

A NEW OSTEOLEPIFORM FISH FROM THE LOWER CARBONIFEROUS RAYMOND FORMATION, DRUMMOND BASIN, QUEENSLAND

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Cladarosymblema narrienense gen. et sp. nov. (Megalichthyidae, Osteolepiformes), herein described from the Lower Carboniferous Raymond Formation, Drummond Basin, Queensland, Australia, is the first megalichthyid described from the Southern Hemisphere. The holotype of *C. narrienense* is preserved in siltstone and is a crushed specimen with skull, mandibles and anterior postcranial elements still together. Paratypes are isolated parts of the skeleton which have been etched with acetic or monochloracetic acid from limestone immediately underlying the siltstone. As a consequence of the detail preserved in these specimens, *C. narrienense* is the best known member of the Megalichthyidae. The sedimentary unit in which the fossils are preserved was probably deposited on a floodplain, in a semi-persistent lagoon which supported abundant calcareous algae and a rich fauna of actinopterygians, acanthodians and crossopterygians. This standing body of water was subject to occasional flooding during which penecontemporaneous sedimentary clasts were washed in, along with silt and sand. The family Megalichthyidae is herein redefined using skull, mandible, pectoral girdle, pectoral fin, and axial ring characters, giving a much broader definition than has been used previously. We include *Megalichthys*, *Ectosteorhachis*, *Cladarosymblema*, an unnamed new genus from Norway and an unnamed species from Turkey. Attention is drawn to great variability of the bone pattern in the roof of the rostral region of the skull in *C. narrienense*. The use of such bone patterns for the diagnoses of genera without a knowledge of their variation in the component species, is questioned. Lateral line canals in the rostral region of *C. narrienense* are discussed, and they are shown to be separated from the ossification centres of some of the bones through which they pass, in some instances lying along the sutures between bones. The significance of these observations for the definition of bones in the nasal and postrostral series is pointed out. Braincase structure of both ethmoid and otico-occipital units, the hyomandibular, and the neural and vascular systems of the mandible of *C. narrienense* are described and figured. More detailed information on the hyomandibular is available than for any other osteolepiform genus apart from *Gogonasmus*; the hyomandibular of that genus is described for the first time. The maxilla has an oblique anterodorsal flange that formed the posterior margin of the choana. A similar structure is described from *Gogonasmus*, already known to be choanate. This condition was probably primitive for osteolepiforms. Other aspects of *Gogonasmus* are described using a new specimen, providing a more secure base for comparison of *Cladarosymblema* with other osteolepiforms. Scale histology and growth of the scales are discussed, particularly in relation to the resorption, deposition and function of cosmine. *C. narrienense* was an elongate animal, that had a mid-body section forming an ellipse with vertical axis slightly the longer, and a slightly more depressed anterior section; this, together with its scale structure, pectoral fin pattern, posteriorly placed median fins, and mouth and dentition, indicate that it was a predatory feeder with subcarangiform locomotion. □ *Megalichthyidae, Osteolepiformes, Cladarosymblema gen. nov., Carboniferous, cranial morphology, Raymond Formation.*

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Fossil fish have been known from the Drummond Basin (Fig. 1) since Smith (in Jack & Etheridge, 1892) reported scales in railway cuttings west of Bogantungan, Queensland. Although attempts were made by geologists from government instrumentalities, oil companies and

universities to collect suitable material for description, adequate collections were never assembled.

In 1966, de Bretzel, a geologist with Aquitaine Petroleum Ltd., reported specimens *in situ* in the Telemon and Raymond formations and sent a

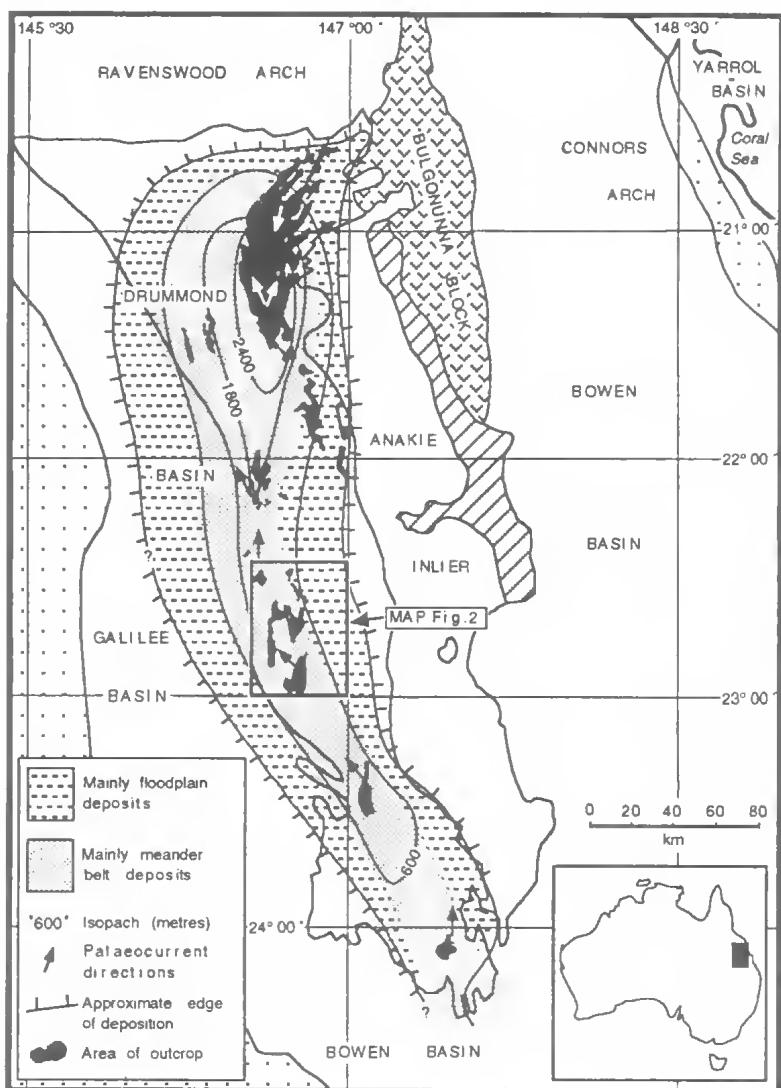


FIG. 1. Map showing the position of the Drummond Basin and its relationship to surrounding tectonic units, and the areas of outcrop, isopachs, and directions of sediment transport of the Raymond Formation. The area covered by Fig. 2 is shown by a rectangle. (Modified from Olgers, 1972).

limestone block full of fish remains, that was collected along a roadside, to the Queensland Museum. Dr Susan Turner of the Queensland Museum made collecting trips to the Narrien Anticline in 1984-5 and found a new fish locality in the Telemon Formation. In 1986, Long prepared a manuscript on the specimens collected by de Bretzel and Turner, but this was never published because he realised that the species involved may have been represented by more

adequate material from the Raymond Formation and was also doubtful about the provenance of the de Bretzel specimen. We here provide a description of that material and compare it with our better localised and more adequate sample. In the same year Long and Arvid Buskas, a postgraduate student at the ANU, located the bed from which the present material has been collected. This had been visited previously by Dr Turner. The collection studied in the present work has been made by Long and Buskas, and by Fox, Barwick, Campbell and William Ellis, a student assistant, in 1986; and Barwick and Campbell in 1990. All the specimens of *Cladarosymblema narrrienense* described herein, except the holotype, have been etched from more than 500 kg of limestone from a single stratum.

The fish fauna from the above locality, which we will refer to as the Police Mountain Track locality (Fig. 2), consists of at least five fish species - one crossopterygian, three actinopterygians and one acanthodian. Long found numerous acanthodian specimens in the de Bretzel block, suggesting that it did not come from our locality. In addition to the specimens definitely identified as fish,

we have found a few large postcranial bones that are large enough to be amphibian but are possibly rhizodontiforms. At present we have too few of these to warrant description.

Herein we describe from the Raymond Formation one osteolepiform fish, with which we compare the osteolepiform from de Bretzel's material. Long (1986) has described some of the acanthodontians from the de Bretzel limestone

