorsal edge of the urohyal (Figure 47).

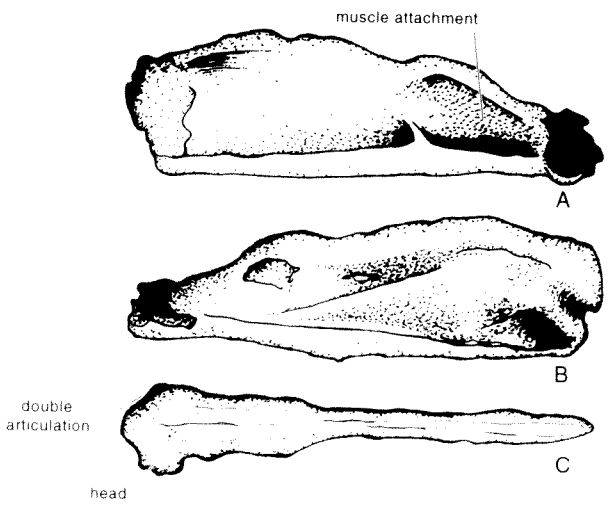


Figure 47 Urohyal of WAM 86.9.661. A and B are lateral views. C is a ventral view.

On the middle part of the lateral face of the unit (Figures 46C, 48D) is a large scar with its long axis vertical. It is separated from the scar in front and the one behind by a broad band of periosteal bone. This scar was for the attachment of the hypobranchial 1 element. The attachment for hypobranchial 2 is not so deep but it is longer, and is situated in the anterior part of the posterolateral excavation. This scar does not extend back to the posterior end of the basibranchial, whereas in *Medoevia* it extends to the posterior edge of the basihyal/basibranchial 1.

The posterior face of the basihyal/basibranchial (Figure 48D) is complex and is best preserved on the right side of the specimen. As is shown on Figure 48D, the entire face is occupied by vesicular bone surrounded by a lip of periosteal bone. Despite this continuity, the scar has joined posterodorsal and posteroventral components. The question is whether this surface is for the articulation of basibranchial 2, or for the articulation of the paired hypobranchial 3 bones? This has important implications because in *Medoevia* the hypobranchial 3 is articulated entirely with the basibranchial 2 (Lebedev 1995, figure 18). Hence there are three options: the break between basibranchials 1 and 2 in *Medoevia*, as interpreted by Lebedev, is a crack; or the two basibranchials in *Gogonasus* are fused; or only one basihyal/basibranchial is present in members of the Osteolepididae, though not in the Tristichopteridae; or the posterior surface is really for the basibranchial 2 which is not preserved in the matrix.

The following points are relevant to such a discussion. The first issue is excluded because checks by both Lebedev and Long confirm the presence of two elements. In the osteolepiform

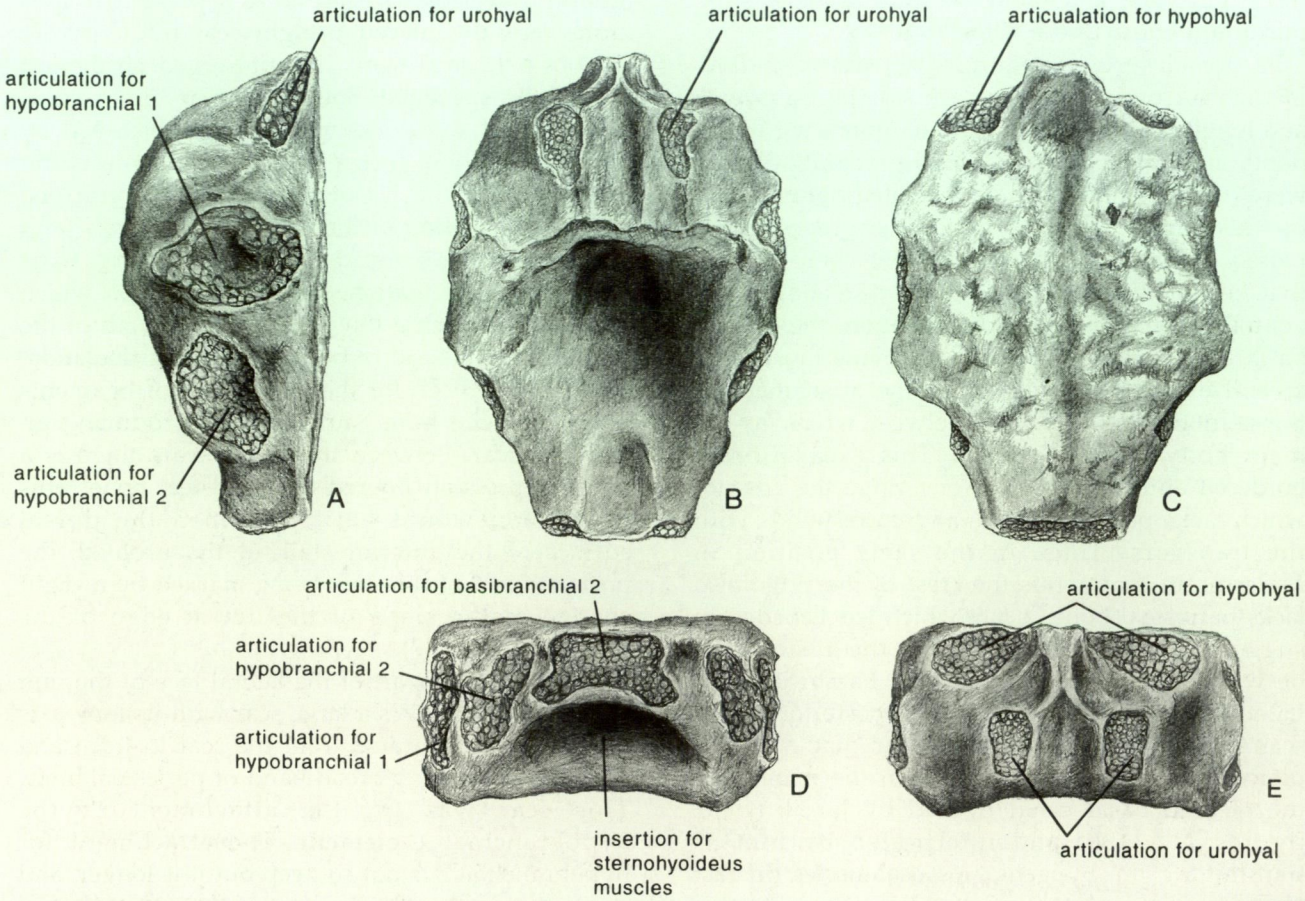


Figure 48 Reconstruction of the basihyal/basibranchial to show details of the scars for the insertion of the various muscles, attachment of the associated bones and details of the surface for the intervening soft tissues. A, left lateral, B, ventral, C, dorsal, D, posterior, E, anterior.

Eusthenopteron (Jarvik 1980, figures 112–113) and also in an undescribed new tristichopterid from Canowindra, N.S.W. (Johanson and Ahlberg, in press) there are two elongate basibranchials, only hypobranchials 1 and 2 are attached to basibranchial 1. [Note, however, that the porolepiform *Glyptolepis* (Jarvik 1972, figure 28) has only one basibranchial/hypohyal and three hypobranchials are attached to it.] The scar on the posterior surface of the basihyal/basibranchial of *Gogonasus* has a bilobed arrangement which is unlike the arrangement we would expect for hypobranchial attachment. And finally, the attachment of hypobranchial 2 in *Medoevia*, which provides the closest basis for comparison with *Gogonasus*, reaches to the posterior limit of what Lebedev refers to as the basibranchial 1, and hypobranchial 3 is attached to the posterior, rather than the lateral, surface of basibranchial 2. Amid all this evidence we see no unambiguous solution. However, the dorsal and ventral surfaces on the continuous attachment area offer the strongest evidence that a single bone was attached, and this can only be the basibranchial 2. This interpretation is also consistent with the view that osteolepiforms have two basibranchials whereas the porolepiforms have one. In this interpretation, hypobranchial 3 would have been attached to basibranchial 2, which is not preserved. It also means that there were larger gaps between the hypobranchial attachments on the basibranchials than occur in *Medoevia*.

The fourth hypobranchial was attached to an articulation on the posterior branch of hypobranchial 3.

In addition to the scars for the attachment of the various items of the branchial skeleton, the surface has small depressions which are suitably placed to have been areas of attachment of muscles. Jarvik (1980, figure 133) has shown genioglossus muscles as running back from the mandibular symphysis to the anterior end of the basihyal/ basibranchial, and the median depression on the front of the bone between the attachment for the hyomandibular scars could well have been for such a muscle. We do not have sufficient data to reach a conclusion.

Urohyal

A single almost complete, but rather poorly preserved, urohyal is known from WAM 86.9.661 (Figures 46F,G; 47A–C). It is so thin that complete extraction from the matrix has proved impossible without destruction of significant features. Hence, as the photographs show, there is still matrix glued to the sides of the specimen.

In lateral view the ventral margin is almost straight, but the dorsal margin shows a slight projection at the posterior end of the short stalk which carries the anterior articulation, and a second, broader projection at the point of maximum depth of the bone. The anterior stalk referred to above permits the urohyal to lie in the groove in the basihyal/basibranchial between the attachment surfaces for the ligaments to the urohyal. The posterior edge of the bone is poorly preserved, but the little remaining suggests that it was truncated rather then rounded. The height/length ratio of the bone is ca 0.3.

Both dorsal and ventral margins are expanded by divergence of the periosteal layers, which are close together over most of the unit. The ventral margin is the more robust, involving a little bone thickening as well. In ventral view, the anterior third is expanded to make a slightly flattened surface, which terminates in what seem to have been two slightly expanded facets, presumably for articulation with the basihyal/basibranchial, as in *Medoevia* (Lebedev 1995, figure 19A). The posterior end is also slightly expanded but much less so than the anterior end, and it terminates in a point only the base of which remains. The entire length of the ventral surface is striated (Figures 46F; 47C).

The dorsal surface is not so expanded as the ventral and it is not flattened, but over the anterior quarter of its length it is slightly expanded to form a buttress for the anterior articulations. It appears that the two perichondral layers do not meet along the entire dorsal edge of the bone, but this could be the result of poor preservation.

The flanks of the bone leave a great deal to be desired in the way of detail, but a groove can be distinguished running from the back of the anterior articulation in a posteroventral direction to fade away near the deepest part of the bone.

In most respects, therefore, the urohyal of *Gogonasus* is like that of *Medoevia* rather than *Eusthenopteron*. It is completely unlike that of *Glyptolepis*.

Branchial arch elements

These are known only from ANU 49259 in which they are dissociated and incomplete. Their positions in the rock as they were being etched are shown in the Frontispiece of this paper.

Hypobranchials

We have identified three hypobranchials from the right side and hypobranchial 2 from the left of ANU 49259. They are all of approximately the same size with wide articulatory facets to the basihyal/basibranchial.

Hypobranchial 1 (Figure 49E) is distinctly more curved in plan view than either 2 or 3. It has shallow furrows on both mesial and lateral surfaces. A short anteriorly directed process like the one on *Medoevia* (Lebedev 1995, figure 18) lies adjacent to the mesial end of the bone. This was for the interarcual ligament (Jarvik 1980, figure 33).

Hypobranchial 2 (Figures 49B,C; 50A,B) is a straight-sided subrectangular bone, with a strongly convex articulatory facet to the basibranchial. Its ventrolateral surface has a longitudinal furrow for the branchial artery, and a short blunt process for the transversalis ventralis muscle, as noted by Lebedev (1995, figure 18) for *Medoevia*. The distal end which articulated with the ceratobranchial, is very compressed and twisted, so that the long axis of the facet is rotated at an angle to the basibranchial facet.

Hypobranchial 3 (Figures 49A; 50 C, D) has a distinctive bent shape and on the bend it carries two short blunt processes. The more dorsal process was probably for the articulation of hypobranchial 4, and the ventral one for the attachment of the muscles which Lebedev in *Medoevia* referred to as the obliquus ventralis, presumably following Jarvik (1980, figure 133A).

The identity of the branchial muscles is a matter of some contention. Wiley (1979) reviewed the distribution of branchial muscles within the osteichthyans, and from our point of view has provided useful new data on sarcopterygians. The extant genera he considered were the dipnoans *Neoceratodus*, *Protopterus* and *Lepidosiren*, and the actinistian *Latimeria*. He 'refuted' the hypothesis that *Latimeria*, and by inference other actinistians, were sarcopterygians because *Latimeria* lacked three paired branchial muscles found in the dipnoans and Recent choanates and actinopterygians, a very dangerous and overstated conclusion in view of the highly specialised buccal, mandibular, and jaw opening features of *Latimeria*, and its remoteness from the time of separation of the actinistians and the other groups in question. If we accept the result of his dissections, and his synonymies, a number of points relevant to our present problem become apparent. Dipnoans have no hypobranchials, and hence they are anything but ideal models for the interpretation of rhipidistian hypobranchials. *Latimeria*, and extant Amphibia are so specialised (i.e., neomorphic) that they too are unlikely models. Even arguing from the common features of extant organisms to produce a primitive sarcopterygian model, as Wiley (1979, figure 5B) has done, is hazardous, simply because of the lack of information.

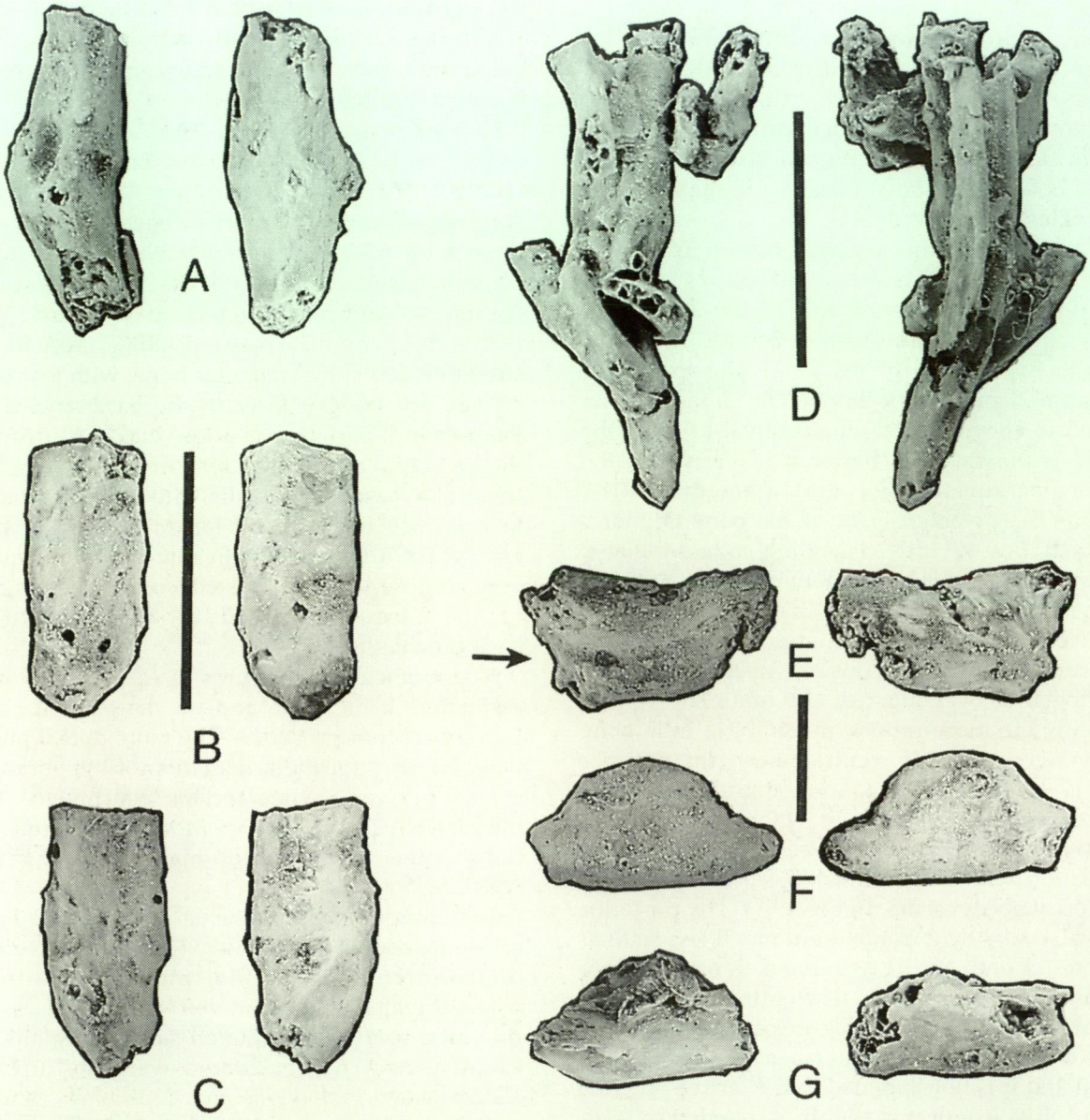


Figure 49 Various parts of the branchial series bones of ANU 49259. Many of these can be partly seen in the frontispiece, and some of them are also illustrated on the next Figure. A, hypobranchial 3. B,C, hypobranchial 2 from both sides of the specimen. D, views of several ceratobranchials and infrapharyngobranchials? E, hypobranchial 1 showing the foramen for the afferent artery of the first branchial unit (black arrow). F, hypohyal? with most of the details slightly impressed. G. One of the more dorsal branchial bones broken through. Scales = 10 mm.