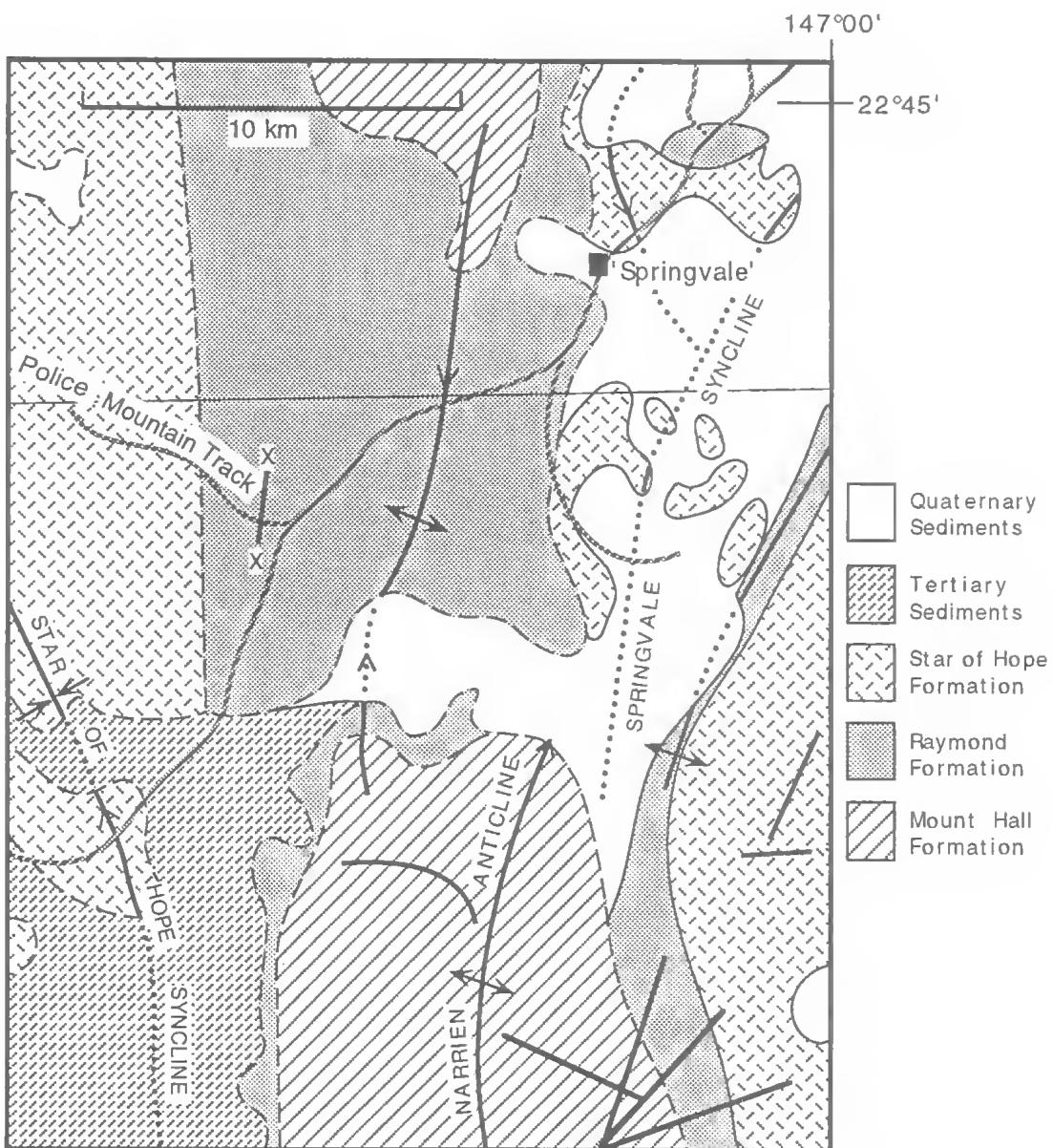


FIG. 2. Generalised geological map of the Springvale area from which the material described was collected. Position of collecting localities shown thus: X—X. (Modified from Vine & Doutch, 1972.)

block, and the other osteichthyans will be the subject of another paper.

Osteolepiforms known from the Devonian of Australia include *Gyroptychius australis* Young & Gorter from the Middle Devonian rocks at Burrinjuck Dam, N.S.W., *Gogonasus andrewsae* (nom.corr. for *G. andrewsi* Long) Long from the Frasnian of the Canning Basin, W.A., and *Marsdenichthys longioccipitus* Long and

Beelarongia patrichiae Long from the Frasnian of Mt. Howitt, Victoria. The problematical *Canowindra grossi* Thomson from the Upper Devonian of New South Wales has been regarded as an osteolepiform by Long (1985b,c) and by Young et al. (1992). The new genus is the first occurrence of a well-preserved osteolepiform from the Australian Carboniferous. The only other crossopterygian fish described from the Carbonifer-

ous of Australia is the rhizodontid *Barameda decipiens* from redbeds near Mansfield, Victoria (Long, 1989). This dearth of crossopterygians is surprising in view of the large number of fishes obtained from the Gogo Formation, and the great thickness of suitable sediments of Devonian and Carboniferous age in all the eastern States. The occurrences reported from both the Telemon and Raymond formations suggest that an aggressive search of the Drummond Basin will produce more freshwater genera, and Long's discovery of rhipidistian fish remains in the Carboniferous rocks of the Canning Basin of Western Australia suggest that more marine genera will turn up there.

STRATIGRAPHY AND ENVIRONMENT

Specimens described herein were obtained from a carbonate bed in the Early Carboniferous Raymond Formation, which crops out extensively in the Drummond Basin (Fig. 1). The fossil bed is exposed on the eastern flank of a small, local anticline whose axis is offset from that of the larger Narrien Anticline and lies west of the Springvale Syncline (Vine & Doutch, 1972; see also Fig. 2). These structures lie about the mid-length of the meridionally oriented Drummond Basin.

The Drummond Basin is an intracontinental structure formed during the Late Devonian and Carboniferous west of the Anakie High in central Queensland. Sediments within it locally overlie the Upper Devonian Silver Hills Volcanics and were deposited in fluvial and lacustrine environments. Sediment transport throughout its history was south to north. As would be expected, the sediments consist mainly of conglomerates, sandstones and shales, all of which show rapid lateral facies changes. The stratigraphic column shown in Fig. 3 has been drawn up from the northern part of the basin where the thickness is greatest. The fossil locality is about 150 km to the south of this depocentre, where the thickness is approximately three quarters of the maximum further north. The rate of sediment accumulation was enormous, the Lower Carboniferous sequence being measured at 12 000 m thick (Olgers, 1972).

The nearest contemporaneous sea was either to the north of the Lolworth-Ravenswood Arch, or at the northern end of the Yarrol Basin, even if allowance is made for the westward translation of that structure in post-Carboniferous times. In both of these areas, Early Carboniferous brachio-

AGE	NORTHERN DRUMMOND BASIN		
	Formation	Max. Thick. In m	Lithology
LATEST CARBONIFEROUS & YOUNGER	GALILEE BASIN SEQUENCE & BULGONUNNA VOLCANICS	—	—
	NATAL FORMATION	1200	Quartzose and feldspathic sandstone, siltstone and mudstone.
	* BULLIWALLAH FORMATION	1800	Lithic and feldspathic sandstone, with minor siltstone, mudstone and tuff
	STAR OF HOPE FORMATION	1800	Varicoloured tuff, sandstone, conglomerate and siltstone
	RAYMOND FORMATION	1000	Quartzose sandstone with minor siltstone and mudstone.
	MOUNT HALL FORMATION	3000	Quartzose sandstone and conglomerate. Minor lithic sandstone and mudstone.
LATE DEVONIAN TO EARLY CARBONIFEROUS	# SCARTWATER FORMATION	1200	Feldspathic and lithic sandstone, mudstone, tuff and algal limestone
	SAINT ANN'S FORMATION	2100	Rhyolite, tuff and algal limestone.
EARLY AND MIDDLE DEVONIAN	UKALUNDA FORMATION	—	Siltstone, sandstone and limestone, metamorphosed in part.

FIG. 3. Generalised stratigraphic column from the depocentre at the northern end of the Drummond Basin. The entire sequence apart from the Ukalunda Formation consists of volcanic and fluvial or lacustrine deposits. * indicates the position of the Ducabrook Formation, a facies equivalent of the Bulliwallah Formation and the # indicates the position of the Telemon Formation, a facies equivalent of the Scartwater Formation. (Modified from Olgers, 1972.)

pods, corals and molluscs are present. However, no Carboniferous marine fossils are known from the Drummond Basin.

The Raymond Formation was named the Raymond Flappy Sandstone by Hill (1957), a name reflecting its overall nature. In the vicinity of the fossiliferous bed, the rocks are mainly grey- or buff-coloured sandstones and siltstones that show many evidences of shallow water deposition. Interference ripples, wind-ripple drift, and channels filled with cross-stratified sands are common within or adjacent to the fossil bed, and there are sporadic sand-filled mud cracks. Moreover, mud clast conglomerates, indicating the break-up and erosion of nearby penecontemporaneous sedi-

ments, demonstrate that the water was so shallow that mud cracking and redeposition were features of the environment. Many of the rocks, including those within which the fish are preserved, contain macrofloral remains, usually lepidodendroid stems. These points, in association with the evidence of the sediments and the palaeogeography, indicate that the fish fossils are of freshwater origin.

The carbonate unit can be traced over a distance of approximately 3km. At its northern extremity the carbonate content gradually decreases; the bed becomes a silty sandstone, containing few fish. At the southern end soil cover obscures the outcrop, but we have been unable to find the bed in the appropriate stratigraphic position further around the structure even where the outcrop improves. Nor have we been able to find it on the other side of the anticline. Consequently, we conclude that the limestone bed was deposited over a restricted area, probably in a restricted environment. It is possible, of course, that the bed was more widely distributed, and was eroded from neighboring areas penecontemporaneously. Because the limestone laterally grades into siltstone at its northern end, and at its southern end it consists of lenticular units, we do not accept that hypothesis.

The fossiliferous limestone is up to about 2m thick, but it varies considerably in thickness over the outcrop. In its northern half the limestone is persistent, and is commonly 1.0-2.0m thick. In the southern part of the outcrop the unit is less persistent and is rarely more than 0.5m thick. It lenses out from 0.5m to nothing within a few metres along strike, and then reappears equally rapidly. This is interpreted as the result of deposition in isolated patches rather than penecontemporaneous erosion.

In the north, the base of the bed is an algal pellet limestone about 0.5m thick, which contains few

fish. The remainder of the unit contains abundant fish remains and is composed of carbonate mud containing quantities of terrigenous sand, silt and, in many places, flat mud and silt clasts up to 10 cm in diameter. Despite the abundance of carbonate, no sign of invertebrate remains has been found. Many of the clasts are carbonate rich, consisting of scattered quartz grains in a mud matrix containing carbonate. Some of the clasts are completely overgrown by algae (Fig. 4A) indicating movement before burial, and others are partly coated with algae (Fig. 4E). Presumably this means that these silt and mud clasts were at least slightly hardened and overgrown before transport. Others were still soft when deposited, because their edges are not sharp, but merge into the surrounding matrix, suggesting partial disintegration during deposition. Occasional small clasts are made of algal carbonate (Fig. 4E), and many of these show the coliform external shape of the growing algal colony (Fig. 4A). The finer-grained matrix consists of mud and silt with large amounts of carbonate; and a carbonate cement. Many fine sand-sized clasts are made of angular quartz. Locally abundant bodies that appear in thin sections as sand-sized groups of radially-arranged calcite crystals, are interpreted as *Microcodium*, structures that are formed as the result of the infilling of root spaces during exposure to the atmosphere (Scholle et al., 1983).

Some larger clasts contain fish fragments (Fig. 4D) indicating that the specimens were disaggregated and deposited in the soft silty sediment. This was then dried out and cracked, and the resulting clasts were redeposited. Such an interpretation implies that some of the isolated fish fragments that are now found in the matrix of the rock were reworked from penecontemporaneous sediment. None of the clasts consists of igneous rocks or of earlier Palaeozoic sediments; this

overleaf on pp. 110-111

FIG. 4. A-E, thin sections of sediment from which the fossils have been extracted. All figures have been prepared by printing the thin section in an enlarger. A, QMF31882, section cut normal to bedding. Shard-like bodies are fish scales. Numerous small white spherical bodies are composed of carbonate. The large mass (a) is a clast still showing bedding. Most other clasts are intraclasts. Those labelled (b) are completely coated with algae. Note some of the clasts have clearly defined boundaries, but those labelled (c) merge into surrounding matrix or show highly irregular boundaries indicating that they were soft when deposited. Cloud-like bodies (d) are algal growths; some are attached to clasts, others have broken free. (e) section through a cartilage bone. B, QMF31883, section parallel with bedding. Most sharp-edged fragments are scales; silty matrix is largely carbonate. C, QMF31884, section normal to bedding; shard-like bodies are scales; dark oolith-like bodies are teeth, appearing as circles demonstrating that they were current-oriented. Note clast (a) has been squeezed out laterally during compaction, indicating that it was soft when deposited. D, QMF31885, section normal to bedding showing large clasts separated by carbonate silt with many fish fragments. Clast (a) itself has an embedded fish fragment; its right margin merges into the matrix. E, QMF31886, section normal to bedding. Upper side of flat clast (a) is encrusted with algae; several well-defined algal balls (b) are present. Scales: 10mm.

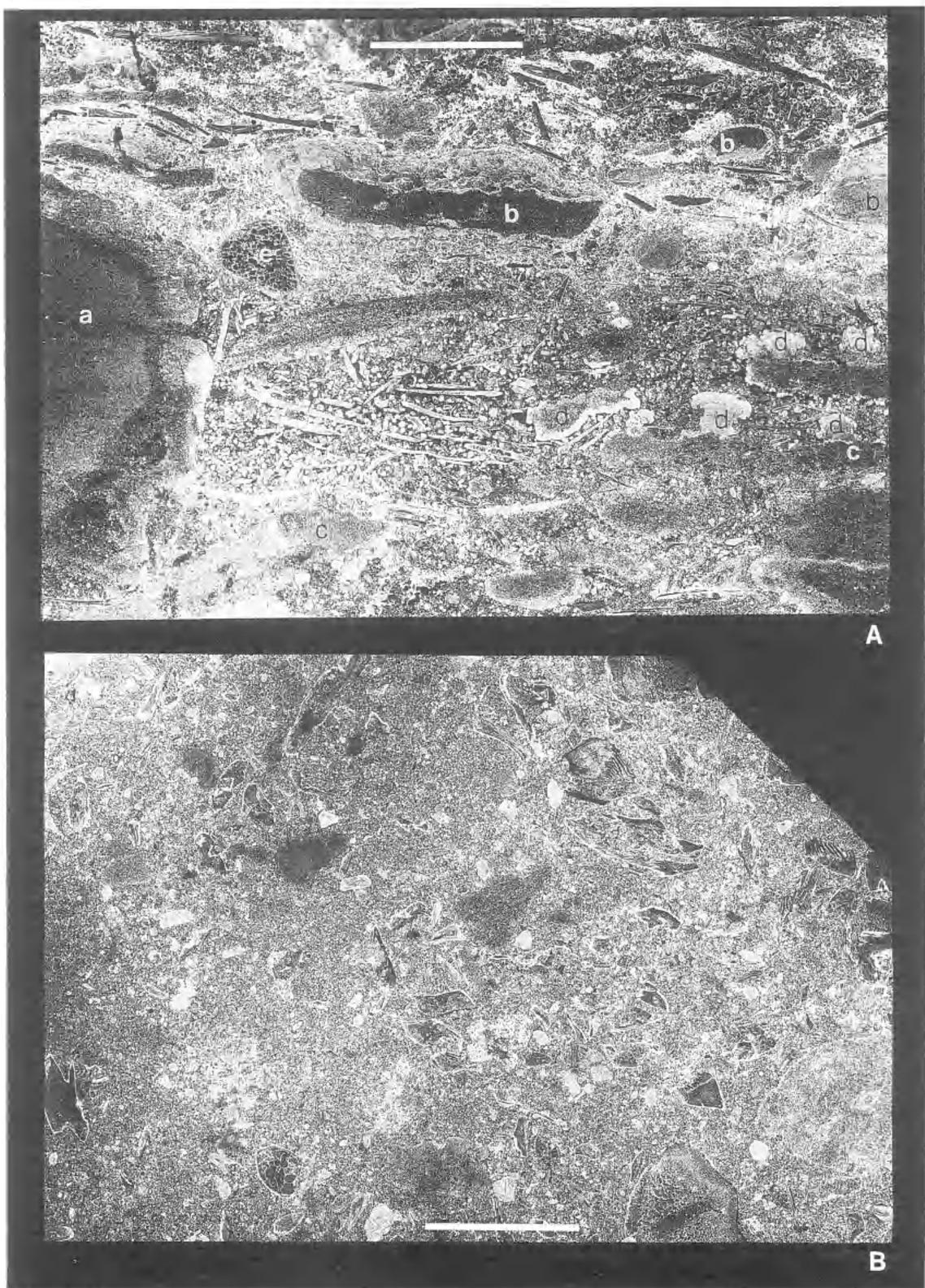


FIG. 4A, B.



FIG. 4C-E.

indicates that no distant transport was involved, and that any currents were of short duration.

Fish remains, whether scales or cranial plates, almost all lie parallel with the bedding, which they help to define in hand specimen (Fig. 4A,C). In thin section many have uniform, small diameter tubes that are now filled with chemically-deposited carbonate. These are of appropriate size and shape to be borings made by either algal hyphae or nematodes. Absence of imbrication indicates low velocity depositing currents. Several well-formed coprolites, cylindrical in form, have been recovered from the etches. These would not have been preserved if they had been subjected to much movement on the bottom. Of course, the nature of the sedimentary clasts also precludes strong persistent currents. We conclude, therefore, that periods of excess energy disrupting bottom sediments were short-lived but rapidly broke up skeletons and caused unconsolidated mud to infiltrate main skeletal cavities.

Sandier units within the limestone are commonly cross-stratified. In places, channels subsequently filled with coarse sediment cause slight thickening of the unit. These channels were cut in the underlying sediments and filled with carbonate and terrigenous clasts.

We interpret the depositional environment as a semi-persistent lagoon formed by a body of overbank water in which freshwater calcareous algae grew, and fish were able to make permanent habitations. During floods, water flowed through and around the lagoon disrupting the carbonate-rich sediments and transporting clasts torn up from the surrounding, recently deposited, sediments. The abundance of *Microcodium* in some sections indicates that plants were growing on the adjacent sediment or perhaps actually on the carbonate itself. On occasions new temporary channels were established, and conglomerates were formed in these.

The fish are almost always fragmentary, and it is uncommon to find whole otico-occipital or ethmoid units. Scales are scattered through the whole deposit. Only one assembled specimen, the holotype, was found, and it was lying in a siltstone/sandstone layer immediately on top of the limestone. Specimens preserved in three dimensions are filled with carbonate mud; none have a crystalline calcite infill. It is concluded that the skeletons were disaggregated before interstitial carbonate precipitation could occur.

As a result of this mud infilling, sediment compaction has resulted in cracking and disruption of

most specimens. This is unlike the fish from the Gogo Formation, Western Australia, where crystallisation of carbonate in the open spaces within and between bones took place during early diagenesis, preventing skeletons from crushing. Most flat specimens of *Cladarosymblema*, such as the roofing bones and operculars, are badly cracked and fall apart during etching. Despite disaggregation, few bones show evidence of abrasion, indicating little transport.

The Drummond Basin is analogous tectonically to the Lambie Basins of New South Wales and Victoria, which are predominantly filled with Upper Devonian redbeds, and contain thick sequences of conglomerates, which, although concentrated near the base of the sequences, occur at many levels. At many horizons freshwater algal pellets are very common, and placoderms are frequently found in such sediments. However, we note that the Drummond sediments include fewer redbeds, and conglomerates are not concentrated in the basal formations. In our opinion, this is not the result of a different tectonic environment, but rather of a wetter climate. Such an interpretation would account for the persistent standing body of water that would be necessary to account for the limestone in which *Cladarosymblema* is found.

AGE OF THE RAYMOND FORMATION

In the absence of marine fossils or volcanic rocks from which radiometric dates could be obtained, spores, plant macrofossils and microvertebrates provide the only means for dating this formation. Only a limited number of palynological determinations have been made on sediments from the Drummond Basin, and all of these were by Dr Geoffrey Playford. The palynostratigraphy was reviewed by Kemp et al. (1977) and Playford (1985). The plant macrofossils have been studied by White (1972).

Lepidodendroids are the common plants in the sequence. *Leptophloem australe* (McCoy) is common in the Late Devonian of eastern Australia, but has never been recorded above the earliest Tournaisian (Jones et al., 1973). In the Drummond Basin, it is not recorded in beds higher than the Mt. Wyatt Formation, which overlies the Lower Devonian Ukalunda Formation and unconformably underlies the Drummond Group in the extreme north of the basin. It is separated from the Raymond Formation by several thousand metres of sediment. Other species of lepidodendroids occur in all the formations between it and the Raymond Formation. The

common species in the Raymond Formation is the long-ranging Carboniferous species *Lepidodendron veltheimianum* Sternberg, which occurs through several formations above and below. The exclusively Carboniferous *Rhacopteris digitata* Etheridge fil. also enters the sequence several thousands of metres below the Raymond Formation, but above the Mt. Wyatt Formation. We conclude that the macroflora gives no more precise age for the Raymond Formation than some level above the base of the Carboniferous.

Playford (1976, 1977) described spores from the Ducabrook Formation, which is higher in the sequence than the Raymond Formation, and has assigned them to his *Anapiculatisporites largus* Assemblage. He considered this assemblage to be of late Viséan age for two reasons: 1, the same assemblage occurs in the Tanmurra Formation and the upper Bonaparte Beds of the Bonaparte Basin, Western Australia, where it is dated by marine invertebrates; and 2, some species of palynomorphs from the assemblage are known elsewhere only from the late Viséan of Britain. Playford (1985), in the most recently published review of Australian Lower Carboniferous palynology, showed the Raymond Formation as late Tournaisian in age, not because he had additional information, but because he spaced the formations between the *Leptophloem australe* Flora and the *Anapiculatisporites largus* Microflora. Thus the macrofloras indicate that the formation is probably younger than Tournaisian, and the microfloras show that it cannot be late Viséan or younger.

Samples of the fish-bearing rock have been etched by Dr Clinton Forster of the Australian Geological Survey Organisation with a view to studying palynomorphs, but no identifiable short-ranging spores have been recognised.