Despite these reservations, the number of options available for the interpretation of the scars on the hypobranchial elements in rhipidistians is small: the interarcuales ventrales muscles which bind the bases of the successive arches together; the obliquus ventrales muscles which connect the hypbranchials to the ceratobranchials; and the transversi ventrales muscles which connect the ceratohyals with a median raphe.

The ceratobranchials are not well preserved, but substantial pieces are recognised by their curved shape and deep branchial furrows (Figures 49D; 50E,F). They resemble the ceratobranchials of the Gogo dipnoans described by Miles (1977). They vary in thickness, some being slab-sided and others rounded on the sides.

The epibranchials and the pharyngobranchials are not definitely recognised, though some fragments that are still cemented to the ceratobranchials shown in Figures 49D and 50E,F, are probably members of these groups. The long element shown as Figure 50F is also probably an epibranchial. None of this material is sufficiently well preserved to be worth description.

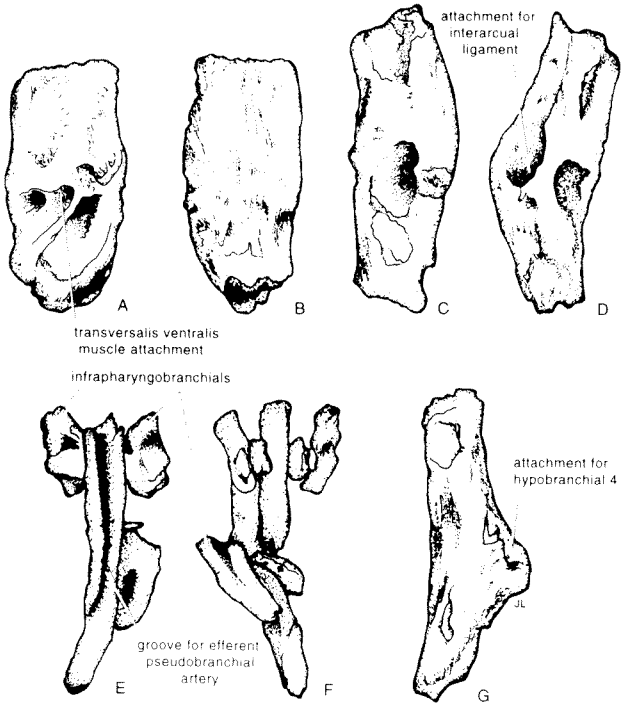


Figure 50 Drawings of various parts of the branchial series, most of which are shown photographically on Figure 49. A–B. Inner and outer views of hypobranchial 2 (Figure 49B,C). C–D. Two views of hypo-branchial 3. E–F. Views of ceratobranchial and infrapharyngobranchials? (Figure 49D). G. Possibly hypobranchial 3.

Scales

We have about 12 scales, some fragmentary, from various parts of the body of WAM 86.9.66. Their exposed parts are all cosmine-covered and are rhombic to sub-rhombic in outline (Figures 51A,B; 52A,C). The overlapped parts are narrow and separated from the cosmine by a gutter in the base of which coarse vesicular bone is exposed. The overlapped surfaces are present on only two edges of the scales; they are smooth, but in places a small number of pores penetrate the surface. Whereas the edge of the cosmine is clearly constructional against the gutter, the opposite edge of the overlapped surface is destructional (Figures 51A,C). The marginal edges of the cosmine are distinctly rolled producing a lip which would lie above the gutter in the overlapped scale (Figures 51E; 52A–C); on flexure of the body of the fish during swimming, the rolled edge would be displaced into the gutter of the overlapped scale providing some resistance to torsion. This seems to be an evolutionary advance on the peg-and-socket articulation of primitive osteolepiforms.

No scale shows any sign of peg-and-socket type articulation. The inner faces of the scales show clear concentric growth lines (Figures 52A–C), and all have either a bar or a plug of raised bone which usually has deeply resorbed edges, and includes one or more perforations (Figures 52A–F). Similar ridges in *Medoevia* have been referred to as the 'articulating ridge and knob' by Lebedev, but their position demonstrates that they could not take part in any articulation, a point which Lebedev himself has made. Ridges of this kind were described in detail on the scales of *Cladarosymblema* by Fox *et al.* (1995). As a result of all these later works, the presence of peg and socket articulations as a synapomorphy of osteolepiforms has to be abandoned.

SEMs of transverse sections of scales show that the usual three layers of hard tissue are present. The outer cosmine layer is thin, being no more than 15–20 microns thick. The flask chambers are squat in comparison with those of other genera (Figures 53A,B; 54A; 55A; 56A–C) and their walls are strongly concave outwards, producing the effect of an oast-house chimney. The mesh canals are well developed and normal; they lie mainly in the dentine layer or in the junction between the dentine and the vesicular bone. As well as having a rolled edge on the free margins, the cosmine has a rolled edge against the gutter. The underlying vesicular layer has very coarse vesicles that extend out, almost undiminished in size, into the overlapped part of the scale (Figures 53A,B,D; 54D; 56A,B). The basal lamellar layer is thin, making up no more than 12% of the scale thickness, except over the median boss. Its character is well seen in SEMs of the inner surface where the flat-lying laminae can be seen in the walls of the nutrient pores (Figures 52B,D–F), and also along some scale margins as shown on Figure 51D. The fibre bundles making up the successive layers are also well seen on specimens in which the layer has been slightly eroded and are usually at a high angle to each other in adjacent layers (see below). The layer is perforated by nutrient pores that are widest at the internal scale surface and become progressively narrower inwards, producing a conical section. These pores are largest mesially on the scale.

Thin sections viewed under polarised light show the standard alternating dark and bright layers which Gross (1956) termed "quergetroffenes" and "längsgetroffenes Fasserbündel". The layers are not continuous across the whole base of the scale, a point well made by Figures 53A,B; 54B; and 56B,C. Some new layers were added marginally and are folded around the overlapped edge of the scale, where they are progressively resorbed from the inside to allow expansion of the vesicular layer (see below). Towards the outer edge of the inner surface the growth layers can be clearly observed by direct observation of the scale (Figures 52A,B), showing that some lamellae were added peripherally; and on the thin sections in polarised

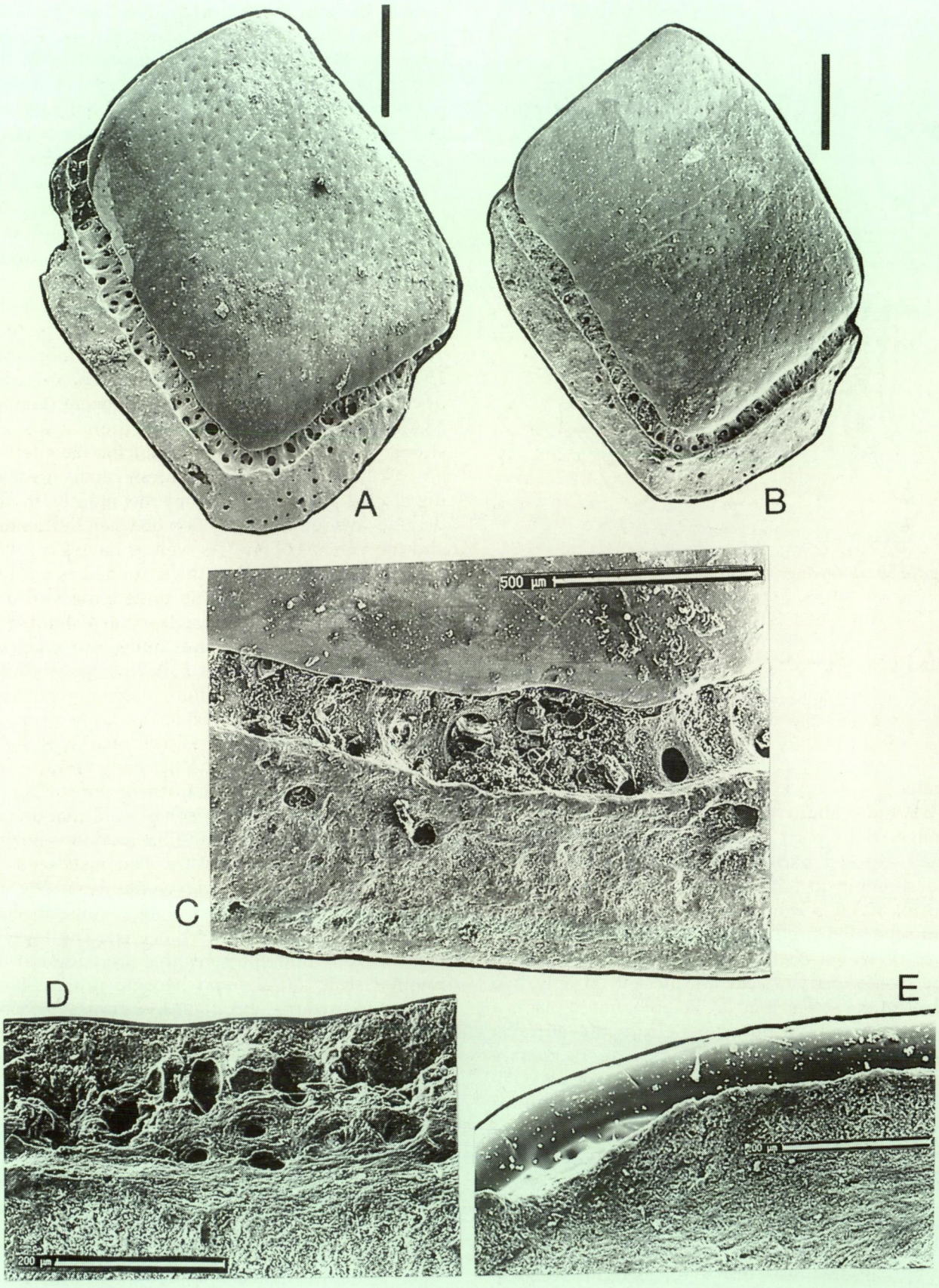


Figure 51 A,B, SEMs of two lateral views of almost lateral median scales of WAM 86.9.661. C, the lateral extremity of B showing the deep furrow and the overlapped area with poorly defined surface. D, the inner edge of the overlapped area of B. It shows that the vesicular edge is exposed along the edge of the scale. E. The same scale viewed at the top of the image (posterior external edge of scale), showing the overfolded edge of the cosmine. Figures 51D,E are from the top of 52B. Scale A–B = 1 mm. Other scales as marked.

light the lamellae can be seen progressively overlapping towards the margin, and folding around it (Figure 56A,B).

Presumably only the last-formed layer of laminar material extends around the scale margin from the inner on to the overlapped surface; as a result of the growth of the vesicles in the vesicular layer, this outer lamellar layer on the overlapped surface was continually being resorbed. This accounts for its thinness in all specimens examined, and for the not infrequent perforations that open down into vesicles. Such a pattern of growth is different from that in *Cladarosymblema* in which new laminae are added widely across the internal surface and around onto the overlapped surface. This means that growth bands are much less visible on the internal surface of scales of that genus.

As in *Cladarosymblema*, the median ridge is composed of lamellate material, but its structure is not simple (Figure 52D–F). Both SEMs and thin sections show that the ridge is underlain by lamellae that are more widely distributed than the ridge itself (Figures 53C; 54B; 56A–C), but the ridge is composed of elongate crystallites set at a high angle to the surface of the ridge and forming a mass of indefinite shape. In places this is overgrown by lamellae that are wider in extent than the ridge itself (Figures 56A–C). The edges of the lamellae forming the ridge are obviously resorbed to varying extents, indicating that it was a feature in continual state of remodelling. This would also account for the variable size of the pores in the ridge and the variable size of the ridge itself in different specimens. The reason for this remodelling is quite unknown.

Teeth and tusks

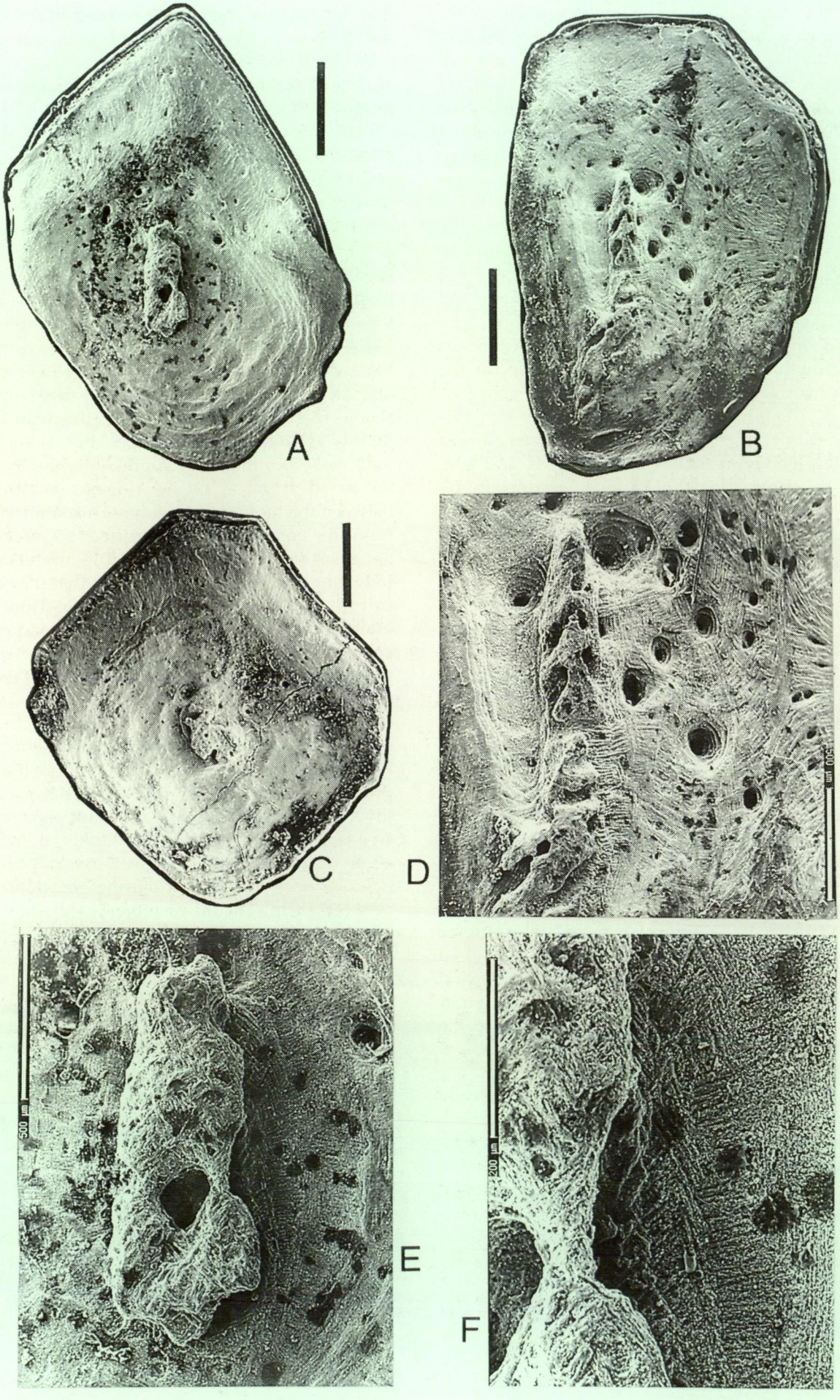
Teeth and tusks are known from the two new specimens, but not from the holotype. Two tusks from WAM 86.9.661 are isolated and are useful for SEM examination (Figures 57, 58). Both have had some material broken from the base, but by and large the remainder is well preserved. The other accessible teeth and tusks are still attached to the bone, and while useful for some forms of examination, are not available for SEM work.

All tusks show folding only at the base only (Figure 57). This is reflected on the external surface where large specimens show ca. 15 folds on a tusk 2.5 mm long. Vacant replacement pits show the same number of folds in the bone of attachment (Figures 57B,E). Looking up into the pulp cavity (Figures 57B,D,E) the folds are seen to be restricted to the basal part of the tusk, although the cavity extends almost to the distal extremity of the tusk as a simple cone. This is apparent in sections and on broken tusks (Figures 57B,E; 58A). The folds extend only a short distance into it the pulp cavity from the sides. In addition, it is important to note that the width of the tissue involved in the dentine infolds is small in comparison with the pulp space between them (Figures 57B,D,E). This is much simpler than even the least complicated megalichthyids.

The external surface of most of the tusk (Figures 57A,C,F,G; 58B–D) shows distinctive ridges and intervening striae. As shown on Figures 57F,G and 58 B,C, at the base of the tusk, where it was embedded in soft tissue, the surface is composed of approximately equidimensional mounds separated by deep but narrow grooves. Distally these mounds become more elongated along the length of the tooth and progressively become dune-like with ridges separated by wider elongated pits. Even more distally, the ridges are elongated and just distal to the basal folds they adopt the final shape. The mounds are present in the depths of the infolds as well as on the ridges, but as shown on Figures 58B,C, their development in the infolds is not as advanced as on the ridges – i.e., the gaps between the mounds are wider. The nature of these mounds cannot be determined by sectioning because of the lack of suitable material, but following Smith (1989) we suggest that they are the initial phases of dentine deposition. This interpretation implies that they are composed of spherulitic aggregates of crystallites, a prediction that is testable when more specimens become available for sectioning.