Turner (1993) studied the microvertebrates of the Raymond Formation at the site from which our material comes. Although there is no precise identity between the Raymond Formation species and those from elsewhere in the world, she considered it possible to draw general conclusions about the age and environment of deposition of the formation. In her opinion the fauna is early to middle Viséan in age, although the control is limited by the range of data available. She further considered that the fish fauna has elements in common with the Scottish Viséan, an interesting point in view of the presence of megalichthyids in the same region. This is slightly younger than suggested by Playford, but is within the range

indicated by plant data. We conclude that the most reliable age estimate available at present is early to middle Viséan, an age consistent with the occurrence of megalichthyids.

MATERIALS AND METHODS

The amount of carbonate cement and matrix can be judged from the mode of preparation we have had to adopt. Each specimen underwent many cycles of immersion in acid for up to seven days, washing for two or three days, drying over a period of days, and finally impregnating with dilute plastic. The matrix does not completely disaggregate under acid treatment, but the rock becomes soft and is easily removed by scraping and/or brushing with a soft hair brush. Many specimens have required immersion and impregnation as many as thirty times.

The specimens were all whitened with ammonium chloride before being photographed. The specimens examined by scanning electron microscope were gold-coated.

The holotype is the only specimen prepared mechanically, and that was done by vibrotool and needle.

Materials cited in this work are registered with the Queensland Museum (QMF), Western Australian Museum (WAM), Australian National University Geology Department (ANU), Royal Ontario Museum (ROM), British Museum Natural History (BMNH), Hancock Museum, Newcastle-on-Tyne (G) and Hunterian Museum, Glasgow (V).

TERMINOLOGY

ETHMOID UNIT: the part of the skull anterior to the intracranial joint, including the skull roof and endocranum of that part of the skull.

OTICO-OCCIPITAL UNIT: the part of the skull posterior to the intracranial joint. As with the ethmoid unit, it includes the skull roof and the endocranum.

NOMENCLATURE OF SKULL ROOFING BONES: We do not wish to become involved in discussion of this matter, as our purpose is to describe a new genus and indicate its relationships with other osteolepiforms. We have chosen the terminology of Westoll (1936), Romer (1937) and several later authors, most recently Ahlberg (1991), which is based on comparison with primitive tetrapods. The matter has been extensively discussed by Borgen (1983).

We wish to comment, however, on the nomenclature of the nasal, rostral and tectal series. Definition of the nasals depends on the presence of

lateral line canals within them, and the other two series lie mesial and lateral to the nasals respectively. Our observations of the snout of *Cladarosymblema* indicate that the position of the lateral line canal is sometimes not clear from observations of the external surface, particularly if reliance is placed on lateral line pores. It is necessary to work from X-radiographs, excavated canals or specially prepared internal surfaces. Even when this is done, it is found that in some specimens the canals run along the sutures between bones in some places, around the centres of ossification in others, and through the centres in yet others. Consequently the identification of the nasal series is sometimes ambiguous. Hence identification of rostrals and tectals is sometimes uncertain. We are wary of some statements in the literature concerning these bones, and advise caution in recognising taxa on the basis of such criteria. A second point concerns the difference in the arrangement of bones of these series on opposite sides of the one specimen. There seems to be little point in trying to homologise individual bones within these series. The taxonomic value of such an exercise is questionable.

PREMAXILLA: Jarvik (1942:346) stated that the infraorbital lateral line canal 'along the ethmoidal region pierces a paired row of bones, the rostrals, in all three main crossopterygian groups'. In osteolepiforms the toothbearing bone around the edge of the mouth also carries the lateral line. Jarvik therefore referred to it as a compound bone, the rostro-premaxilla, except in species in which he considered that the first nasal was also incorporated. For such forms he used the name naso-rostro-premaxilla. Jarvik claimed to be able to show that in some specimens of *Eusthenopteron* the premaxilla is an independent bone sutured against the rostrals. In all our specimens of *Cladarosymblema* the tooth-bearing bone is large and has a projection extending over the area that is covered by the first nasal bone in such genera as *Osteolepis*. However, the bone in question has a single centre of ossification; hence we have no observable evidence of fusion. We prefer to refer to it as the premaxilla.

PRENASAL FOSSA: Jarvik (1966: figs 17 et seq.) referred to deep fossae roofed with thin endocranial bone and lying anteromesially to the nasal cavities, as 'divisio prenasalis communis of the neural endocranum'. In a complicated terminology of this region, he also used the terms prenasal pit, intervomerine pit and anterior palatal fenestra. We are unable to discriminate detail of this sort on our specimens. In addition, Jarvik has

used the structures he recognised to imply relationships that have not been accorded general agreement. Hence, to avoid confusion, we have not accepted his terminology. The two deep, sub-hemispherical depressions in the endocranum that are clearly separated by a broad median ridge of endochondral bone which is slightly overlapped anteriorly by the posterior process of the premaxilla, are given the non-committal name of 'prenasal fossae'.

SYSTEMATIC PALAEONTOLOGY

Order OSTEOLEPIFORMES Jarvik, 1942

REMARKS

The possibility of defining this taxon has been disputed by Rosen et al. (1981), who considered that it was paraphyletic. Long (1985b,c, 1988, 1989) and Panchen & Smithson (1987), working within a cladistic framework, are among the few who have continued to take this work seriously, and even they have contested its conclusions. Restricting the families included in the taxon to the Osteolepididae and the Eusthenopteridae as then understood, Long claimed that the Osteolepiformes are unique in having a small vertical preopercular, seven bones forming the cheek with the lachrymal as large as the jugal, a dermal shoulder girdle with an exposed anocleithrum, and scutes at the bases of the fins. Panchen & Smithson (1987: 358-362) independently considered that the seven cheek bones were autapomorphic for the Osteolepiformes. In addition, they accepted the presence of scutes at the base of median and paired fins, and a single external naris, from the list provided by Andrews (1973). This composite list of disparate characters does not commend itself to some of us as the basis for the recognition of a major taxon. In our view, osteolepiform and rhizodontiform genera should be analysed in terms of functional systems before an adequate classification is possible, but we do not have access to a complete range of characters that can be interpreted functionally (but see below). Hence we do not attempt the definition of taxa at the level of the Osteolepiformes. On the other hand, we consider the Megalichthyidae to be closer to the Osteolepididae than to any other family, and so we classify them under the order Osteolepiformes simply to indicate that point. We note, however, that the Megalichthyidae falls within the definition of the Osteolepiformes as defined by Long (1985b).

Family MEGALICHTHYIDAE Hay, 1902

DIAGNOSIS

Skull low and wide; no pineal opening; anterior narial opening slit-like, embraced in front by lateral rostral and behind by anterior tectal bones; separate bones dorsal and ventral of this opening absent; maxilla high, with its highest point posterior, leaving only a short edge for junction with the squamosal; outline of squamosal approximately equidimensional; preopercular short and standing vertically. Opercular large, subquadrate in outline, with a H/L ratio of approximately 1; two suboperculars, (see discussion of operculars below), both abutting posteriormost submandibular; subopercular 1 only half the size of opercular; lateral extrascapulars wide. Posterior endocranial wall of trigeminofacialis chamber approximately transverse (see REMARKS below). Tusk on premaxilla positioned behind variably developed row of small teeth; posterior process on premaxilla lying on endocranial palatal lamina of ethmoid shield; pres nasal fossa divided by endocranial bone partly covered by posterior process of premaxilla. Vomer transverse in outline, lacking posterior process, but with mesial process meeting, or almost meeting, its fellow in midline. Well-developed, deep anterior mandibular fossa; strong postglenoid process; strong symphysial tusk on dentary, and teeth reduced or absent in front of it. Scales rhombic but lacking peg-and-socket articulation. Scapulocoracoid very large, and with extensive attachments to cleithrum. Pectoral fins large and fan-shaped.

REMARKS

The diagnosis has been prepared with a view to differentiating the family from other osteolepiform families, and consequently we have used only those osteolepiform characters that are individually unique, or which form complexes unique to the Megalichthyidae. We are aware that it is possible to find outside the family an odd genus that has one or more of the features listed above as unique. In our view this is not significant: the definition of any higher taxon is likely to include statements about characters that have developed independently in unrelated taxa, i.e., homoplastic characters.

For this reason it is necessary to emphasise character complexes, as illustrated by the following three examples.

(A) We acknowledge that the squamosal of some members of other families is almost

equidimensional in outline and that some others have high maxillae, and that yet others have steeply inclined preoperculars, but these features in megalichthyids inter-relate to make a distinctive cheek.

(B) The outline of the opercular in some members of *Osteolepis macrolepidotus* is similar to that of the megalichthyids (Jarvik, 1948: fig. 41). However, note that the opercular in that species is highly variable, it is small in comparison with that of megalichthyids of similar size, subopercular 1 is of like dimensions to the opercular, and that these two bones sit high on the side of the head with the long axis of the opercular inclined to the long axis of the fish. Although we have no specimens of megalichthyids with the opercular series in position relative to the cheek and the shoulder girdle (but see Borgen's illustration of the cheek and operculars of his new genus [MS]), it is clear that the long axis of the opercular must have been almost horizontal and that it covered a large part of the side of the gill chamber, its ventral edge being at about the level of the mandibular articulation; and that subopercular 1 is small in comparison with the opercular. All these features imply significant differences between megalichthyids and *Osteolepis* in the dynamics of the gill chamber.

(C) The significance of the two bones around the anterior naris is that they are placed anterior and posterior to the opening rather than dorsal and ventral. Although this bald statement is made in isolation, the position of these bones was only achieved by a complex rearrangement of the surrounding bones as compared with other osteolepiforms. Yet the diagnosis contains only terse statements about the positions, shapes and relative sizes of all the bones in question, making it possible to object that individual characters are not unique. This illustrates our previous point that the listing of uninterpreted characters such as is found in standard cladistic analyses is almost valueless.

One feature we have left in the diagnosis is the large, flat, fan-shaped pectoral fins, despite the fact that some osteolepidids, such as *Gyroptychius groenlandicus* (see Jarvik, 1985, fig. 8), have similar fins. *Gyroptychius* is a member of the Osteolepididae, which do not normally have fins of this type. We conclude that *Gyroptychius* has evolved this fin type independently. Thus, although the shape of the pectoral fins cannot be said to be unique to the Megalichthyidae, it is a feature that permits a

separation of most members of the Osteolepididae from the Megalichthyidae.

Some characters have not been found in all the named taxa, but we have included them in the diagnosis because we have reason to believe, on the basis of incomplete evidence, that they are so distributed. Other features have been included although they have not yet been discovered in all the included taxa, because we consider that they are very distinctive in the genera in which they are known, and the probability of their occurrence in taxa with correlated characters is high. For example, with regard to the shape of the vomers we note that although only incomplete bones have been found for *Cladarosymblema narrienense*, the shape of the endocranial surface to which the vomers were attached shows that they were very wide, like those of *Megalichthys*. This shape ties in well with the unusual breadth of the rostral unit, and so it has been included as diagnostic.

Other features that may prove useful when better descriptions become available are as follows: (1) The cheek is apparently short in *Megalichthys*, *Ectosteorhachis*, *Cladarosymblema* and a new genus of megalichthyid from the ?Permian of Norway being described by Ulf Borgen (Borgen, MS), but details are lacking.

(2) It appears that the squamosal is equidimensional in outline, and from the position of the orbit as inferred from the jugal, the postorbital and the jugal must be more elongate than in other osteolepiforms.

(3) The ornament of the dermal pectoral girdle of both *Cladarosymblema* and *Ectosteorhachis* is distinctive, but *Megalichthys* itself is too poorly known to permit the character to be used diagnostically for the family.

(4) A strong oral lateral line canal branches from the mandibular canal in *Eusthenopteron* and it may be a widespread feature in osteolepiforms, but adequate material has never been prepared. *Cladarosymblema* has no oral canal, and from the absence of pits in the surangular of *Ectosteorhachis* and *Megalichthys*, we conclude that the same applies to those genera also. However, absence of an oral canal may be more widespread than that, and so caution has been exercised in using it as a family character.

(5) In *C. narrienense*, the angle between the olfactory tracts in dorsal view is only about 45°, and the dividing point is behind the mid-length of the ethmoid unit. In fact, the division is so far back that the canal for the optic nerve exits from the side of the olfactory tract instead of from the

wall of the braincase proper. The same arrangement has been described for *Ectosteorhachis nitidus* (Romer, 1937: figs 8, 9). The British *M. hibberti* requires dissecting before the olfactory tract configuration is certain, but we consider that specimen V3040 from the Hunterian Museum, Glasgow, although crushed, suggests a posterior divergence like that described above. Should this prove to be so, it is another feature by which the Megalichthyidae may be distinguished from other osteolepiforms.

(6) In megalichthyids, the gutter around the cosmine cover of the scales usually exposes the vesicular bone that forms the core of the scale, and the overlapped part of the scale is lamellar bone on its inner and outer surfaces. A gutter in which vesicular bone is exposed is also known in *Latvius* (Gross, 1956), but the histology of the whole scale has not been described. The value of this feature requires investigation.

We also note that a feature which has not attracted attention in differentiating the Megalichthyidae, probably because it is so rarely preserved, is the form of the endolymphatic sacs and ducts. The only other osteolepiforms in which these structures are confidently known are *Eusthenopteron foordi* and *Ectosteorhachis nitidus*. As Jarvik (1975) has pointed out, in *E. foordi* the supraotic cavities of the two sides converge mesially in a discrete arch that extends posteriorly over the brain stem and exits from the braincase to form an extension down the spinal cord. Romer (1937) showed that no such arch is present in *Ectosteorhachis nitidus*, which has a relatively flat-topped sac without a vertebral extension. Our observations of *Cladarosymblema narrienense* (see below) indicate a different pattern from that of *E. nitidus*. We still lack detail for this region in *Megalichthys hibberti*, detail that can be obtained only by dissecting an appropriately preserved specimen.

Unusual features of *Cladarosymblema* are the large lateral extrascapulars and post-temporals. We have not been able to confirm the presence of similar bones in *Megalichthys*, *Ectosteorhachis* or Borgen's new genus. Borgen, however, has figured a specimen of *M. hibberti* (BMNH P 5231) that has a large lateral extrascapular, and all of these genera have large quadrate-shaped operculars whose size and orientation suggest that the post-temporals were also large. We expect that these features will prove to be diagnostic of the family when more material is discovered.

Finally, we draw attention to the point that the components of the ring centra of *Megalichthys*,

Ectosteorhachis and *Cladarosymblema* are solidly fused, although they may be incomplete dorsally along part of the vertebral column. Andrews & Westoll (1970b: 427–429) considered that this type of structure represents the culmination of ‘a trend of increasing consolidation of the axial skeleton within the Rhipidistia’, and that it also occurs within other stocks such as the one leading to *Rhizodopsis*. It may yet be possible to distinguish between the centra of *Rhizodopsis* and megalichthyids using such features as the nature of the lateral grooves and the lack of a periosteal surface on *Rhizodopsis*. For this reason we prefer not to list the character of the centra as a possible diagnostic feature until further investigation is complete.

In preparing the above diagnosis of the family some previously used features have had to be ignored in the light of new observations, and others have been stressed now that we have access to information derived from better preserved specimens. In particular, we note that Bjerring (1972), followed by Jarvik (1985), indicated that within the Osteolepiformes, the crista parotica of osteolepidids differs from that of rhizodontids in that it runs posteromedially beneath the skull roof, leaving the lateral parts of the supratemporal and the entire extratemporal unsupported by endocranum. To arrive at this conclusion they used the endocranum of *Ectosteorhachis nitidus* on which they superimposed the roof of *Megalichthys laticeps* as interpreted by Bjerring (1972). Their view has been confirmed, at least for osteolepids, by the genus *Gogonasmus andrewsae* Long, new specimens of which are under description by us; but in our specimens of *C. narriense* the crista parotica runs posteriorly along the outer edge of the supratemporal, and our observation of *E. nitidus* indicates that it is precisely similar. Hence we do not accept that the position of this structure is consistent in all osteolepiforms, and it cannot have the significance they proposed. However, the position of the transverse wall of the endocranum at the rear of the trigeminofacialis chamber is probably a feature that will permit the differentiation of the Osteolepididae from the Megalichthyidae. The sharp lateral turn of this part of the endocranum where it attaches to the roofing bones, does seem to be a distinctive feature of the Megalichthyidae, even though the angle may be somewhat less than a right angle in *E. nitidus*. Romer (1937) figured this structure as oblique rather than transverse in its orientation, but we consider he was in error; the chamber has been partly excavated in

MCZ6499 without reaching the wall, which must therefore be more nearly transverse than he considered it to be.

Borgen (MS) pointed out that the first use of a family-level designation involving the use of the stem name *Megalichthys* was in a list published in 1902 by Hay. However, Hay did not define the family, and he included a number of genera that today would be regarded as only distantly related to *Megalichthys*. In 1962, Vorob'jeva considered that *Megalichthys*, as she then conceived it, was a Carboniferous form derived from an *Osteolepis* stock in the Middle Devonian, and she retained *Megalichthys* in the Osteolepididae. The discovery of Late Devonian megalichthyids in Turkey (Janvier, 1983) showed that the Devonian origin of the group is correct, although it may not extend back to the Middle Devonian. Vorob'jeva (1977) considered the Megalichthyinae to be one of a number of subfamilies, although she did not assign genera to it.

Young et al. (1992) defined the Megalichthyidae so as to include *Megalichthys*, *Ectosteorhachis*, *Megistolepis* and their new genus *Mahalalepis*. They used eight characters to diagnose the family. Seven were roofing characters of the ethmoid shield and the eighth was the presence of tusks on the premaxilla. Apart from the notching of the parietal to receive the posterior nasal, which is a very variable character (Thomson, 1964a: fig. 6), we accept this list but, with the exception of Long, we consider that it is too incomplete to meet the needs of an effective classification.

In this family we include *Megalichthys* Agassiz, *Ectosteorhachis* Cope, *Cladarosymblema* gen. nov., the new genus being described from Norway (Borgen, MS), and a form referred to as Megalichthyidae gen. et sp. nov. by Janvier (1983). The diagnostic characters cannot be observed on all these genera, but they are almost certainly present on *Megalichthys*, *Cladarosymblema* and Borgen's new genus. Most of the characters are known on the other two listed, and the apparent absence on the others is the result of a lack of data rather than the presence of different structures. Janvier's Turkish specimens consisted of an ethmoid unit and part of a mandible only, and consequently it is impossible to be certain of the assignment. However, it does have the characteristic flat snout, the tusk and pit on the premaxilla, the semblance of a divided prenasal fossa, a slit-like anterior naris, and olfactory canals separating at a low angle from a point behind the mid-length of the ethmoid unit. There

is a high probability that it is correctly assigned to the Megalichthyidae, although we remain uncertain about its generic relationships.

Megistolepis and *Mahalalepis*, which were placed by Young et al. (1992) in the family are, in our opinion, too poorly known to assign to the Megalichthyidae with confidence. *Megistolepis* is known from two Late Devonian species from Russia, neither of which shows adequate diagnostic features. However, we note that there is no tusk on the premaxilla and that, although the vomers are transverse in outline, they have two tusks or pits on each. The prenasal fossa is divided, and the figure given by Vorob'jeva (1977: fig. 35B) seems to show that the olfactory canals extend back to the posterior third of the ethmoid unit; both of these characters are known at present exclusively in members of the Megalichthyidae. Our view is that until more material is found, there are sufficient differences from the standard *Megalichthys* to make it unwise to assign this genus to a higher taxon. Vorob'jeva (1977) assigned it to the subfamily Megistolepinae of the family Osteolepididae.

Mahalalepis is known from a single fragmentary ethmoidal shield. Most of the characters we consider to be diagnostic of the family have not been preserved and so three of the authors of this paper are not prepared to comment further on its assignment. Long, however, still considers that on balance it is probably a megalichthyid.

Schultze (1988) placed *Lohsania* (Thomson & Vaughn, 1968) with *Ectosteorhachis* in the Megalichthyinae. Thomson & Vaughn made comparisons of the otico-occipital roof and the scales of *Lohsania* with *Ectosteorhachis*, but they pointed out that the structure of the vertebral centra differs in the two genera (Thomson & Vaughn, 1968: cf. figs 2 & 8). *Lohsania* lacks the structure of the centra found in *Ectosteorhachis*, *Megalichthys* or *Cladarosymblema*. In addition, the mandible of *Lohsania* is short and deep compared with that of *Ectosteorhachis*, but information on its other features remains unknown; no ethmoid or otico-occipital units were recovered from the same locality as the holotype, and hence the homogeneity of the paratype sample cannot be guaranteed. Although Schultze (1988) compared the new form he was describing from the Pennsylvanian of Kansas with *Lohsania*, the evidence of a relationship is restricted to a similarity in external outline, and even that is not great. We consider the mandible figured by Schultze (1988) cannot be definitely assigned. Until new data become available no worthwhile judgments can

be made about the taxonomic relationship of *Lohsania*.