As indicated above, more distally, but still between the basal folds of the tusk, short ridges lying parallel with the length of the tooth are present (Figures 57F,G), implying that growth of the mounds proceeded as tusk eruption continued. At a level still between the basal folds, an indefinite edge of a thin tissue is seen overlapping the mounds and partially obscuring the depressions between them. This must represent the first phase of enamel deposition. The surface of the tusk at this level is still dune-like, simply because the enamel is so thin and reflects the underlying surface morphology of the dentine mounds. Distal to the basal folding, the ridges are longer and show a variety of sizes and patterns right to the tip of the tusk. Because no alteration to the surface can take place once it has moved through the surrounding soft tissue, this implies that a cuff of epithelium encompassed the tusk up to the distal edge of the folds.

In general the ridges on the fully formed surface are not as pronounced as those on *Megalichthys* or *Cladarosymblema*, and they number a minimum of 125 per mm as compared with 60 per mm in *Cladarosymblema* and 12–15 in *Megalichthys*. What is more, the ridges are not of uniform size, but large and small individuals are interspersed to varying extents, even on adjacent parts of the same tusk. In places they bifurcate and in others they are


A
B
C
D
E
F
500 µm
200 µm

interpolated, but nowhere do they form continuous lines as in *Cladarosymblema*.

Detailed data on the structure of the tusks of *Medoevia* are not available, but Lebedev's figure (1995, figure 10) shows that a smooth-walled pulp cavity extends up high in the tusk, and a small number of simple folds occurs towards the base.

FUNCTIONAL MORPHOLOGY

In the following discussion we have attempted to separate out features that are related to the main functional aspects of vertebrate organisms that leave traces on the skeleton, viz. feeding, respiration, sensory systems and locomotion. Of course, none of these is entirely independent of the others. For example, respiration and feeding are closely related to the capacity of the organism to pump water through the buccal cavity, and as a result it is necessary to evaluate all the factors responsible for buccal pump activity together. This is why we have begun the discussion with one of the generalised morphological characteristics applicable to both functional interpretations, viz. intracranial kinesis. A second point is that we lack most of the post-cranial data relevant to a discussion of locomotion. Despite this, some inferences can be drawn from the overlapping pattern of the scales, and these inferences are then available for testing as further information on post-cranial structures becomes available.

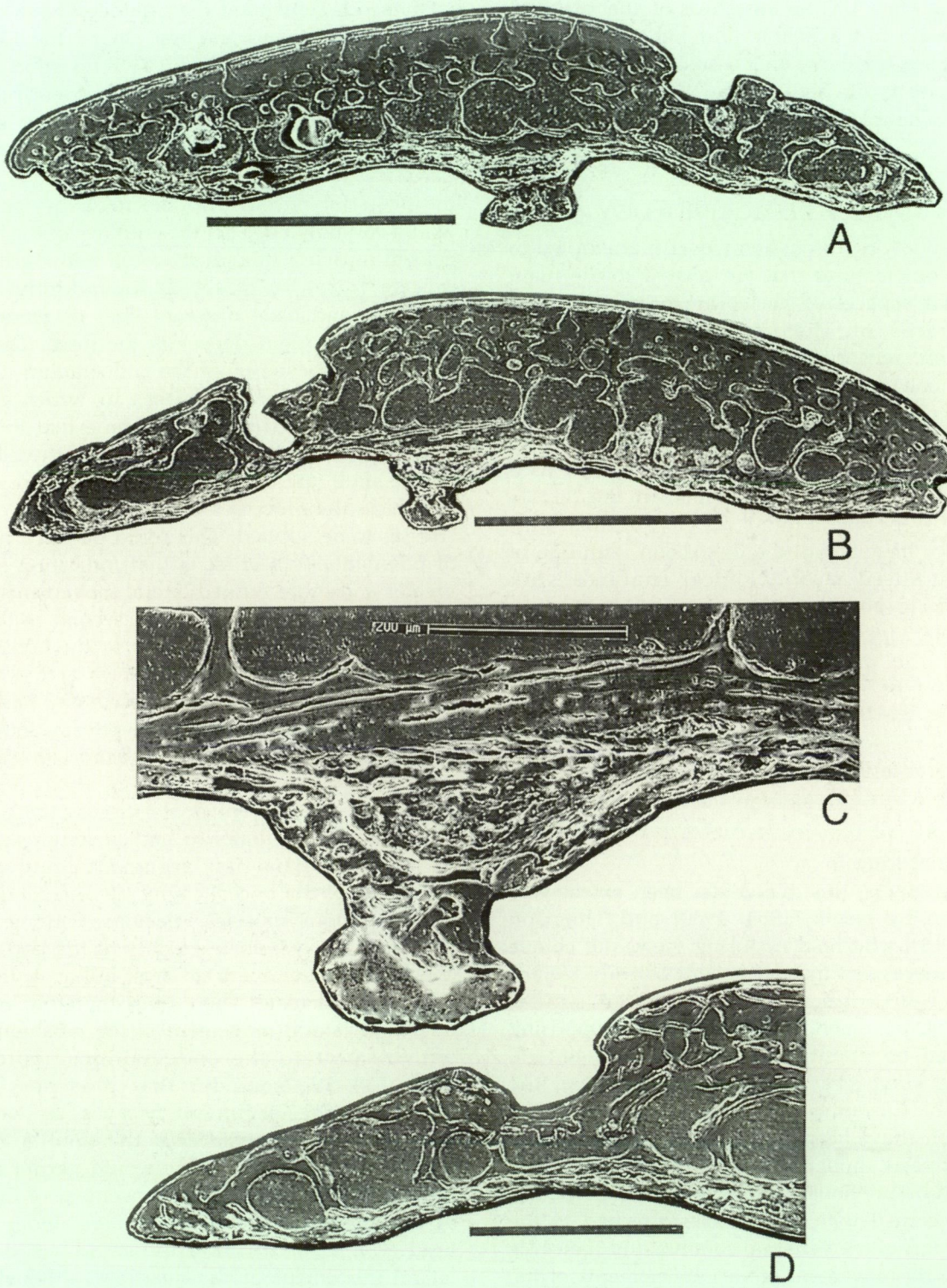
Intracranial kinesis

Among others, this matter has been extensively canvassed by Jarvik (1954, 1980) and Thomson (1967, 1969), who hold opposing views. Of course it is not necessary that all genera of rhipidistians that have an intracranial joint shared similar degrees of movement; it is possible that opposing views can be maintained for different genera. Recently, Hitchcock (1995) has re-examined the material of *Eusthenopteron*, on which most of the conclusions have been based, and has advocated a limited kinesis, though of a different kind from that described by previous authors. In particular, he has been concerned with the muscles attached to the anterior part of the vertebral column, and their role in activating movement of various elements of the head. This view needs further examination especially in view of the availability of new specimens for which most moveable parts of a single specimen are known, i.e., *Medoevia* and *Gogonasus*.

Hitchcock contended that the deep fossa Bridgei in *Eusthenopteron* implies that the epaxial musculature had a large area of insertion on the lateral and posterior faces of the braincase as in *Amia* and *Latimeria*. This conclusion may well be justified for *Eusthenopteron*, but we note that *Gogonasus* has a pair of processes partially covering the posterior entrance to the fossa Bridgei. This would certainly obstruct the entrance of the bulk of epaxial muscles, though it would allow groups of muscle fibres to attach independently to the processes and have different lines of action from those taking origin deeper in the fossa. The large faces on the posterior of the endocranium of both genera also provide surfaces to which epaxial muscles could attach. We conclude that the main mass of muscles that would have attached directly on the skull, are similar in the two genera, but in *Gogonasus* the processes would allow more oblique stresses to be applied. This could permit a number of possibilities: the first is that indicating slightly greater and more refined lateral movements of the head relative to the body; the second is that the movement of the head relative to the body could have been increased. So far as we are aware, no processes of the kind we are discussing have been described from any other osteolepiform, and so our interpretation has to be based on general principles.

Hitchcock then went on to discuss the possible movement of the anterior and posterior elements of the skull. His first argument involved the expansion of the buccal cavity by retraction of the sternohyoideus muscles, placing a 'strong lateral force on the posterior extremity of the jaws..., and consequently the quadrate must follow or the jaws would disarticulate. There must therefore be some degree of lateral movement of the palatoquadrate with respect to the endocranium' (Hitchcock 1995:281). We consider that it is possible to controvert this argument because, as we have shown for *Cladarosymblema*, the double glenoid articulation of the mandible would permit a great deal of lateral or rotational movement of the rami of the mandible relative to the remainder of the head (Fox *et al.* 1995). This would not demand lateral movement of the quadrate, although such movement would be possible unless constrained by some other mechanism. At least this part of Hitchcock's argument is not conclusive.

◀ **Figure 52** A–C. SEMs of three internal views of lateral scales showing the great variation of the internal boss. D, an enlargement of B. Note the lamellae of the inner bony layer exposed in the pores and across the broad surface layer. This may heve been produced by the resorption of the innermost layer, or it may be part of the growth process. E. An enlargement of A showing the details of the fine lamellae as in D. F, a further enlargement of E to show the variation of the fibres of the adjacent layers to show the basis for the layers outlined in Gross's characterisation. Scale A–C=1 mm. Other scales as marked.



Figures 53 SEMs of cut surfaces of scales of WAM 86.9.661. A–B, sections from the polished and etched opposite sides of a saw cut through an embedded scale, cut obliquely so that a complete cosmine edge is present on one side and an overlapped surface on the other. Note the overfolded edges of the cosmine on the free edge and adjacent to the groove, and the disposition of large vesicles in the vesicular layer. C, enlargement of the median ridge to show the lack of conformity of the lamellae forming the ridge (compare Fox *et al.* 1995, figure 68B). D, enlargement of the overlapped surface of another scale showing the arrangement of the laminae on the inner surface and their discontinuous diatribution on the outer surface. Scales A–B = 1.0 mm, C as marked, D = 0.5 mm.

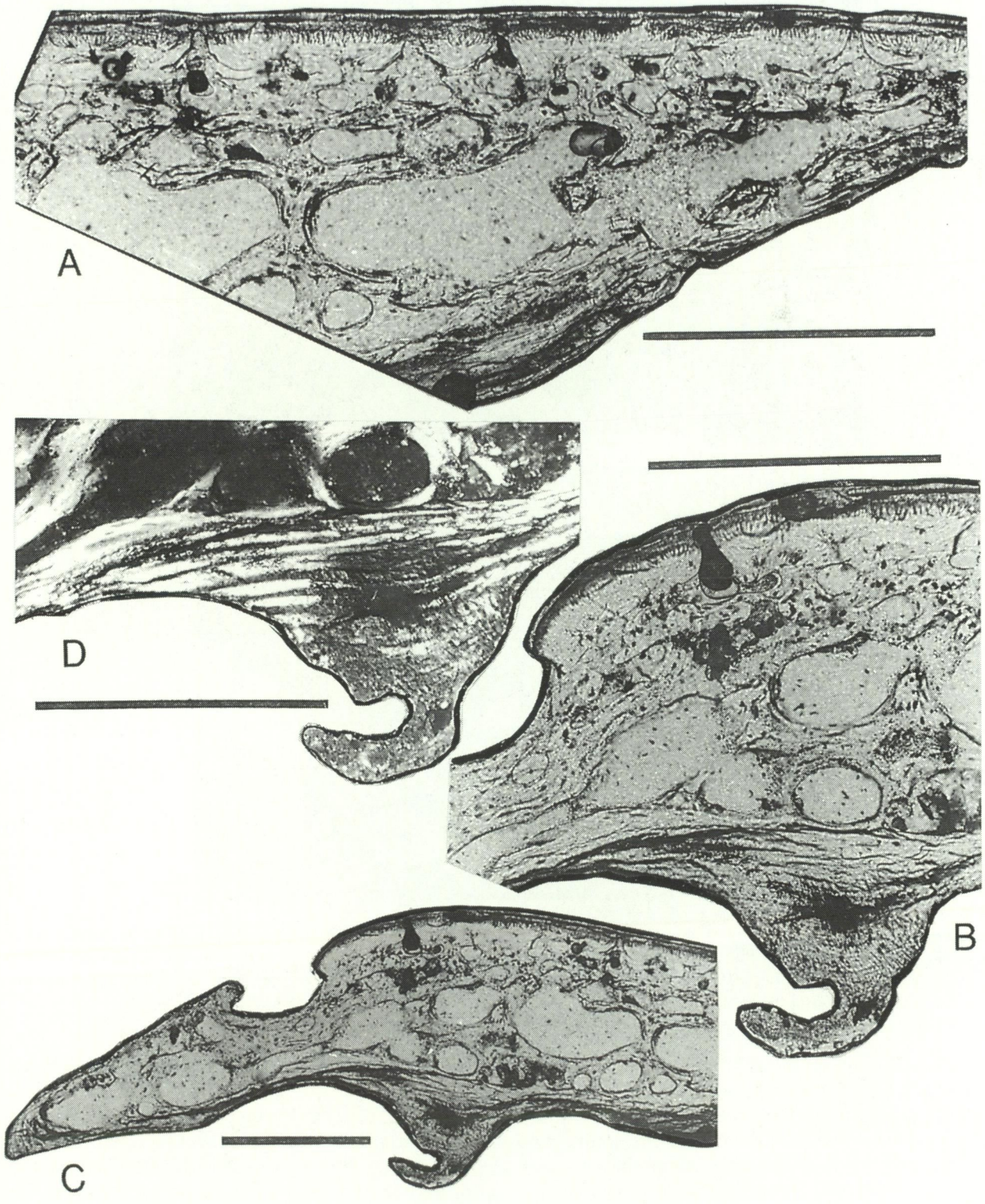


Figure 54 Optical photographs of a vertical thin section of a scale. A, the main surface of the cosmine showing the enamel, the dentine with the flask chambers and the mesh canals. The dentine tubules in the outer part of the cosmine layer are emphasised by mineral staining. B, section to the left of A showing the median ridge which has been strongly resorbed on the left side, and the fibrous nature of the inner part of the ridge (compare Fox *et al.* 1995, figure 68C). The black flask chamber contains an air bubble introduced during preparation of the section. C, same at smaller magnification. Note the discontinuity of the laminae on the inner surface and the folding of laminae around the end of the overlap. D, the median ridge and surrounds photographed in crossed polarised light to show the arrangement of the laminae. Scales A–C = 1.0 mm, D = 0.75 mm.

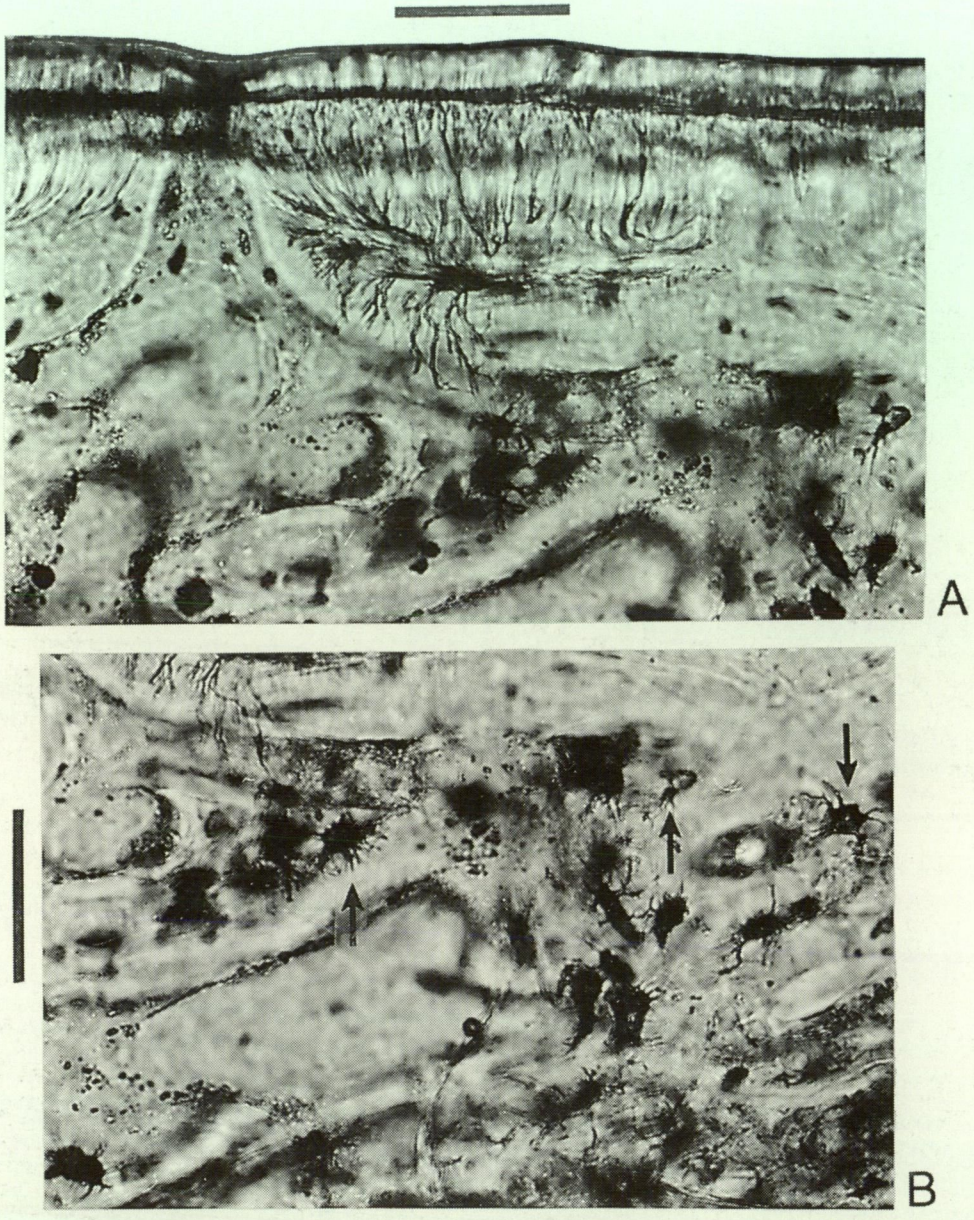


Figure 55 Optical photographs of the upper right corner of Figure 54A. A, enlargement to clarify the relationship between the dentine tubules derived from the horizontal pulp canal, together with the crystallites of the enamel. The shape of the flask chamber is clear. B, section a little deeper into the scale showing the mineral-filled osteocyte spaces with their cell processess still intact. Scales = 0.1 mm.