Cladarosymblema gen. nov.

TYPE SPECIES

C. narriense sp. nov. from the Raymond Formation, Early Carboniferous (Viséan), in the Drummond Basin, Queensland.

DIAGNOSIS

Lateral line canal in front of posterior nasal sharply deflected mesially. Lateral extrascapulars and post-temporals large. Denticulated anterior part of parasphenoid long, very acute, but terminating well behind median processes of vomers. Wide parasympophysial plate turned posteriorly at lateral extremities, and covered with small denticles; lateral ridge on coronoids reduced and devoid of denticles; postglenoid process large and well-rounded; pre-articular produced into acute anterior termination, usually non-denticulate; lateral line pores large; no oral branch of lateral line canal in surangular.

ETYMOLOGY

Kladaros (Gr) = weak; sym (Gr) = together; blema (Gr) (n) = cover. Referring to the fact that the dermal bones and scales of the specimens have fallen apart during preservation.

REMARKS

The above diagnosis is a minimal statement distinguishing this new genus from other members of the family Megalichthyidae. We now discuss in detail the means by which the genus can be distinguished in turn from *Megalichthys*, *Ectosteorhachis* and the new Norwegian genus described by Borgen (MS), and we comment on other features likely to become useful with the advent of new knowledge.

Because material from the type locality of this new genus has been referred to previously as *Megalichthys*, or as being akin to *Megalichthys*, for example by Long (1989) and Turner (1993), it is important to be explicit about the differences between the two genera. Comparison between *Cladarosymblema* and *Megalichthys*, as represented by the type species *M. hibberti*, leaves no doubt that the two are distinct, although many differences are only in the relative proportions of various elements. We have examined some of the specimens in the Royal Scottish Museum, two in the Hancock Museum in Newcastle-upon-Tyne,



FIG. 5. *Cladarosymblema narrienense*. Dorsal view of the holotype, QMF21082. Scale: 10mm.

and a cast of the specimen from the Hunterian Museum, Glasgow, on which Jarvik's (1966) description was based. In addition we have used an advance copy of Borgen's review of the European species of *Megalichthys* (Borgen, MS).

One obvious difference is the size of the pores in the snout, those of *Megalichthys* being very large, and those of *Cladarosymblema* much smaller. We have considered the possibility that this difference is related to size of the specimens examined, or to resorption of tissue from the rims of the pores during cosmine replacement, but it seems more likely to be a taxonomic feature. A second obvious difference is the more anterior position of the external narial opening in *Cladarosymblema*, a feature it shares with *Ectosteorhachis* and Borgen's new genus from Norway. The posterior process on the prearticular that carries the tusk is shorter in *Cladarosymblema* than in *Megalichthys*, the tusks are more anteriorly placed, and the teeth on the margin of the premaxilla anterior to the tusks are more reduced or even absent. The number and position of the postrostrals is also a possible means of differentiating *Megalichthys* from *Cladarosymblema*, but in both genera the number of specimens in which the bone boundaries are not obscured by cosmine is small, and among the useful ones the variation is too large for definite conclusions to be reached. (We have already noted our reservations about the taxonomic use of these bones.)

More information is needed on the endocranum of *M. hibberti* to make an adequate comparison of the endocranum of *Cladarosymblema*; the main description available is that of Jarvik (1966), which deals with the ethmoid unit only. We disagree with Jarvik about some important parts of the anatomy of this unit. In particular, we consider it possible that the posterior process of the vomer is not as he claimed; it seems more likely that the bone he interpreted as this process is a cracked piece of the surface of the endocranum. We do not accept that there is an intervomerine pit in the position he indicated. There are other foramina on the endocranum lateral to the posterior end of the parasphenoid, in addition to those indicated by Jarvik. These will be commented upon in the appropriate places below. We now comment on differences between *Megalichthys* and *Cladarosymblema* in dermal characters.

Examination of well-preserved specimens of *M. hibberti* has convinced us that no inter-premaxillary bone (Schultze, 1974) is present, and that the tusk and pit seen in this region are on the premaxilla. Several specimens of *C. narrienense* in which the radiation centres and boundaries of the bones can be discerned on internal and external surfaces (Fig. 27A,D), show no evidence of

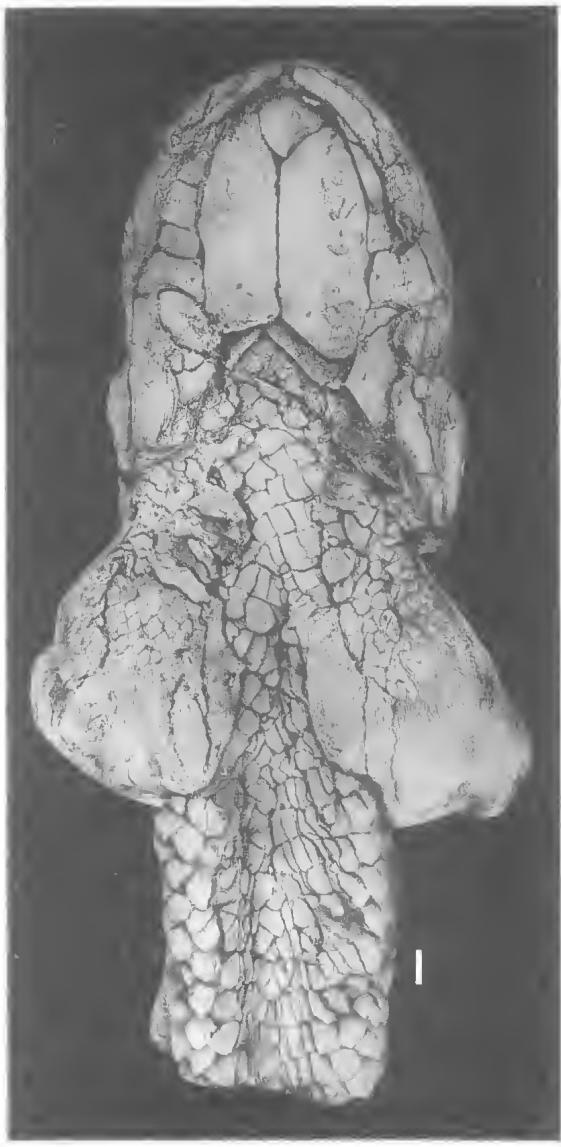


FIG. 6. *Cladarosymblema narrienense*. Ventral view of a cast of the holotype, QMF21082, made prior to the removal of the left gular and submandibular plates and the scales on the ventral surface of the lobe of the left pectoral fin. Scale: 10mm.

an inter-premaxilla either, and hence we do not consider this point further.

C. narrienense and some specimens of *M. hibberti* have similarly shaped parietals, which are deeply notched anterolaterally to receive the posterior nasal and are widest immediately behind the nasal. Thomson (1964a: fig. 6) illustrated several variants of this basic shape in *M. hibberti*, but the usual form is very similar to that in *C.*

narrienense. Hence we do not consider this to be a useful feature for distinguishing the two genera.

The skull roof of the otico-occipital unit of *Megalichthys* is best known from *M. laticeps* (Bjerring, 1972) and the work on *M. hibberti* by Borgen (MS). The relationship between *M. laticeps* and *M. hibberti* is not well understood, and indeed the two may be conspecific. Bjerring (1972) described a remarkable branch of the supraorbital lateral line canal extending into the postparietal, and Borgen (MS) has illustrated a specimen of *M. hibberti* in which remnants of the canals are visible on the visceral surface of the postparietal. X-rays, and the broken surfaces of bones, show that no such canal is present in *C. narrienense*. The transverse pit-line on *C. narrienense* is continuous across the postparietal and tabular bones, and turns backwards slightly at its lateral extremity. A shorter posterior line runs posterolaterally from near the inner end of the main line, but the two do not join. In *M. hibberti* the transverse line is variable (Borgen, MS); in some specimens it is continuous across the postparietal and tabular bones, but in others it is a short discrete segment on each bone. Bjerring also inferred from the shape of the tabular (his supratemporal) that a small extratemporal must have been present, although it had not been observed by previous workers. All of our specimens of *C. narrienense* in which this part is preserved, show an edge on the supratemporal for the articulation of an extratemporal, and on some specimens a small branch of the lateral line canal extends into the space that would have been occupied by such a bone. We conclude that an extratemporal was present, but its shape remains conjectural.

The endocranum of the otico-occipital unit of *M. hibberti* is so poorly known that comparisons with *C. narrienense* are not possible.

According to Schultze (1974), the olfactory tracts of *Megalichthys* sp., cf. *M. hibberti* from the U.S.A. diverge from the braincase at c.90°, the division lying about one-third of the length of the ethmoid unit from its anterior end. Jarvik (1985) considered that the evidence for this was dubious, and certainly it is true that the preservation of the specimen figured by Schultze leaves something to be desired. However, *C. narrienense*, preserved in the same way, shows that Schultze's interpretation of that specimen is probably correct. Despite this we consider that it is necessary to confirm that the British specimens of *M. hibberti* share this arrangement. The limited available evidence implies that they do not do so.

In comparison with *Cladarosymblema*, *Ectosteorhachis* has less club-shaped postparietals, a weaker notch in the parietals for the posterior nasals, strongly tuberculate cosmine (Thomson, 1975), wider and less acute anterior denticulate part of the parasphenoid (Thomson, 1964a,b), an otico-occipital unit making a strong processus connectens (Romer, 1937), a more oblique orientation of the endocranum forming the posterior wall of the trigeminofacialis chamber (Romer, 1937). (Our direct examination of Romer's material, shows that his reconstruction is inaccurate in respect to the last point, and the wall in question is more nearly transverse than he showed.)