Hitchcock also commented that 'the articulation of the palatoquadrate to the otical shelf lies in line with the processus connectens and therefore would not prevent movement of the intracranial joint'. We assume that he used the term otical shelf in the sense of Jarvik (1980, figure 88). So far as *Gogonasus* is concerned (Figure 60), such a statement would be difficult to follow because the reassembled specimen shows clearly that there is no firm attachment of the palatoquadrate to the otical shelf; in fact there is a clear gap between the otical shelf and the palatoquadrate, and presumably the space was filled with connective tissue. Even if there were a contact of the type postulated by Hitchcock, the fact that the edge of the otical shelf and the processus connectens are on the same line, tells us nothing about the possibility of intracranial movement, apart from the point that the two could make a hinge for intracranial rotation. However, if the palatoquadrate were firmly attached to the otical shelf it would limit the movement on the intracranial joint because the palatoquadrate is firmly attached to the ethmosphenoid unit at the points discussed below. Nor does it tell us anything about the possibility of lateral movement of the palatoquadrate, because the basipterygoid, autopalatine and processus ascendens articulations are not collinear; thus they do not provide a more or less horizontal hinge around which the whole bone could rotate laterally. The reassembled

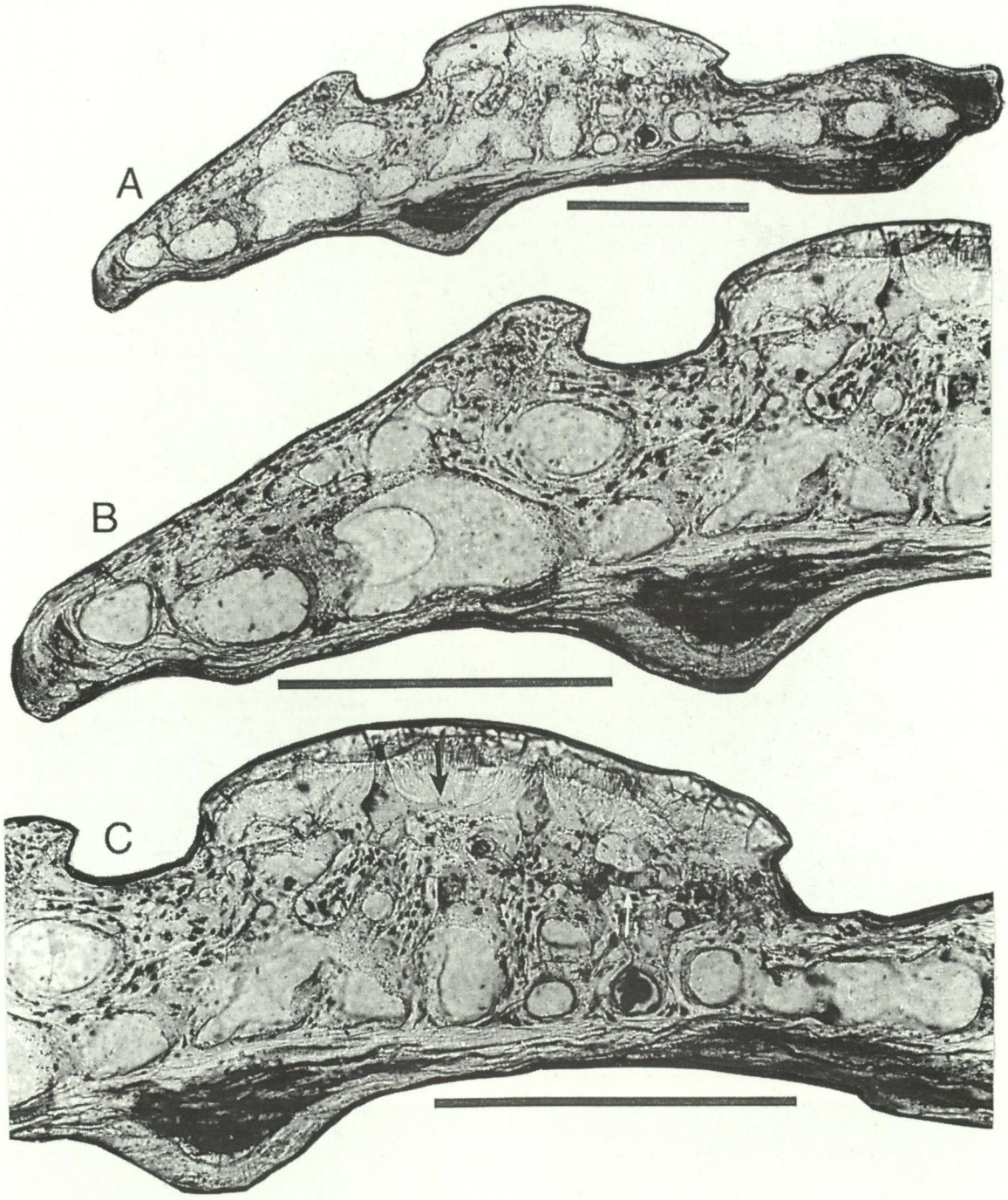
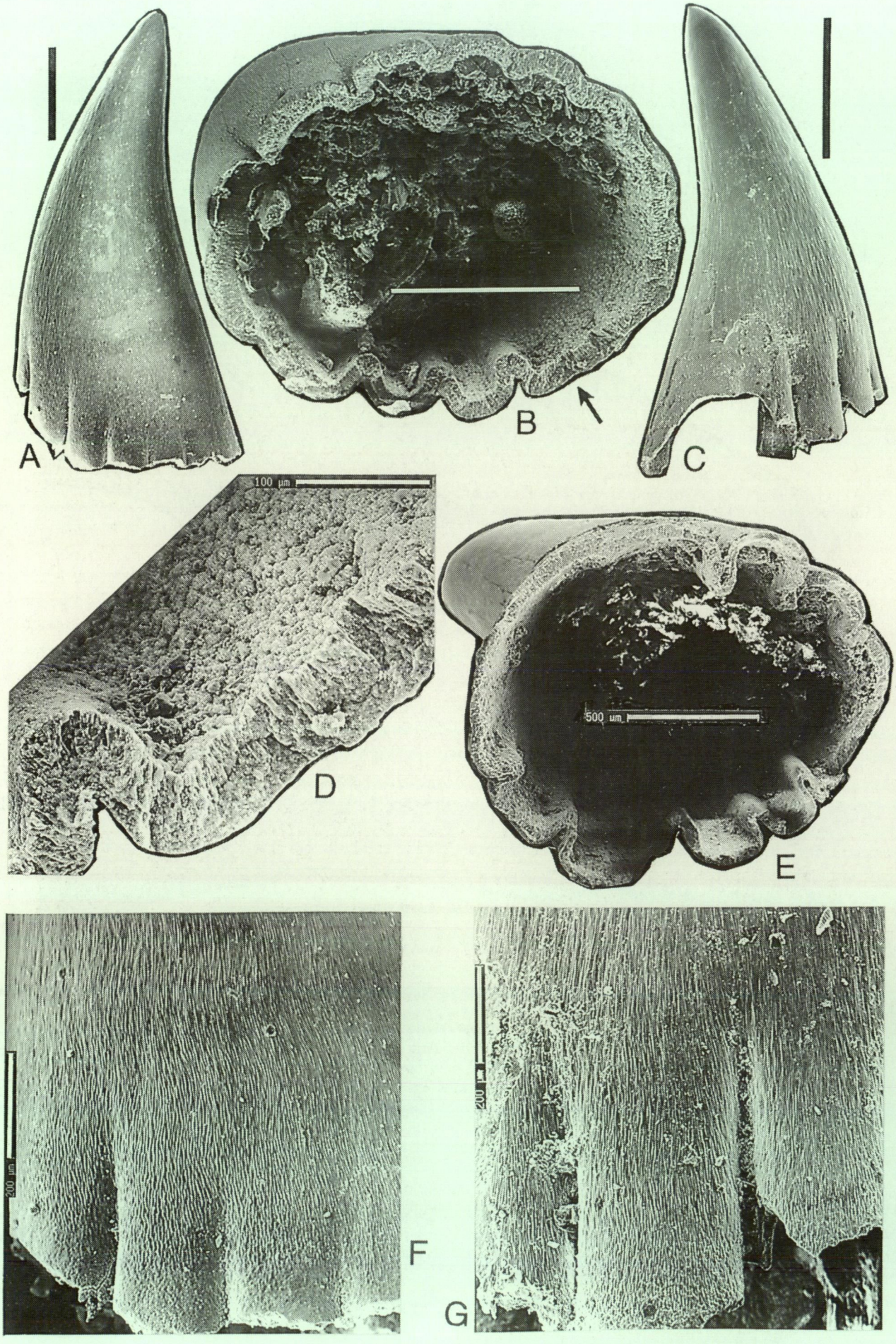


Figure 56 Optical sections across the end of the cosmine-covered scale surface with overlapped surfaces on each side. A, complete section. The right end has been partly destroyed. B, left end of same enlarged to show the laminae of the inner surface incomplete and new laminae added at the extremity folded around on to the upper surface. Note the presence of osteocytes associated with the vesicular bone at the upper surface indicating that the laminae have been removed. C, section to the right of the one above showing the flask chambers, the mesh canals and the cross canals (arrowed). Note the shape of the median ridge and the laminae beneath and forming it. Scales = 1 mm.

specimen shows a tight stable three-point articulation at the three processes mentioned above, and that would have precluded rotational or translational movement of the palatoquadrate on the ethmosphenoid unit of the skull. All these comments are based on *Gogonasus* in the first instance, but similar arguments apply to *Medoevia*, as an examination of the specimen shows. It seems probable that they would also apply to *Eusthenopteron*, the genus on which Hitchcock's argument is based.

So now we are left with an otico-occipital unit


A
B
C
100 µm
D
500 µm
E
200 µm
F
200 µm
G

which could move on a hinge with the ethmosphenoid unit unimpeded by attachment to the palatoquadrate. The only remaining constraints to intracranial movement are the junction between the dermal roofing bones of the two units, the junction at the processus connectens, and the notochord which extended from one unit to the other. Jarvik (1980, figure 88) has figured the processus connectens of *Eusthenopteron* as a long structure fitting back inside the flange of the otical shelf. In *Gogonasus*, and probably also *Medoevia*, judging from Lebedev (1995, figures 1D, 2), the process is much shorter and does not fit back so far. In fact, even though the surface in neither of the new specimens of *Gogonasus* is well preserved, the holotype has a clear vesicular bony surface well differentiated from the surrounding periosteally covered surfaces, and suggestive of a ligamentary or a cartilaginous junction with the inner anterior face of the otical shelf (Figure 10C). In other words, the junction would not make a precise hinge that allowed rotation in a vertical direction only. In *Medoevia* the surface of the process also consists of unfinished vesicular bone, indicating a ligamentary or cartilaginous junction with the inner face of the otical shelf.

As shown in the description above, the supratemporal articulation in *Gogonasus* is very weak; it is unlikely to have served as a major hinge for intracranial movement, as it apparently did in megalichthyids (Bjerring 1972; Fox *et al.* 1995, figures 29; 31; 32; 36). The situation in *Medoevia* is similar to that in *Gogonasus*. In any case, we must take into account the fact that the lateral line canal crosses the junction between the two moieties at the above hinge, and that this implies only slight pull apart at this point if the hinge of intracranial movement was at the processus connectens.

The third of the listed points is the strength of the notochord. Whilst this would probably have resisted bending, and hence would have acted to return the two units to a resting position if flexure did occur, this is unlikely to have been its primary function. More probably it gave stability to the intracranial joint while permitting limited movement (see below).

The final point at issue is the strength of the basicranial muscle between the two cranial units. In *Gogonasus* this muscle had a large cross-section, as can be shown from its attachment surface on the endocranium adjacent to the notochordal pit. On ANU 49259 these surfaces are ridged showing that the muscle was firmly attached to the bone. Presumably this means that the muscle was strong. It could have had any one of three functions: to hold the two units in position during the stress of a bite; to provide a counter to the flexor tendency of the notochord under compression; or to provide a flexor muscle for the intracranial kinesis. The first of these possibilities seems to be inconsistent, at least superficially, with the fact that the insertion is well below the hinge point formed by the processus connectens, and any strong muscle contraction would tend to rotate the ethmosphenoid unit downwards with respect to the otico-occipital unit, rather than just clamping the two units together. However, it should be considered in association with the second possibility which depends on the elastic properties of the notochord; because its axis lies above the hinge formed by the processus connectens, the notochord would tend to rotate the ethmosphenoid unit upwards with respect to the otico-occipital unit. Thus it is possible that the basicranial muscle and the notochord acted together to hold the two units in a stable position during a bite. The third possibility, that the muscle was entirely to produce flexure at the intracranial joint is improbable, in the light of our observations that neither of the possible hinges are designed to act as a load-bearing structure.

This examination does not preclude the possibility of some intracranial kinesis, but if such did occur, it would have been minor. Observation of the Gogo *Onychodus* specimens demonstrates that this fish had extreme degree of intracranial kinesis – the intracranial gap is very large, the otico-occipital unit is never ossified (presumably being cartilaginous and flexible in life), the gill arches are also poorly ossified and the large anterior symphysial tooth whorls indicate that the gape must have been large for the animal to capture prey. Conversely *Gogonasus* shows limitation in all these features, suggesting that intracrnial kinesis was much more limited.

◀ **Figure 57** Two tusks of WAM 86.9.661. A–B, SEMs of lateral and basal views of the smaller of the two tusks available for scanning. Note the simple folds which extend for only a short distance into the pulp cavity. D, enlargement of the edge of the tusk marked in B (arrowed), showing the arrangement of the dentine tubules and the surface of the growing dentine in the pulp cavity. C, E, lateral and basal views of the larger of the two tusks available. F, lateral view of the left base of A. F, similar view of central part of base of C. Both show the transition from the exposed ends of the first formed dentine columns at the base, to the zone with thin enamel, to the first-formed striae on the more distal part near the top of the folds. Scales A–B=500 microns; C= 1 mm. Other scales as marked.

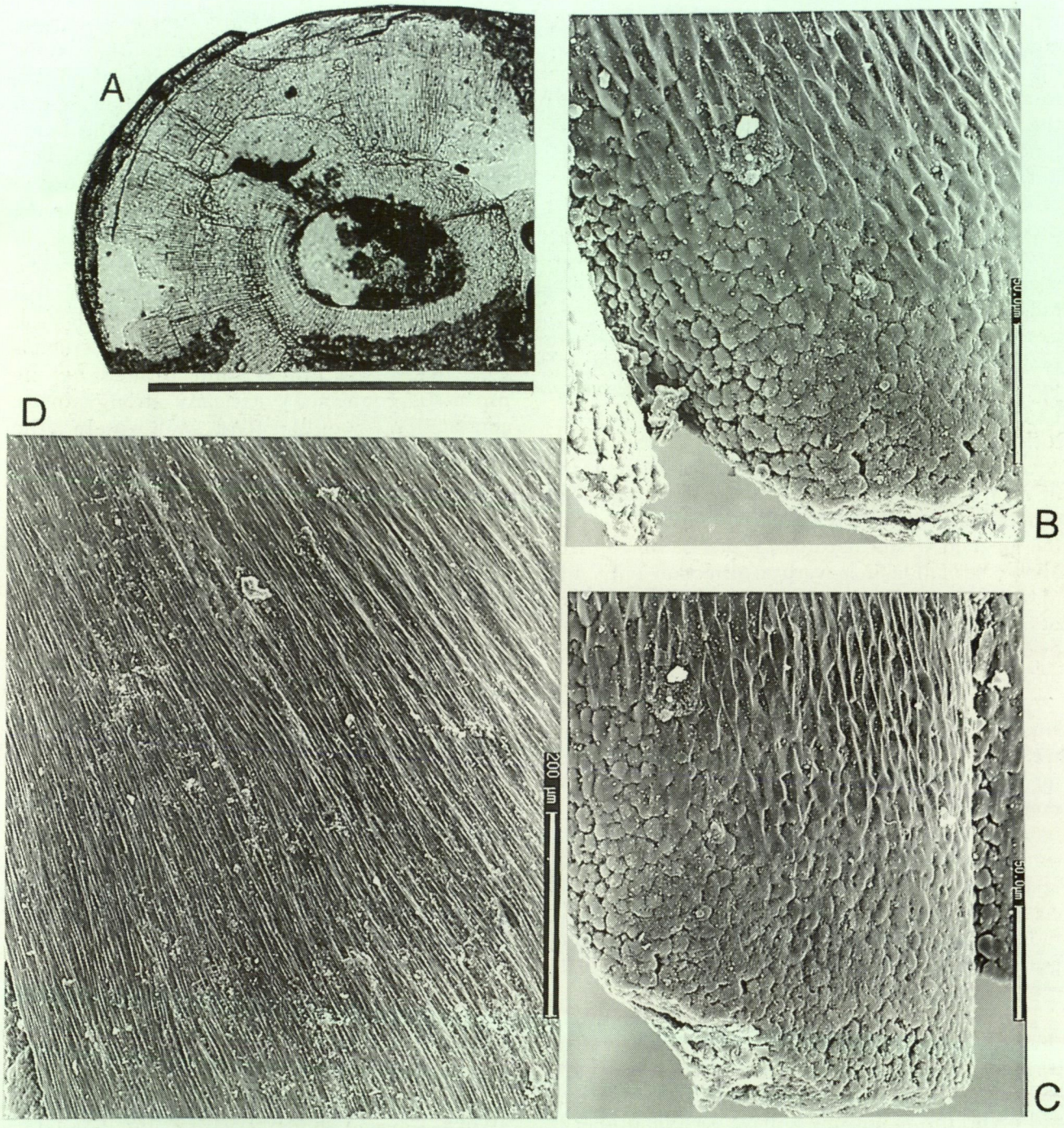


Figure 58 Tusks of WAM 86.9.661. B–C, two SEMs of lateral views of the base of the tusk in 57A,F, images made at slightly different angles to show the different size and spacing of the dentine mounds on the ridges and in the furrows. Note the proximal edge of the thin enamel coating distal to which the surface topography is reduced and the shapes of the dunes is modified. D. SEM of the surface of the specimen in Figure 65C, distal to the basal folds. A, thin cross section near to isolated tip of a tusk showing a remnant of enamel and the well-banded dentine. Scale of A = 0.5 mm; others as marked.

Attachment of palate to maxilla and its possible limitation of movements

As shown in the appropriate section of the text we have not found any evidence that the maxilla was not firmly attached to the adjacent dermopalatine and ectopterygoid, though the anterior process fits very broadly into a groove on the inner face of the dermopalatine, and a ridge dorsal to the tooth row fits broadly into a much larger groove on the ectopterygoid. These structures would not have had much stabilising control on the movement of the maxilla. Jarvik has indicated that in *Eusthenopteron*, the maxilla was probably separated from the other bones by a layer of connective tissue in which vessels passed; this would have permitted some movement. Anteriorly

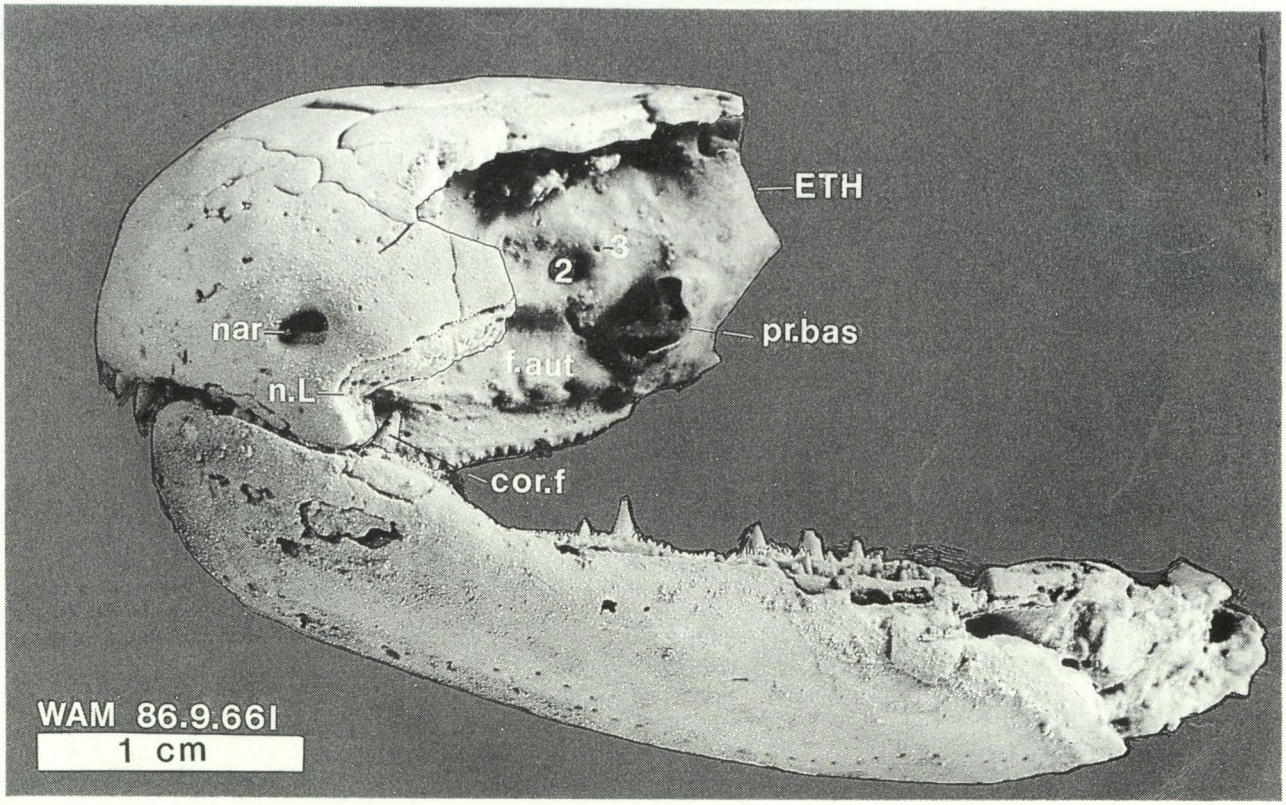


Figure 59 Lateral view of the ethmosphenoid region and attached mandible of WAM 86.9.661 showing the first coronid tusk and how it fits into the ethmosphenoid, and the arrangement of the mandible in relation to the anterior end of the ethmosphenoid unit. *Abbreviations:* 2, 3 foramina for cranial nerve II (optic) and NIII (oculomotor); ETH, ethmosphenoid unit; cor.f, coronoid fang; f.aut, fossa autopalatina; n.L. notch for lachrymal, nar, naris; pr.bas,m basipterygoid process.

the maxilla fitted into a notch in the edge of the premaxilla and the lachrymal, but the bones were not tightly sutured together. Both of these observations suggest that some movement between the palate and the cheek was possible, though it may have been limited by connective tissue. It is also clear that the palatoquadrate was not firmly attached to the part of the endocranium to which the vomers were attached, and hence a rocking movement between these two elements would have been possible. We note however that this junction is very oblique to the midline, and so the suggestion of Rosen *et al.* (1981: 191) that the dermopalatine/vomer and the lachrymal + maxilla/premaxilla + lateral rostral are in the same transverse plane, is not applicable to *Gogonasus*. It is probably not applicable to *Eusthenopteron* either, the genus on which their judgment was based, because they apparently did not understand the articulation mechanisms between the palatoquadrate and the endocranium in that genus. They proposed that the palatoquadrate articulated with the vomer via three small articulatory surfaces, but as is shown by our Figure 25, 26, the articulation is between the palatoquadrate and the endocranium along an oblique groove and ridge, and at the autopalatine articulation. These ensure that the amount of movement is limited. The relation between the palatoquadrate and the vomer is at a small overlap which is present in one specimen of *Gogonasus* but not the other. This has nothing essential to do with the articulation of the two bones. Our conclusion is that the amount of vertical movement between the maxilla, the palatoquadrate and the rostral part of the ethmosphenoid unit is limited, and its probable function was to absorb the shock of a biting strike. It did not affect the size of the mouth gape.

In relation to possible lateral movements of the maxilla, we have already indicated that such movement was possible but limited. However, it should be noted also that once the jaw had closed to the level where interlocking of the teeth of the dentary and the maxilla occurred, rotation of the mandible via the double glenoid fossa would have been possible. The teeth on the dentary would have locked into the groove between the maxillary teeth and the edges of the coronoids, and the tusks of opposing upper and lower jaws would have fitted into large open cavities that would not have restricted rotational movement (see below). During jaw closure, the coronoid fangs and dermopalatine/ectopterygoid fangs fitted into fairly large pits on their opposing jaw, thus a small

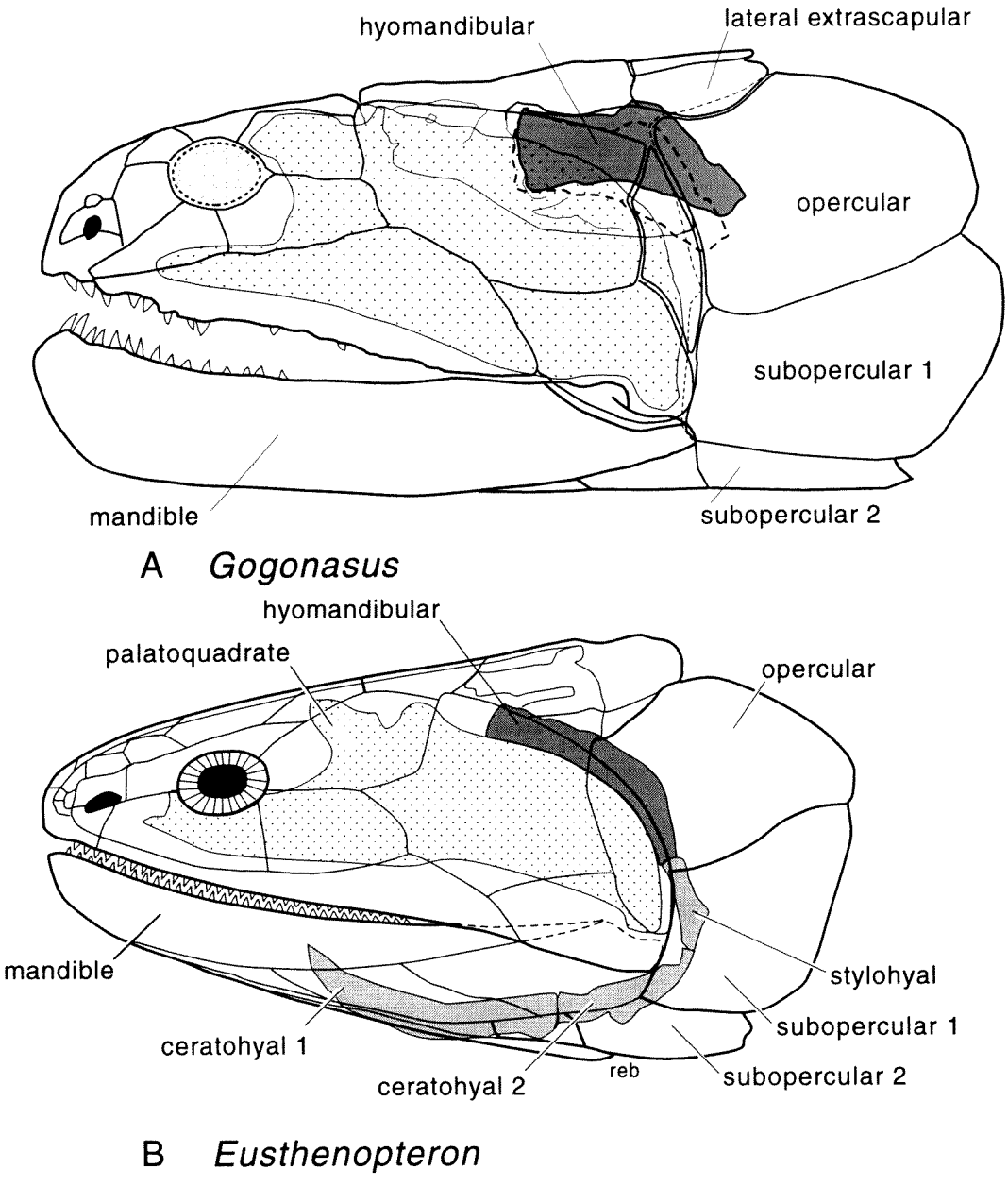


Figure 60 Lateral views of *Gogonasus* and *Eusthenopteron* to show the arrangement of the opercular series and known position of the hyoid arch in relation to the remainder of the skeleton. Note in particular the dorsal position of the orbit in *Gogonasus;* the highly inclined slope of the hyomandibular in *Eusthenopteron;* the low height of the skull at the posterior end of the skull in *Eusthenopteron;* and the difference in orientation of the operculars in the two genera. *Eusthenopteron,* after Jarvik (1980).

degree of movement would have been possible, if this factor only is considered.

Respiration

Height of skull

One of the features of *Gogonasus* and *Medoevia* is the great height of the skull from the denticulated surface of the parasphenoid to the skull roof immediately above it, the height being ca. 50% of the length. The corresponding value in the megalichthyid *Cladarosymblema* is ca. 44%. Profiles of some other osteolepiforms were figured by Long (1985a, figure 7), but these were taken from the work of previous authors and, in at least some instances, involved considerable reconstruction. They are more depressed than *Gogonasus*, the only exception being *Thursius estonicus* which was based on a species which was not necessarily correctly assigned to that genus, and in any case also involved reconstruction. A second point related to the skull height is that the palatoquadrate is steeply inclined down to the quadrate articulation, making

the skull at the jaw articulation unusually high relative to its width. What is the significance of this difference in proportions between *Gogonasus* and other osteolepiforms?

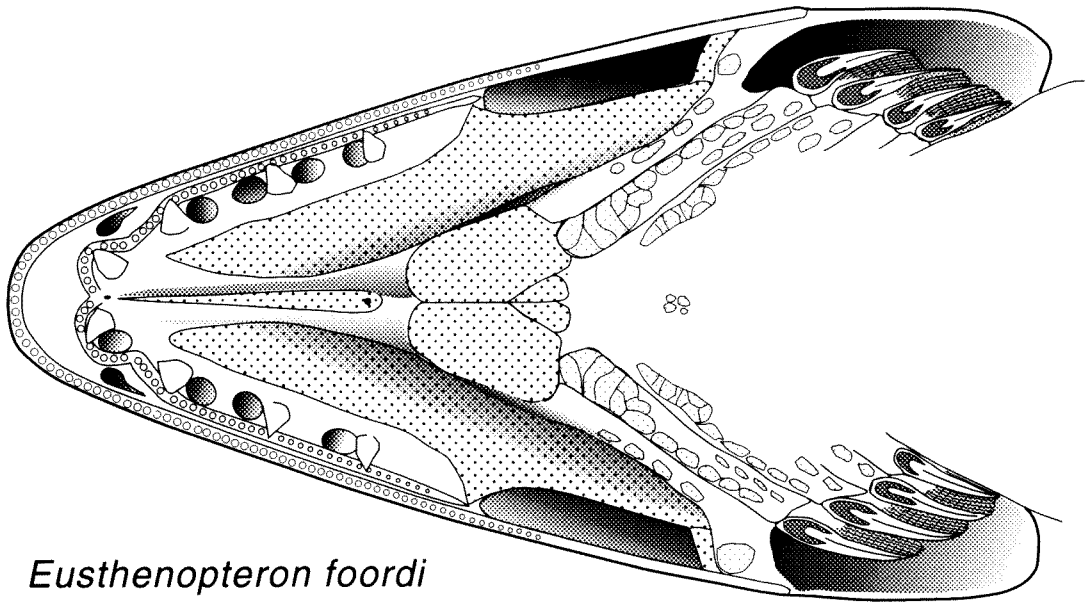
1. It means an enlarged space is available for the adductores mandibulae.
2. The posterior part of the buccal cavity is unusually high, indicating a large volume available for the storage of water before expulsion over the gills.
3. The palatoquadrate walls that form the steep lateral margins of this part of the buccal chamber are devoid of denticles, unlike the corresponding walls in *Medoevia* and *Eusthenopteron*. Embedded in this soft tissue was a strong mandibular branch of the trigeminus nerve. Therefore, the soft tissue cover over these surfaces must have been moderately thick. This implies that the extra space in the posterodorsal part of the buccal cavity was not for food manipulation, but rather to increase the volume for water.
4. The height of the buccal chamber is also related to the height of the gill chamber immediately behind it. This is confirmed by the position and relative size of the opercular (see reconstruction in Figure 60).
5. The gill chamber is related to the size and position of the basihyal/basibranchial. The basibranchial is short and kite-shaped, and has the branchial arches articulating at an angle of about 45%. Water would be forced across them at an angle as shown in Figure 61. Like *Medoevia*, but unlike *Eusthenopteron*, *Gogonasus* had a very short basihyal-basibranchial, and it seems that the more posterior gill arches were articulated with the ceratobranchials immediately in front. From the size and shape of the ceratohyals we infer that the basibranchial was situated about mid-way along the length of the mandibular rami, and not as in *Eusthenopteron* (see Figure 60). This is further emphasised by the fact that in tristichopterids (e.g. *Eusthenopteron*; and a new genus from Canowindra, Johanson and Ahlberg in press) there is a much longer sublingual rod and relatively smaller urohyal compared with *Gogonasus* and *Medoevia* (Lebedev 1995, figures 18, 19).
6. The intermandibular muscles, as indicated above, were attached along the entire length of the mandibular rami, indicating that they were able to apply pressure along the whole length of the bottom of the buccal and gill chambers. Such a design would express water across the gills in a regular way.
7. The orientation of the gill arches is quite different from the ones in *Eusthenopteron*, as shown in Figure 61 (redrawn from Jarvik 1954, figure 27). In *Eusthenopteron* the gill arches are distributed at about 60° to the long axis of the animal. In contrast to *Medoevia*, and probably *Gogonasus*, the angle is about 40°–50° (based on measurement of the angles shown from the ventral articulated gill arches in Lebedev 1995, figure 18).