The mandibles of the two genera provide several useful distinguishing features. The adductor fossa is longer and broader in *Ectosteorhachis*, the coronoids have a row of denticles along their lateral edges, and these are continuous with the denticles on the parasymphysial plate; *Cladarosymblema* has no denticles on the lateral edges of the coronoids. In *Ectosteorhachis* the denticles on the prearticular are more robust and extend to the anterior end of that bone, whereas in *Cladarosymblema* they are much weaker and, if they reach the anterior end, they are limited to the dorsal edge. One of Romer's specimens, MCZ6999, has an unknown number of small, approximately equidimensional submandibulars that are certainly more numerous than the 6 - 7 in *Cladarosymblema*. On the other hand, Thomson (1975: fig. 36) has illustrated a specimen with submandibulars not unlike those of *Cladarosymblema*, although still numbering 8-9. We are unable to judge the significance of these data.

Cladarosymblema narrienense sp.nov.

MATERIAL EXAMINED

HOLOTYPE: QMF21082, the anterior part of a fish including the skull, pectoral fins, and part of the scale-covered trunk (Figs 5-6); collected from the fine-grained sandstone immediately above the limestone about 1km north of the Police Mountain Track (Fig. 2). **PARATYPES:** QMF21083-21111; 26537-26576; 31858-31907; 33046-33058: Same locality as the holotype.

DIAGNOSIS

As for genus.

ETYMOLOGY

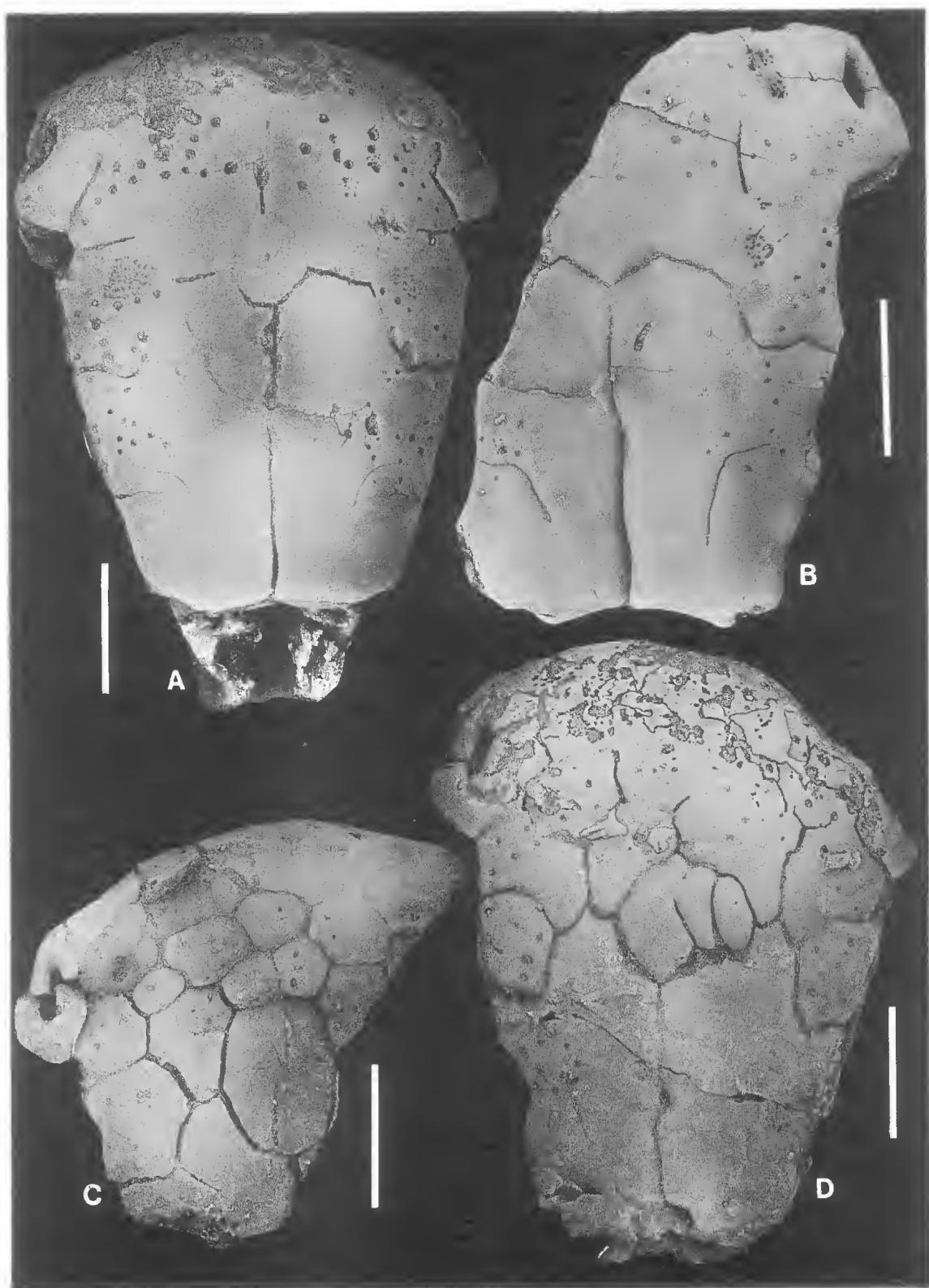
From the Narrien Range, the dominant topographical feature in the vicinity of the outcrop at the type locality.

DESCRIPTION

EXTERNAL DERMAL BONES OF THE SKULL

Ethmoid Unit. Two relatively complete roofs of the ethmoid unit (QMF21083 and 21110), seven other large fragments, several smaller fragments including an isolated premaxilla, and several detached rostral ends are known. The ethmoid unit withstands erosion better than the more posterior parts of the skull because it has a downturned rim and a marginal thickening of the premaxilla. The dermal bones of the unit are completely covered with cosmine; an occasional plate shows a weak blister, but none shows the blistered texture that accompanied regrowth in *Ectosteorhachis*. On the anterior half of the roof cosmine has obliterated sutures making identification of individual bones difficult. However, QMF21097 (Figs 7C,E; 8C), 21095 (Fig. 7F-I) and 21111 (Fig. 27C-D) show these bone outlines almost completely, the first on the external surface and the others on the internal surface.

On QMF21083, 21108 and 21110 the parietals are well preserved (Figs 7A,B,D; 8A,B,D); on the holotype, weathering has removed detail from central parts of the parietals, and lateral outlines are indistinct. Parietals occupy slightly more than half the length of the ethmoid unit. The interparietal suture is almost straight, but with a slight irregularity over its posterior half in some individuals. There is no pineal foramen. The parietal outline is distinctive with an anteromesial projection and a deep anterolateral angle to accommodate the most posterior nasal. The widest part of the parietal is at the suture with the posterior nasal, behind which is a gradual taper to the posterior margin of the shield. In some specimens this taper is straight-edged and in others it has a slight double embayment. We assume that a supraorbital and an intertemporal articulated with the parietal, although no examples of these bones have been found. The supraorbital part of the lateral line canal passes from a posterolateral direction into the parietal, slightly anterior to the midlength of the intertemporal notch, and exits through the anterolateral edge of the parietal. A strong arcuate anterior pit-line lies on the posterior third of the bone but fails to reach the median suture.



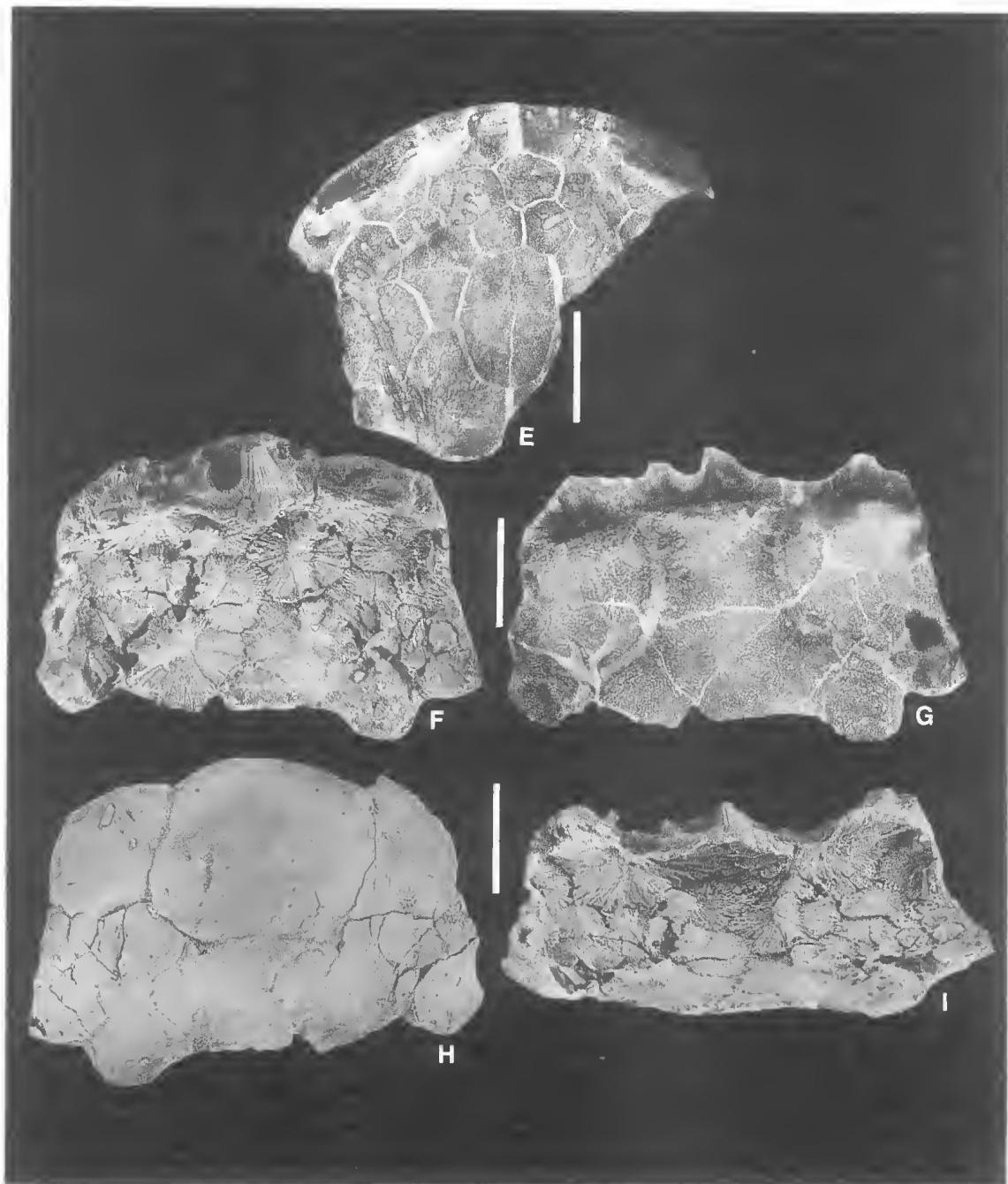


FIG. 7. *Cladarosymblema narrienense*. A-I, views of the roofs of isolated incomplete ethmoid units showing variation of dermal bone patterns. In A and B, QMF21083 & 21108, the more rostral sutures have been obliterated by cosmine. C, QMF21097 shows the most extensive suture pattern found. D, QMF21110 has incomplete sutures rostrally, but shows extensive resorption of cosmine in patches and growth of a number of cosmine blisters. E, X-radiograph of QMF21097 figured in C. F-G, QMF21095 in ventral view and X-radiograph in same orientation, showing radiation centres of dermal bones and the course of the lateral line canals. H,I, dorsal and posteroventral views of the same specimen. Note radiation centres and lateral line canals in F and I, and cutaneous sensory pore clusters on all dorsal views except D. Scales: 10mm.