In *Gogonasus* it is difficult to find the precise attachment points of the epipharyngobranchials to the skull, but it is clear that the points were much more transverse to the long axis of the animal than in *Eusthenopteron*. One of our specimens has a short epibranchial attached to the end of the ceratobranchial, and its orientation is not at the high angle depicted by Jarvik (1954, figure 17). Instead it lies at a much more acute angle indicating the attachment to the epipharyngobranchial was much more acute. We also have several ceratobranchials which have only a gentle curvature, indicating that they did not form a long arc as in *Eusthenopteron*. Finally, in addition, the attachment points of the basihyal/basibranbchial were much closer together and formed into a shorter band than in *Eusthenopteron*. From all these points we conclude that the arrangement of the gills in *Gogonasus* were much more transverse than in *Eusthenopteron*, and hence they were more like *Polypterus* and *Amia* (Figure 61). The effect of this was to make a narrower pharynx, and to make the passage of water across the gills less divergent than in *Eusthenopteron*.

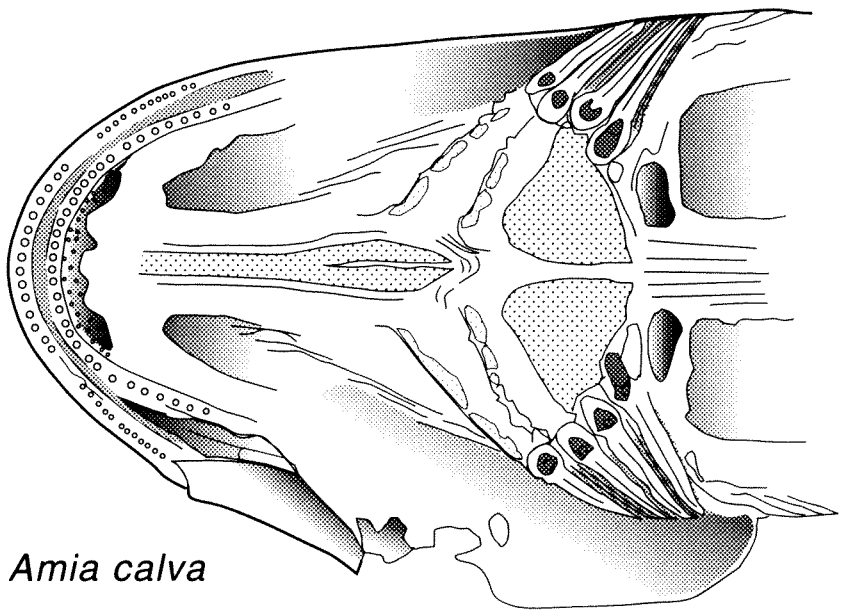
In summary, this complex of interrelated characters is involved with a mechanism for pumping water over the gills from an unusually large buccal reservoir, which presumably was refilled relatively infrequently.

Angle of hyomandibular and palatoquadrate

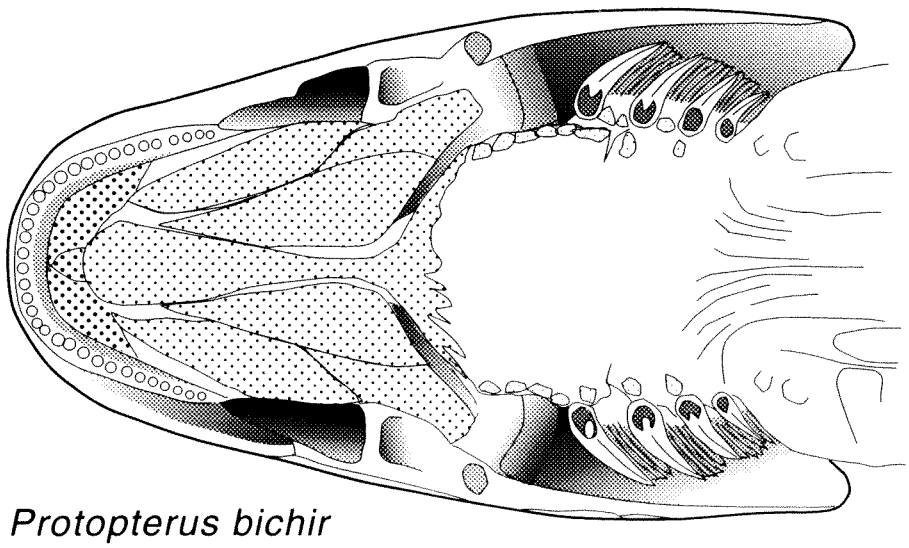
The hyomandibular is attached with its anterior part almost horizontal, and fitted up high under the skull roof. Its posterior part was turned posteroventrally at a high angle. Much of the structure lies adjacent to a smooth furrow in the palatoquadrate, thus confining its movement, but there is clearly no firm connection between the hyomandibular and the palatoquadrate (Figure 62). At this point we are in agreement with Hitchcock, and contra Thomson (1967) and Smithson and Thomson (1982). As discussed above, vertical movement of the palatoquadrate relative to the skull of the ethmosphenoid braincase and roof could have been only minor because of the autopalatine, the suprapterygoid, and the basisphenoid articulations, and the distinct notch in the dorsal rim of the palatoquadrate around the ventral edge of the foramen for nerve $V_{2,3}$ where it emerges from the otico-occipital braincase. Hence this nerve permitted only minor lateral flexure to be transmitted from the palatoquadrate to the



A *Eusthenopteron foordi*



B *Amia calva*



C *Protopterus bichir*

hyomandibular. In addition the attachment of the hyomandibular to the otico-occipital skull is double headed in the normal way and the attachment surfaces are strong and almost vertical, being laterally compressed. Hence, it is quite clear that the vertical movement of the hyomandibular was limited; the lateral movement of the hyomandibular was greater. It is of interest, therefore, that the distal end of the hyomandibular was formed in cartilage, and that it was situated a fair distance dorsal to the mandibular articulation (Figure 62). This implies a long link, probably a symplectic, between the hyomandibular and the ceratohyal, as suggested by Veran (1988). We do not have this bone preserved, and indeed it may not have been well ossified. The so-called 'opercular process' was situated in a very dorsal position ventral to the lateral extrascapular, well out of position for possible contact with the opercular, though there remains the possibility of a horizontally aligned ligamentary or muscular connection.

Restoration of the various elements of the skeleton indicates that the distal end of the hyomandibular lay posterior to the muscle scar for the dilator operculi on the inner face of the opercular. Although it was not well ossified, the ventral end of the hyomandibular served for the attachment of a muscle, or more probably a ligament, that mediated the opening of the opercular. Adduction would then be effected by the contraction of an adductor operculae attached to the more dorsal part of the opercular. The postulated arrangement is illustrated in Figure 62.

Movement of opercular series

The overlapping arrangements of these bones implies a definite sequence of movements. The opercular is overlapped only at its anterodorsal and anterior edges. The anterodorsal overlap is made by the lateral extrascapular which overlies it at an angle, and is itself a mobile bone. Hence it would restrict, but not prevent, lateral movement of the opercular around its anterior edge as a hinge. The opercular, therefore, could move laterally without moving the subopercular. Subopercular 1, however, is strongly overlapped by the opercular, and it could not move laterally around its anterior marginal hinge without moving the opercular. Similarly the subopercular 2 which has a large overlap from subopercular 1, could not move laterally without moving that element. We note that the large overlapped surface on subopercular 2 is partly accounted for by the fact that it surmounts a subangular flexure and hence lateral movement would also cause downward slippage of subopercular 2 relative to subopercular 1, and disconnection would take place unless the overlap were large.

Eusthenopteron is reconstructed in such a way as to place a process on the stylohyal (interhyal of our account) in an appropriate place to make a connection with the subopercular 1 (Jarvik 1980, figure 123C). The interhyal of *Gogonasus* remains unknown, but subopercular 1 has a definite scar towards the anterodorsal corner, implying that a ligament (or possibly a muscle) was attached from it to the adjacent element of the hyoid arch, and that could only be the interhyal. The interpretation of this ligament is of concern. Was it involved in opening or closing the opercular? As has been shown above, the subopercular 1 could not have been opened by movement of the opercular because of their overlapping relationship. This suggests that the ligament in question was involved in opening the subopercular 1, a feat accomplished by the outward rotation of the interhyal. It follows that the return of the interhyal to its resting position would close the subopercular. The ligament would then be involved in both opening and closing the bone.

All this is of interest in relation to the position of the hyomandibular opercular process, which we have noted is not in the same position relative to the opercular as in *Eusthenopteron*. In this genus it is situated beneath the opercular to which it is presumably attached by a direct connection. In *Gogonasus* it is situated too high to be beneath the opercular, and there is little opportunity to have it functioning to open and close that bone. It becomes difficult to understand why the hyomandibular had moved so markedly in a dorsal direction to lose its contact with the opercular. Westoll (1943) attempted to show how the opercular process moved dorsally relatively to the opercular during the evolution of the Amphibia, indicating how this might have happened. Westoll's work has been largely overturned by Clack's work on *Acanthostega* (Clack 1994), an aquatic amphibian from Late Devonian of Greenland. This shows that the

◀ **Figure 61** Ventral view of the roof of the palate of A, *Eusthenopteron* B, *Amia* C, *Polypterus* (redrawn from Jarvik 1954, figure 27). These diagrams illustrate the vast differences in orientation of the gill arches relative to the openings in the buccal cavity and the pharynx. In *Polypterus* the gill arches lie along the pharynx; in *Amia* they are across the length of the pharynx; and in *Eusthenopteron* they are elongated and are appoximately oblique. In *Medoevia* and *Gogonasus* they are similar in orientation to those in *Amia*.

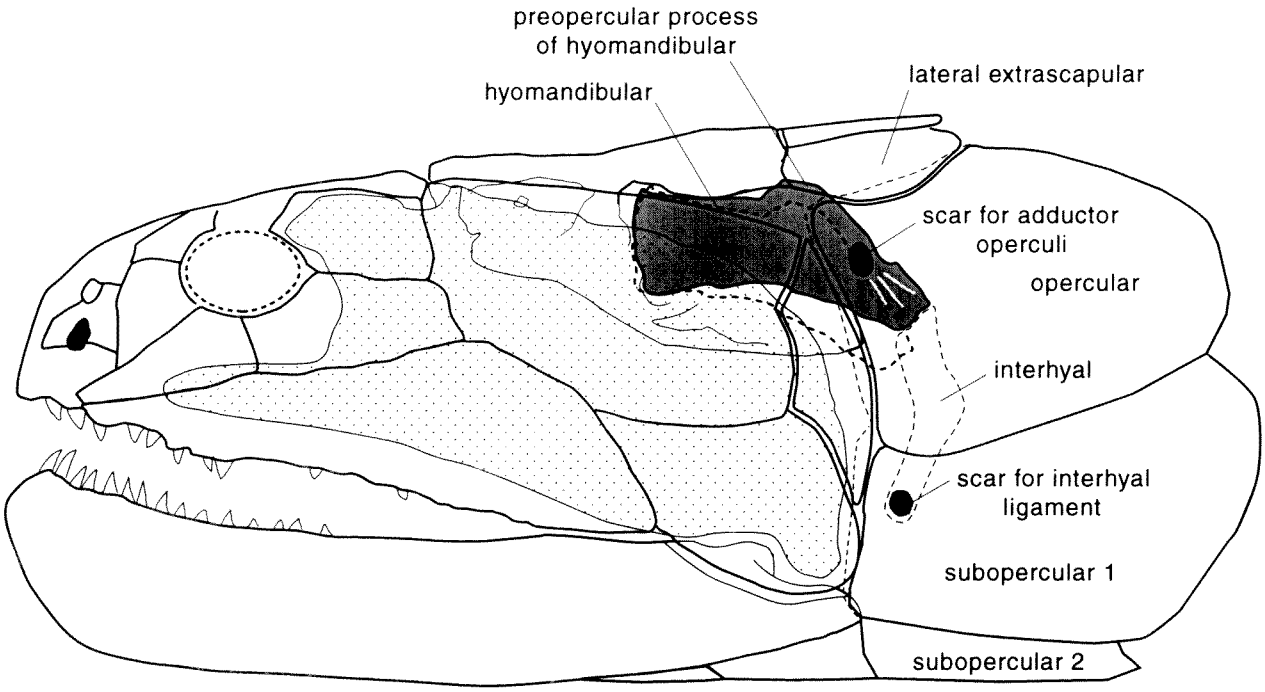


Figure 62 Lateral view of the reconstructed head of *Gogonasus*, based on ANU 49259, showing attachment of muscles and ligaments to the hyomandibular. The white lines on the hyomandibular are for the attachment of muscles which joined the bone to the opercular. Stippled area shows the position of the palatoquadrate complex on the left side. The most ventral position of the hyomandibular is dotted in.

previous work on the early amphibians was completely incorrect in suggesting that they were autostylic; in fact they were primarily amphistylic, and this requires that the hyomandibular remained in contact with the palatoquadrate. The hyomandibular (=stapes) supported the articulation between the roof and the palate in *Acanthostega* (Clack 1994). The dorsad position of the hyomandibular in both *Gogonasus* and *Medoevia* is not related to the dorsad position of the stapes in some tetrapods (suggested by Westoll 1943) because in early tetrapods like *Acanthostega* the stapes articulates low on the braincase against the stapedial footplate, positioned within the festibular fontanelle (Clack 1994). An alternative explanation will have to be found for the similar position of the hyomandibular in *Gogonasus* and *Medoevia*.

It is our view that the whole structural complex of features is related to the high vaulted skull. As indicated previously, the high skull increases the size of the gill chamber, which was used to house elongated, higher gills. This size is also increased by the high angle of the posterior corner of the palatoquadrate, around which the hyomandibular bends. This bending of the hyomandibular is the basis for the high position of the opercular process on the hyomandibular, which is forced up under the lateral extrascapular. The outcome of this is the position of the ventral part of the hyomandibular under the opercular, and it is this which is related to the opening of the opercular. Thus it appears that the opercular process of the hyomandibular is not associated with any attempt to move towards an amphibian organisation, but rather with a new means of opening the gill chamber.

We note that in *Gogonasus* and *Medoevia* the spiracular notch is a smooth, downturned embayment in the lateral margin of the postparietal shield. It makes a tight junction with the endocranium, but leaves a gap between the dermal skull roof and the cheek plates. Unlike the condition seen in *Eusthenopteron* or *Eusthenodon*, where there is a smooth downturned lamina of bone from the tabular into the spiracular slit, on *Gogonasus* and *Medoevia* there is no dermal expression of the slit seen in the postparietal shield. Functionally the spiracular slit may be used to either intake water for respiration when the mouth is ventrally located (e.g. batoids) or to eject sediment from the bucco-pharyngeal chamber. Osteolepidids may occur together with tristichopterids in the same fauna (e.g. Andreyevka fauna, Lebedev 1992), leading us to suggest that this morphological difference in the spiracular slit is not indicative of an environmental difference, but probably reflects a major distinction in the feeding/respiratory mechanism in the two groups. Tristichopterids, having a larger and better

sculptured spiracular groove, presumably had a more efficient mechanism for the intake of water during feeding or, alternatively, the expulsion of particles from the bucco-pharnygeal chamber during food reduction. The use of the spiracle to intake water may be advantageous in an ambush predator in a stillwater environment which tries to remain immobile whilst stalking prey.

Feeding

Opening and closing the mouth

This topic has been reviewed recently by Hitchcock (1995). So many factors are involved with the process of jaw opening that it is unlikely that a complete interpretation can be produced from bones alone, but in this work he showed that the muscles attached to some of the anterior neural arches were of greater significance than previously thought. He also concluded that the movement of the jaws was similar to that outlined by Lauder (1980b) for *Latimeria*. One of the real difficulties with *Latimeria* is that its hyoid arch is so differently constructed from that of the rhipidistians, and although it may be one of the most closely related living genera to rhipidistians, this provides no guarantee that it will provide the best functional analogy. However, comparison with such forms as *Latimeria*, together with an understanding of the geometry of the ventral side of the head and analogy with muscle action in living fishes in general, enable us to pinpoint at least some of the most significant factors involved. These include the coracomandibularis muscles from the jaw symphysis to the girdle, the sternohyoideus muscles, the geniohyoideus muscles, the epiaxial muscles, and the mandibulohyoid ligament. These will now be considered.

We have only fragments of vertebrae in our specimen, and so we can offer no direct comments on that aspect of Hitchcock's hypothesis. However, we have pointed out that there are two large openings across the posterior ends of the fossa Bridgei in *Gogonasus*, which suggests that the epaxial muscles did not have so strong attachment into the skull as Hitchcock (1995) suggests that they had in *Eusthenopteron*. This does not mean that they had no function in opening the jaws, but it suggests that it did not have the major role Hitchcock suggests.

On the other hand we agree with him that there was no connection between the maxilla and the endocranium, allowing a clear movement of the endocranium relative to the endocranium. As shown above, a strong mandibulohyoid ligament ran ventromesially from the posteroventral part of the mandible; it probably was connected to the ceratohyal or the ventral end of the stylohyal (Figure 60). As indicated above, the shape of the articulation of the attachment on the mandible suggests that the mandible would be dropped if this ligament was moved posteriorly. It is suggested therefore that at least part of the opening proceedure would involve the posterior movement of the hyoid arch.

The anterior part of the mandible shows strong attachment for longitudinal muscles in the symphysial region and, as these would be operational below the mandibular glenoid fossa, we conclude that they had a strong influence on jaw opening.

The closing of the mouth was almost certainly largely dominated by the large adductor mandibulae. The role of the basicranial muscles in initiating the closure as suggested by Hitchcock cannot be supported by any evidence we have.

Tusks and their fossae in the opposing jaws

Because we have individual specimens for which both palates and mandibles are available, we are able to make precise reconstructions of the interrelationships of tusks and their fossae. As was pointed out by Long (1988a), and shown here on Figure 26, there is no prospect of a tusk fitting into the choana (see also Fox *et al.* 1995). The tusk on the anterior coronoid, which is dorsomesially directed, fits into a fossa mesial to the choana and in front of the tusks on the dermopalatine, as is shown in Figure 59. The fit is quite imprecise, as would be expected given the lateral movement of the mandible implied by the double glenoid articulation (Fox *et al.* 1995). The same can be said of the fit of the dermopalatine and ectopterygoid tusks into the fossae in the mandible. As indicated in the previous point, the lateral rotation of the mandible resulting from the double glenoid articulation and the flexible medial symphysis of the mandible, means that significance can be ascribed to the furrows between the dentary and the coronoids on the one hand, and the maxilla and the dermopalatine – ectopterygoid on the other. In one mandibular position the dentary teeth would fit into the furrow on the upper jaw, the maxillary teeth passing outside the dentary; but when the mandibular ramus rotated laterally, the maxillary teeth would pass into the furrow on the mandible, the dentary teeth passing outside the maxilla. This arrangement gave exceptional holding power to the bite in either position.

Sensory systems

Distribution of tubules from lateral-line canals

What is the significance of the fact that tubules on one side of the main cheek canals are developed in a paling-fence-like way, whereas those on the other side of the main canal are derived at a limited number of points, and then branch to produce

brush-like arrays (e.g., bones of the cheek, Figure 19)? We note that in the squamosal the arrangement is slightly different in that the posterior array of canals below the lateral line canal is different from those in front, consisting of units that are branching and crossing some of the anterior canals.

The tubules in all bones that lie ventrally to the main canal, open to the exterior *via* two or three pores; in addition there are occasional openings where they join the canal itself. In the group of canals that open dorsal to the main canal, branching is much more common and the pores through which they open have no definite arrangement. Within a single bone both types are represented.

As is well known from work on living species, the receptors open to the surface in a variety of ways, one of which is through a pore in the canal wall itself (Coombs *et al.* 1989; Denton and Gray 1989). As is the case of extant forms, we assume that the receptor cells are buried between the bases of two adjacent pore openings. The passage of water over the surface of the animal would produce turbulence around the pores, and thus produces the movement of the hairs on the neuromasts as water moves over the external surface. Motion is then detected because a sequence of pores is activated as the current moves along the surface. To have a linear series of pores along the length of the animal suggests that the means of detecting speed at which the current moves over the surface is enhanced, and produces a strong unidirectional signal, with its intensity and attenuation enhanced. This leaves the more random arrangement of pores elsewhere to be interpreted. Presumably the irregular distribution of pores would pick up diffuse signals from a variety of different directions, and would alert the animal that there was movement of water in the general vicinity.

Of course we know nothing about the range of frequency received by individual pores, and these may have an effect on the features we have considered. On the other hand we notice that there are no obstructions in the lateral line canals. As is well known from Denton and Gray (1989, figure 23.6) such obstructions cause considerable variations in frequency reception, but in the present instance we have a simple opening extending the whole length of the head. Obviously, the whole matter of receptivity of canals in such fishes as *Gogonasus* requires continued research on extant fishes before conclusions about their effectivity can be reached.

Absence of sensory pore clusters

Such clusters are widely distributed among osteolepiforms. For example, *inter alia*, in *Osteolepis*, *Thursius*, *Latvius*, *Gyroptychius*, *Megalichthys*, *Cladarosymblema*, *Koharalepis* and *Platyethmoidia*. No doubt they occur also in other genera for which data are not easily accessible. The interesting thing about *Gogonasus* is that it is definitely a marine genus, whereas all those in which sensory pore patches occur are mostly from fresh water deposits. According to Lebedev (1996, pers. comm.) *Medoevia* has sensory pore clusters although they are not clearly shown and are filled with silt; and though its provenance is not established, its limestone matrix contained a tooth of the shark *Phoebodus australienesis*, a genus known only so far from marine deposits. We have discussed the function of the pores previously (Fox *et al.* 1995) without reaching any conclusions, but we drew attention to the existence of abundant pore clusters in North American paddlefish. In that group they are electrosensory receptors (Grande and Bemis 1991). The greater electrical conductivity of marine water may mean that the electrosensory receptors in marine forms were more efficient, and that the sensory pore clusters were less useful. In any case, we suggest that our data indicate that taxonomists should exercise caution in using the presence or absence, or even the abundance of sensory pore clusters as features of taxonomic value. They may merely indicate the salinity of the water in which the animals lived.

Prenasal fossae

The prenasal fossa is a feature of most osteolepiforms so far investigated, although the matter of its subdivisions and their functions remains contentious. For example, Jarvik (1942, 1980) used several terms to cover what to us seems to be a single structure, and he proposed that it housed an intermaxillary gland. Fox *et al.* (1995) were of the opinion that such structures could not be recognised in *Cladarosymblema*. *Gogonasus* is unusual, therefore, in that no clearly defined fossa is present, though a small but variable number of foramina occur within the region normally occupied by the whole fossa. This suggests two options: that the genus did not possess any special organ in the nominated space, which was occupied by tissue, the function of which was simply to protect the passage of nerves and vessels; or alternatively, that the tissue had some special sensory function.

The issue can be approached in the first instance by the examination of the variation of the shape and size of the space in question, and by examining the vascular and nerve supply to the area. If some special organ were present, and it had the significance attached to it by Jarvik, there should be a recognisable space for it across the range of osteolepiforms. If, on the other hand, the space was occupied by undifferentiated soft tissue, it could

vary in size and shape depending on a variety of features, such as the shape of the surrounding elements like the vomers and the parasphenoid. In this respect, a comparison between *Gogonasus* and *Medoevia* has something to offer because, not only are they similar in many respects, they are so well preserved that the spaces in question can be unambiguously defined, and their relationships to the surrounding structures can be determined. In the first place, the space between the vomers and the premaxilla is remarkably different in shape in the two genera. The canals into the space differ in many respects, and so the supply of nerves and vessels was probably not identical (but see below). We can only conclude that the tissue occupying the space was not dependent on having the same form, blood supply or innervation. This argues for a generalised rather than some specialised soft tissue in the space.

In the second place *Gogonasus* and *Medoevia* show that there is no correlation between the size of the tusks on the anterior part of the dentary and the presence of a prenasal fossa. *Medoevia* has fossae but no anterior tusks, whereas *Gogonasus* has larger tusks and no fossae. Thus it is not possible to use the dental data to support the view that the space was occupied by fossae for reception of mandibular teeth. It may be conjectured that this could be explained by differences in closure pattern, but we judge such an explanation to be improbable.

Thirdly, we note that in both genera, as in *Eusthenopteron* and megalichthyids, a covered space exists between the vomers presumably for the transmission of nerves or vessels or both, from the posterior to the prenasal space. These would most probably be the palatine nerves and arteries. Such an interpretation would imply the presence of soft tissue having a significant sensory function. In attempting to decide what this tissue might be, we prefer to examine the matter from general principles rather than from a direct comparison with an extant animal; the latter is a procedure which in our view is more likely to prejudice the outcome. So the question then devolves into a discussion of the known function of the palatine nerves. Finally, *Gogonasus*, *Eusthenopteron*, megalichthyids, and probably *Medoevia* (judging from Lebedev 1995, figure 1D), have foramina opening into this space through the posterior flange of the premaxilla or the anterior edge of the palatal lamina. In *Cladarosymblema* such foramina can be shown to open into the deeply buried lateral line canal, and there is good reason to think that in *Gogonasus* they do the same thing, although we do not have sufficient material to confirm this by excavation. As Fox *et al.* (1995) pointed out, this is a most unlikely arrangement for seismosensory neuromasts, and an alternate view must be sought consistent with the openings being inside the mouth.

We are left with the information that although the form of the prenasal space and the foramina opening into it differ between genera, two nerve systems are invariably present – the palatinus VII and the profundus V; and foramina that open into the lateral line canal through the premaxilla are probably also invariably present. Both the profundus V and palatine VII nerves have sensory functions, as obviously do the neuromasts of the lateral line system. This suggests that some special sensory function has to be ascribed to the tissue occupying the prenasal area.

Jarvik (1980, vol.2: 31–33) has pointed out that the taste bud and accustico-lateralis systems have a great deal in common, not only in bud and neuromast structure, but also in their distribution during development. In the larval stages of *Amia*, for example, 'the external taste buds of the head may be arranged in lines suggestive of and running along the lateral lines', and the 'ganglia and nerves of both systems are derived from ectodermal placodes'. A possible explanation of the tissue occupying the prenasal space is that it had a chemosensory or taste function. This interpretation seems to account for more observations than either the glandular or the tusk fossa hypotheses.

Locomotion

As indicated above, we have no useful information on fins or vertebral column that would assist with an interpretation of locomotion. However, work by Pridmore and Barwick (1993) on the scales of Devonian dipnoans, shows that the degree of overlap of the scales may be a good index of body flexibility. Because most osteichthyans, apart from those with an eel-like and some with a compressed deep-bodied shape, use caudal locomotion as their main propulsive mechanism, body flexibility is one of the most significant indices of movement. The shape of the posterior end of the head indicates that the body of *Gogonasus* was thick and ovate in section, quite unlike either of the above forms. It is important, therefore, to note that the exposed parts of the scales of *Gogonasus* are large in comparison with the overlapped parts and the number of scales overlapping at any one point is small in comparison with the number in Devonian dipnoans. In addition, there are three features of the scales that support the view that the body was highly flexible.

A) They have lost the peg-and-socket arrangement previously thought to be characteristic of some primitive osteolepiforms (e.g. *Beelarongia*, Long 1987b). The peg-and-socket pattern would have severely limited the mount of body flexure.

B) The overlapped surfaces are cambered in such a way as to facilitate inter-scale movement.

C) The deep grooves around the cosmine-covered surfaces allowed the edges of adjacent scales to interlock at the points of maximum flexure. The limited data available, therefore, suggests that the body of *Gogonasus* was capable of body flexure consistent with carangiform or subcarangiform movement.

ACKNOWLEDGEMENTS

We wish to acknowledge our indebtedness to a the following people from the Geology Department, Australian National University: Norman Fraser and John Vickers, for the preparation of thin sections; Tony Phimphisane for assistance with photographic darkroom procedures; Peter Pridmore and Val Elder for support in the field; and Val Elder for assistance with the acid etching of the Australian National University specimen and curation of the material. Wallace Ambrose of the Research School of Pacific Studies, Australian National University, and Susan Morrison of the Aquatic Zoology Department, Western Australian Museum, prepared the X-ray negatives. Roger Heady of the Electron Microscope Unit, Australian National University, was responsible for the Scanning Electron Microscopy. In the Department of Earth and Planetary Science at the Western Australian Museum, Kristine Brimmell prepared some of the photographs, and Danielle Hendricks produced some of the stippled drawings used as text-figures from J.A.L.'s camera lucida drawings. John Long would like to thank the organisers of "The Great Russian Dinosaurs Exhibition" for bringing Oleg Lebedev, Palaeontological Institute of the Russian Academy of Sciences, Moscow, Russia, and his *Medoevia* specimen out to the Western Australian Museum in 1995, and he acknowledges the helpful discussions on this work from both Oleg and Per Ahlberg, Natural History Museum, London. The WAM *Gogonasus* skull was found on field work sponsored by the National Geographic Society (grant #3364–86, awarded to JAL). The work of Barwick and Campbell has been supported by a grant from the Australian Research Grants Council.

REFERENCES

Ahlberg, P.E., Clack, J.A. and Luksevics, E. (1996). Rapid braincase evolution between *Panderichthys* and the earliest tetrapods. *Nature* **381**: 61–64.

Andrews, S.M. (1973). Interrelationships of crossopterygians. In Greenwood, P.H., Miles, R.S. and Patterson, C. (eds), *Interrelationships of Fishes:* 138–177, Linnean Society, London.

Andrews, S.M. and Westoll, T.S. (1970a). The postcranial skeleton of *Eusthenopteron foordi* Whiteaves. *Transactions of the Royal Society of Edinburgh* **68:** 207–329.

Andrews, S.M. (1970b). The postcranial skeleton of rhipidistian fishes excluding *Eusthenopteron. Transactions of the Royal Society of Edinburgh* **68:** 391–489.

Bjerring, H.C. (1972). Morphological observations on the exoskeletal skull roof of an osteolepiform from the Carboniferous of Scotland. *Acta Zoologica* **53:** 73–92.

Borgen, U. J. (1983). Homologizations of skull roofing bones between tetrapods and osteolepiform fishes. *Palaeontology* **26:** 735–753.

Borgen, U.J. (1989). Cosmine resorption structures on three osteolepid jaws and their biological significance. *Lethaia* **22:** 413–424.

Borgen, U.J. (1992). The function of the cosmine pore canal system. In: Mark-Kurik, E. (ed.), *Fossil Fishes as Living Animals:* 141–150, Academy of Sciences of Estonia, Tallinn.

Campbell, K.S.W. and Barwick, R.E. (1982). A new species of the lungfish *Dipnorhynchus* from New South Wales. *Palaeontology* **25:** 509–527.

Campbell, K.S.W. and Barwick, R.E. (1984). *Speonesydrion*, an Early Devonian dipnoan with primitive toothplates. *Palaeoichthyologica* **2:** 1–48.

Campbell, K.S.W. and Barwick, R.E. (1987). Paleozoic lungfishes – a review. *Journal of Morphology* Supplement 1: 93–132.

Chang, M. (1982). *The braincase of* Youngolepis, *a Lower Devonian crossopterygian from Yunnan, South-Western China*. Unpublished PhD Thesis, Stockholm University.

Chang, M. (1991). "Rhipidistians", dipnoans, and tetrapods. In: Schultze, H-P and Trueb, L. (eds), *Origins of Higher Groups of Tetrapods:* 3–28, Comstock Publishing Associates, Ithaca and London.

Chang, M. and Smith, M.M. (1992). Is *Youngolepis* a porolepiform? *Journal of Vertebrate Paleontology* **12:** 294–312.

Chang, M. and Zhu, M. (1993). A new osteolepidid from Qujing, Yunnan. *Memoir of the Association of Australasian Palaeontologists* **15:** 183–198.

Clack, J.A. (1992). The stapes of *Acanthostega gunnari* and the role of the stapes in early Tetrapods. In: Webster, D.B., Fay, R.E. and Popper, A.N., *The evolutionary biology of hearing:* 405–420, Springer-Verlag, New York.

Clack, J.A. (1994). Earliest known tetrapod braincase and the evolution of the the stapes and fenestra ovalis. *Nature* **369:** 392–394.

Cloutier, R. and Ahlberg, P.E. (1995). Sarcopterygian interrelationships: how far are we from a phylogenetic consensus? *Geobios* **19:** 241–248.

Coombs, S., Janssen, J., and Webb, J.F. (1989). Diversity of lateral line systems: evolutionary and functional considerations. In: Coombs, S, Görner, P. and Munz, H. (eds),*The Mechanosensory Lateral Line: Neurobiology and Evolution*:593–592 , Springer Verlag, New York.

Denton, E.J. and Gray, J.E.B. (1989). Mechanical factors in the excitation of lateral line of fishes. In: Coombs, S, Görner, P. and Munz, H. (eds),*The Mechanosensory*

Lateral Line: Neurobiology and Evolution: 565–617, Springer Verlag, New York.

Eaton, T.H., Jr. (1939). The crossopterygian hyomandibular. *Journal of the Washington Academy of Science* **19:** 109–117.

Fox, R.C., Campbell, K.S.W., Barwick, R.E. and Long, J.A. (1995). A new osteolepiform fish from the lower Carboniferous Raymond Formation, Drummond Basin, Queensland. *Memoirs of the Queensland Museum* **38:** 97–221.

Grande, L. and Bemis, W.E. (1991). Osteology and phylogenetic relationships of fossil and recent paddlefishes (Polyodontidae) with comments on the interrelationships of the Acipenseriformes. *Society of Vertebrate Paleontology*, Memoir **1:** 1–121.

Goodrich, F.S. (1958). *Studies on the structure and development of vertebrates.* 2 Vols. Dover Publications, New York.

Gross, W. (1941). Über den Unterkiefer einige Devonischer Crossopterygier. *Abhandlungen der Preussische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse* **7:** 1–51.

Gross, W. (1956). Über Crossopterygier und Dipnoer aus dem Baltischen Oberdevon im Zusammenhang einer vergleichenden Untersuchung des Porenkanalsystems Paläozoischer Agnathen und Fische. *Kungliga Svenska Vetenskapsakademiens Handlingar* **5:** 1–140.

Hitchcock, E.C. (1995). A functional interpretation of the anteriormost vertebrae and skull of *Eusthenopteron. Bulletin de la Musée Nationale d'Histoire Naturelle, Paris, Série* **17,** Section C **1–4:** 269–285.

Janvier, P. (1980). Osteolepid remains from the Devonian of the Middle East, with particular reference to the endoskeletal shoulder girdle. In: Panchen, A.L. (ed), *The terrestrial environment and the origin of land vertebrates:*223–254, Academic Press, London.

Janvier, P. (1983). Les vertébrés Dévoniens de la Nappe Supérieure d'Antalya. (Taurus Lycien occidental, Turquie). *Géologie Méditerranéene* **10:** 1–13.

Jarvik, E. (1942). On the structure of the snout of crossopterygians and lower gnathostomes in general. *Zoologiska Bidrag Från Uppsala* **21:** 234–675.

Jarvik, E. (1944). On the dermal bones, sensory canals and pit-lines of the skull in *Eusthenopteron foordi* Whiteaves, with some remarks on *E. säve-söderberghi* Jarvik. *Kungliga Svenska Vetenskapsakademiens Handlingar* **21:** 1–48.

Jarvik, E. (1948). On the morphology and taxonomy of the Middle Devonian osteolepid fishes of Scotland. *Kungliga Svenska Vetenskapsakademiens Handlingar* **25:** 1–301.

Jarvik, E. (1950a). On some osteolepiform crossopterygians from the Upper Old Red Sandstone of Scotland. *Kungliga Svenska Vetenskapsakademiens Handlingar* 2: 1–35.

Jarvik, E. (1950b). Middle Devonian vertebrates from Canning Land and Wegeners Halvö (East Greenland), II. Crossopterygii. *Kungliga Svenska. Meddelelser øm Grønland* 96 (4): 1–132.

Jarvik, E. (1954). On the visceral skeleton in *Eusthenopteron* with a discussion of the parasphenoid and palatoquadrate in fishes. *Kungliga Svenska Vetenskapsakademiens Handlingar* **5:** 1–104.

Jarvik, E. (1963). The composition of the intermandibular division of the head in fish and tetrapods and the diphyletic origin of the tetrapod tongue. *Kungliga Svenska Vetenskapsakademiens Handlingar* **9:** 1–74.

Jarvik, E. (1966). Remarks on the structure of the snout in *Megalichthys* and certain other rhipidistid crossopterygians. *Arkiv för Zoologi* **19:** 41–98.

Jarvik, E. (1972). Middle and Upper Devonian porolepiformes from East Greenland with special reference to *Glyptolepis groenlandica* n.sp. *Meddelelser øm Grønland* **187:** 1–295.

Jarvik, E. (1980). *Basic structure and evolution of vertebrates,* 2 Vols. Academic Press, London and New York.

Jarvik, E.(1985). Devonian osteolepiform fishes from East Greenland. *Meddelelser øm Grønland, Geoscience* **13:** 1–52.

Jessen, H. (1967). Die Crossopterygier Oberen Plattenkalks (Devon) der Bergisch- Gladbach-Paffrather Mulde (Rheinisches Schiefergebirge) unter Berückichtigung von amerikanischem und europäischem *Onychodus*-material. *Arkiva Zoologica* **(2) 18:** 305–389.

Jessen, H. (1973). Weitere Fischreste aus dem Oberen Plattenkalkes der Bergish-Gladbach- Paffrather Mulde (Oberdevon, Rheinische Scheifergebirge). *Palaeontographica* **143A:** 159–187.

Jorgensen, J.M., Flock, A. and Wersall, J. (1972). The Lorenzian ampullae of *Polyodon spathula.. Zeitschrift für Zellforshung und Microscopische Anatomie* **130:** 362–377.

Johanson, Z. and Ahlberg, P. E. (in press) . New Tristicopterid (Osteolepiformes; Sarcopterygii) from the Mandagery Sandstone (Famennian) near Canowindra, N.S.W., Australia. *Transactions of the Royal Society of Ediburgh, Earth Sciences.*

Kerr, T. (1955). The scales of modern lungfish. *Proceedings of the Zoological Society of London* **125:** 335–345.

Lauder, G. (1980a). Evolution of the feeding mechanism in primitive actinopterygian fishes: a functional anatomical analysis of *Polypterus, Lepisosteus,* and *Amia. Journal of Morphology* **163:** 283–317.

Lauder, G. (1980b). The role of the hyoid apparatus in the feeding mechanism of the coelacanth *Latimeria chalumnae. Copeia* **1980** (1): 1–9.

Lauder, G. (1985). Functional morphology of the feeding mechanism in lower vertebrates. *Fortschritte der Zoologie* **30:** 179–188.

Lebedev O.A. (1992). The latest Devonian, Khovanian vertebrate assemblege of Andreyeveka-2 locality, Tula region, Russia. In: Mark-Kurik, E. (ed.), *Fossil fishes as living animals:*265–272, Estonian Academy of sciences, Tallin.

Lebedev, O.A. (1995). Morphology of a new osteolepid fish from Russia. *Bulletin de la Musée National d'Histoire Naturelle, Paris, Série* **17,** Section C **1–4:** 287–341.

Long, J.A. (1985a.) A new osteolepidid fish from the Upper Devonian Gogo Formation, Western

Australia. *Records of the Western Australia Museum* **12:** 361–377.

Long, J.A. (1985b). The structure and relationships of a new osteolepiform fish from the Late Devonian of Victoria, Australia. *Alcheringa* **9:** 1–22.

Long, J.A. (1985c). New information on the head and shoulder girdle of *Canowindra grossi* Thomson, from the Late Devonian Mandagery Sandstone, New South Wales. *Records of the Australian Museum* **37:** 91–99.

Long, J.A. (1987). Late Devonian fishes from the Gogo Formation, Western Australia – new discoveries. *Search* **18:** 203–205.

Long, J.A. (1988). Late Devonian fishes from Gogo, Western Australia. *National Geographic Research* **4:** 436–450.

Long, J.A. (1989). A new rhizodontiform fish from the Early Carboniferous of Victoria, Australia, with remarks on the phylogenetic position of the group. *Journal of Vertebrate Paleontology* **9:** 1–17.

Meinke, D.K. and Thomson, K.S. (1983). The distribution and significance of enamel and enameloid in the dermal skeleton of osteolepiform rhipidistian fishes. *Paleobiology* **9:** 138–149.

Miles, R.S. (1971). The Holonematidae (placoderm fishes), a review based on new specimens of *Holonema* from the Upper Devonian of Western Australia. *Philosophical Transactions of the Royal Society of London* **263B**: 101–234.

Millot J. and Anthony, J. (1958). *Anatomie de Latimeria chalumnae.* (3 Vols). Centre National de la Recherche Scientifique, Paris.

Nelson, G. J. (1969). Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates. *Bulletin of the American Museum of Natural History* **114:** 475–552.

Northcutt, R.G. (1986). Electroreception in non-teleost bony fishes. In: Bullock, T.H. and Heiligenberg, W. (eds), *Electroreception:* 257–285, Wiley, New York.

Panchen, A.L. (1967). The nostrils of choanate fishes and early tetrapods. *Biological Reviews* **42:** 374–420.

Panchen, A.L. and Smithson, T.R. (1987). Character diagnosis, fossils and the origin of tetrapods. *Biological Reviews* **62:** 341–438.

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

Romer, A.S. (1937). The braincase of the Carboniferous crossopterygian *Megalichthys nitidus. Bulletin of the Museum of Comparative Zoology* **82:** 1–73.

Romer, A.S. (1941). Notes on the crossopterygian hyomandibular and braincase. *Journal of Morphology* **1:** 141–160.

Rosen, D.E., Forey, P.L., Gardiner B.G. and Patterson, C. (1981). Lungfish, tetrapods, paleontology and plesiomorphy. *Bulletin of the American Museum of Natural History* **167:** 159–276.

Schaeffer, B., (1968). The origin and basic radiation of the Osteichthyes. In: Ørvig, T. (ed.), *Current Problems in Vertebrate Phylogeny, Nobel Symposium 4:* 207–222, Interscience Publishers, New York.

Schultze, H.-P. (1969). Die Faltenzahne der Rhipidistien Crossopterygier der Tetrapoden und die Actinopterygier Gattung *Lepisosteus. Palaeontographica Italica* **65:** 63–137.

Schultze, H-P. (1974). Osteolepide Rhipidistia (Pisces) aus dem Pennsylvanian von Illinois, USA. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **146:** 29–50.

Schultze, H-P. (1987). Dipnoans as Sarcopterygians. *Journal of Morphology Supplement* **1:** 39–74.

Schultze, H-P. (1988). An osteolepidid rhipidistian in Upper Pennsylvanian deposits of Hamilton, Kansas. *Kansas Geological Survey Guidebook Series* **6:** 181–183.

Schultze, H-P. (1994). Comparison of hypotheses on the relationships of sarcopterygians. *Systematic Biology* **43:** 155–173.

Smith, M.M. (1989). Distribution and variation in enamel structure in the oral teeth of sarcopterygians: its significance for the evolution of a protoprismatic enamel. *Historical Biology* **3:** 97–126.

Smith, M.M., Hobdell, M.H. and Miller, W.A. (1972). The structure of the scales of *Latimeria chalumnae. Journal of the Zoological Society of London* **167:** 501–509.

Smithson, T.R. and Thomson, K.S. (1982). The hyomandibular of *Eusthenopteron foordi* Whiteaves (Pisces Crossopterygii) and the early evolution of the tetrapod stapes. *Zoological Journal of the Linnean Society* **74:** 93–103.

Thomson, K.S. (1964). The comparative anatomy of the snout in rhipidistian fishes. *Bulletin of the Museum of Comparative Zoology* **131:** 313–357.

Thomson, K.S. (1965). The endocranium and associated structures in the Middle Devonian rhipidistian fish *Osteolepis. Proceedings of the Linnean Society of London* **176:** 181–195.

Thomson, K.S. (1967). Mechanisms of intracranial kinetics in fossil rhipidistian fishes (Crossopterygii) and their relatives. *Zoological Journal of the Linnean Society* **46:** 223–253.

Thomson, K.S. (1969). The biology of the lobe-finned fishes. *Biological Reviews* **44:** 91–154.

Thomson, K.S. (1975). On the biology of cosmine. *Bulletin of the Peabody Museum of Natural History* **40:** 1–59.

Traill, T.S., (1841). Notice of the fossil fishes found in the Old Red Sandstone formation of Orkney, particularly of an undescribed species, *Diplopterus Agassis* [sic]. *Transactions of the Royal Society of Edinburgh* **15:** 89–92.

Véran, M. (1988). Les éléments accessoires de l'arc hyoidïen des poissons téléostomes (Acanthodiens + Ostéichthyens) fossiles et actuels. *Mémoires du Muséum national d"Histoire naturelle,* Paris, 4 ème ser. **54:** 1–98, 7 pls.

Vorob'jeva, E.I. (1962). Rhizodontid crossopterygians of the main Devonian field in the USSR. *Trudy Paleontologicheskogo Instituta. Akademiya Nauk SSSR* **94:** 1–139. [In Russian].

Vorob'jeva, E.I. (1977). Morfologiya i osobennosti evolyutsii kisteperykh ryb. *Trudy Paleontologicheskogo Instituta. Akademiya Nauk SSSR* **163:** 1–240. [In Russian].

Warren, A.A. and Davey, L. (1992). Folded teeth in temnospondyls – a preliminary study. *Alcheringa* **16:** 107–132.

Watson, D.M.S. (1926). The evolution and origin of the amphibia. *Philosophical Transactions of the Royal Society of London* **204:** 189–257.

Webb, P.A. (1982). Locomotor patterns in the evolution of actinopterygian fishes. *American Zoologist* **22:** 329–342.

Westoll, T.S. (1936). On the structures of the dermal ethmoid shield of *Osteolepis*. *Geological Magazine* **73:** 157–171.

Westoll, T.S. (1937). On a specimen of *Eusthenopteron* from the Old Red Sandstone of Scotland. *Geological Magazine* **74:** 507–524.

Westoll, T.S. (1940). New Scottish material of *Eusthenopteron*. *Geological Magazine* **77:** 65–73.

Westoll, T.S. (1943). The hyomandibular of *Eusthenopteron* and the tetrapod middle ear. *Proceedings of the Royal Society of London* **131:** 393–414.

Young, G.C., Long, J.A. and Ritchie, A. (1992). Crossopterygian fishes from the Devonian of Antarctica: systematics, relationships and biogeographic significance. *Records of the Australian Museum, Supplement* **14:** 1–77.

Guide to Authors

Subject Matter:

Reviews, observations and results of research into all branches of natural science and human studies will be considered for publication. However, emphasis is placed on studies pertaining to Western Australia. Longer papers will be considered for publication as a Supplement to the *Records of the Western Australian Museum*. Short communications should not normally exceed three typed pages and this category of paper is intended to accommodate observations, results or new records of *significance*, that otherwise might not get into the literature, or for which there is a particular urgency for publication. All material must be original and not have been published elsewhere.

Presentation:

Authors are advised to follow the layout and style in the most recent issue of the *Records of the Western Australian Museum* including headings, tables, illustrations and references.

The title should be concise, informative and contain key words necessary for retrieval by modern searching techniques. An abridged title (not exceeding 50 letter spaces) should be included for use as a running head.

An abstract must be given in full length papers but not short communications, summarizing the scope of the work and principal findings. It should normally not exceed 2% of the paper and should be suitable for reprinting in reference periodicals.

The International System of units should be used.

Numbers should be spelled out from one to nine in descriptive text; figures used for 10 or more. For associated groups, figures should be used consistently, e.g. 5 to 10, not five to 10.

Spelling should follow the *Concise Oxford Dictionary*.

Systematic papers must conform with the International Codes of Botanical and Zoological Nomenclature and, as far as possible, with their recommendations.

Synonymies should be given in the short form (taxon, author, date, page) and the full reference cited at the end of the paper. All citations, including those associated with scientific names, must be included in the references.

Manuscripts:

The original and two copies of manuscripts and figures should be submitted to the Editors, c/- Publications Department, Western Australian Museum, Francis Street, Perth, Western Australia 6000. They must be in double-spaced typescript on A4 sheets. All margins should be at least 30 mm wide. Tables plus heading and legends to illustrations should be typed on separate pages. The desired position for insertion of tables and illustrations in the text should be indicated in pencil. Tables should be numbered consecutively, have headings which make them understandable without reference to the text, and be referred to in the text.

High quality illustrations are required to size (16.8 cm x 25.2 cm) or no larger than 32 cm x 40 cm with sans serif lettering suitable for reduction to size. Photographs must be good quality black and white prints, not exceeding 16.8 cm x 25.2 cm. Scale must be indicated on illustrations. All maps, line drawings, photographs and graphs, should be numbered in sequence and referred to as Figure/s in the text and captions. Each must have a brief, fully explanatory caption. On acceptance an IBM compatible disk containing all corrections should be sent with amended manuscript. The disk should be marked with program (e.g. WordPerfect, Wordstar, etc).

In papers dealing with historical subjects references may be cited as footnotes. In all other papers references must be cited in the text by author and date and all must be listed alphabetically at the end of the paper. The names of journals are to be given in full.

Processing:

Papers and short communications are reviewed by at least two referees and acceptance or rejection is then decided by the editors.

The senior author is sent one set of page proofs which must be returned promptly.

The senior author will receive fifty free offprints of the paper. Additional offprints can be ordered at page proof stage.