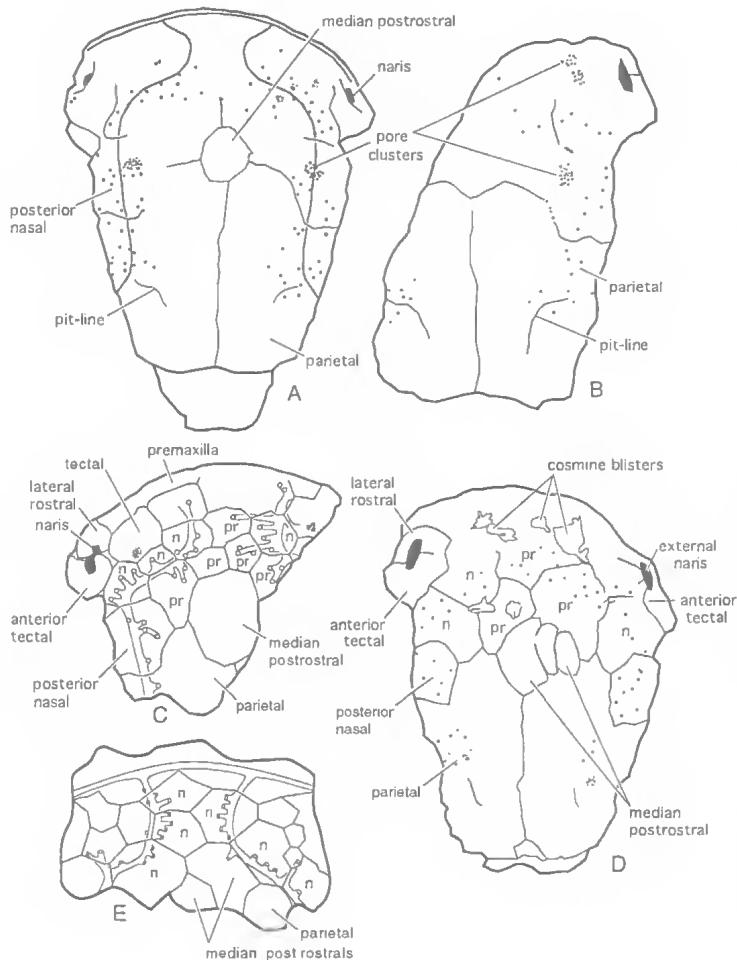


FIG. 8. Outline diagrams of specimens shown in Fig. 7. Lateral line canals are drawn from X-radiographs, and the bone outlines reconstructed from all sources. A, QMF21083. B, QMF21108. C, QMF21097. D, QMF21110. E, QMF21095. n = nasals; pr = postrostals.

QMF21083, 21097, 21111 and 21547 each have a single symmetrically placed median postrostral, but QMF21110 (Figs 7D; 8D) has three asymmetrical bones occupying the same space; in QMF21108 overgrowth by cosmine has almost obliterated the sutures between the median postrostral and surrounding bones (Figs 7B; 8B). Between the premaxilla, the median postrostral and the anterior tectals and lateral rostrals, the roof is covered by small irregular bones (Figs 7C,D,E; 8C,D,E; 27A,C,D). Identification of the bones of the nasal and postrostral series is a problem. Nasals are normally recognised by the presence of the lateral line canal, and the postrostals lie between the canals

anterior to the median postrostral. QMF21095, 21097, 21111 and 26540 are very instructive in this context, because the endocranial material has been stripped away revealing the pores opening to the external surface, the centres of radiation of the dermal bones and, deeply buried in the dermal bones, the lateral line canals whose position and size can be checked by X-radiography. These canals do not pass through the centres of ossification of most of the bones (Figs 7E,F,G; 8C,E). Instead, they often bypass the bone centres or run along the sutures. For example, the left side of Fig. 7E and 8C shows the canal lying along the suture between the most posterior postrostral and the neighboring small nasal, and Fig. 7F-G show the canals partly along sutures on both sides of the specimen. The variable distribution of lateral line pores reflects great variation in the length of the tubules from the main canals. For example, the right side of Fig. 7E shows extremely long tubules from the supraorbital canal extending mesially into bones we label as postrostals, and Fig. 27D also shows long mesially directed tubules. This variation makes it impossible to use the pores to locate the canals precisely. Be-

cause the canals cannot be unambiguously positioned from a study of the pores on the external surface, and in places the canal is not unequivocally in one bone or its neighbour, the recognition of nasals and postrostals is frequently ambiguous.

In Figs 7F,G, 8C,E and 27D, the canal swings sharply anteromesially on emerging from the posterior nasal, but its course relative to the bones of this region varies from specimen to specimen. On the left in Figs 7F,G and 8E it passes through the anterolateral corner of the bone flanking the median postrostral. Presumably, therefore, strict application of the definitions implies this bone has to be a nasal. On the right the bone that

unambiguously carries the canal is not in contact with what appears to be the median postrostral if only one of them is present. As shown in Fig. 7D and 8D, however, more than one may be present. We therefore consider that one interpretation of Fig. 8E is that it has two median postrostrosals. Alternatively, the right one of the pair so labelled could be a postrostral like that on the left of the median postrostral in Fig. 8C. In the more anterior nasals, the canal turns forwards and slightly laterally to join the infraorbital canal in the premaxilla in the usual osteolepiform manner. The nasals from the two sides meet medially, and so in this specimen the only definite postrostral is the median. A similar absence of postrostrosals has been inferred for QMF21111 (Fig. 27D), although the situation is not so clear. However, in QMF21097 (Fig. 7C, E), which has all the bones visible on the external surface, three small bones lie between the nasals and in front of the median postrostral; these can only be postrostrosals. In addition, the bone anterolateral to the median postrostral on the left side has the canal along its suture, whereas the equivalently placed bone on the right clearly has the canal in its anterolateral corner. The bone on the left could be considered a postrostral and the one on the right a nasal. This seems to us to be entirely arbitrary, and we label them both as postrostrosals. In this specimen, the nasals do not meet medially, and the intervening space is occupied by at least three small postrostrosals. We conclude that the number of postrostrosals is highly variable in this species.

Small tectals are present on all specimens, between the lateral line canal-bearing bones and the circumnariales, although these are usually not visible on the external surface due to the cosmine cover. They are best observed by X-ray or by cleaning the internal surface (Figs 7E-1; 8C,E; 27A,C,D). Their number and size varies between specimens and on opposite sides of a single specimen. On Fig. 7G a strong offshoot from the supraorbital canal enters the posteriormost of these bones on each side of the specimen. On the left side of Figs 7C and 8C,E, a small tectal bearing a sensory pit cluster lies on the mesial side of the lateral rostral, and on the right side a similarly placed bone is present, although no lateral rostral is preserved. Also, on the flank of the left premaxilla in Fig. 27A, tectals can be recognised from their radiation centres. We see no value at present in trying to homologise individual bones in the series.

The premaxilla is complete or near complete in three individuals in which the whole roof of the

ethmoid unit is preserved (the holotype, QMF21083, and 21110), as well as in five fragments (QMF21095, 21097, 21104, 21105, 21111) consisting of the bone itself and a few small more posterior bones adhering to its edge (Figs 7A,C,F-I; 8A,C,E; 21A,C; 22; 27A-D). In all of these specimens, cosmine has obscured the sutures between the premaxilla and its neighbours. The premaxilla is transverse and follows a broad arc across the front of the upper jaw. It has a strongly thickened bar across its inner surface, and this joins the endocranum; this rim produces a distinct furrow along its inner surface behind the teeth. On each side of the midline along the edge of the bone there are 16-20 small teeth, all of approximately the same size. Towards its lateral extremities the posterior face of this inner bar of premaxillary bone is marked by a posterior-facing area of horizontal grooves and ridges (Figs 21A; 22; 25D) that seem to have met the similarly ridged anterolateral surface of the vomers. At the median suture, some specimens (QMF21097, 21104) show a tusk on one side and a pit on the other (Fig. 20A), but in others two tusks are present side by side (Figs 21A; 22). To make room for these two tusks, the premaxilla is swept back into a short process that lies on the endocranial internasal ridge. This median process is relatively much shorter than its equivalent in *Megalichthys hibberti*, and does not extend back almost to the parasphenoid as Jarvik (1966: figs 17,19) indicated for that species. In some of our specimens, the row of small marginal teeth does not extend across the front of the tusks, but on QMF21083, 21095 and 26541, small teeth do occur in this position, and on QMF26540 a row of even smaller teeth crosses in front of at least the left tusk, the edge of the right bone being missing. These differences are probably individual variants.

The deeply buried infraorbital canal, which runs in the thickened bar across the inner face of the premaxilla, is joined by the supraorbital canal at the ossification centre of the bone. The infraorbital canal opens laterally either in the apex of the lachrymal notch or along the limb of the premaxilla that borders the notch ventrally, but never in the lateral rostral. Consequently, the maxilla, which does not carry the lateral line, must have met the premaxilla only below the opening for the canal; most, if not all, of the notch would therefore have been occupied by the end of the lachrymal. We can find no evidence of a premaxillary canal in the position shown by Jarvik (1966: fig. 14C) for *Megalichthys hibberti*.

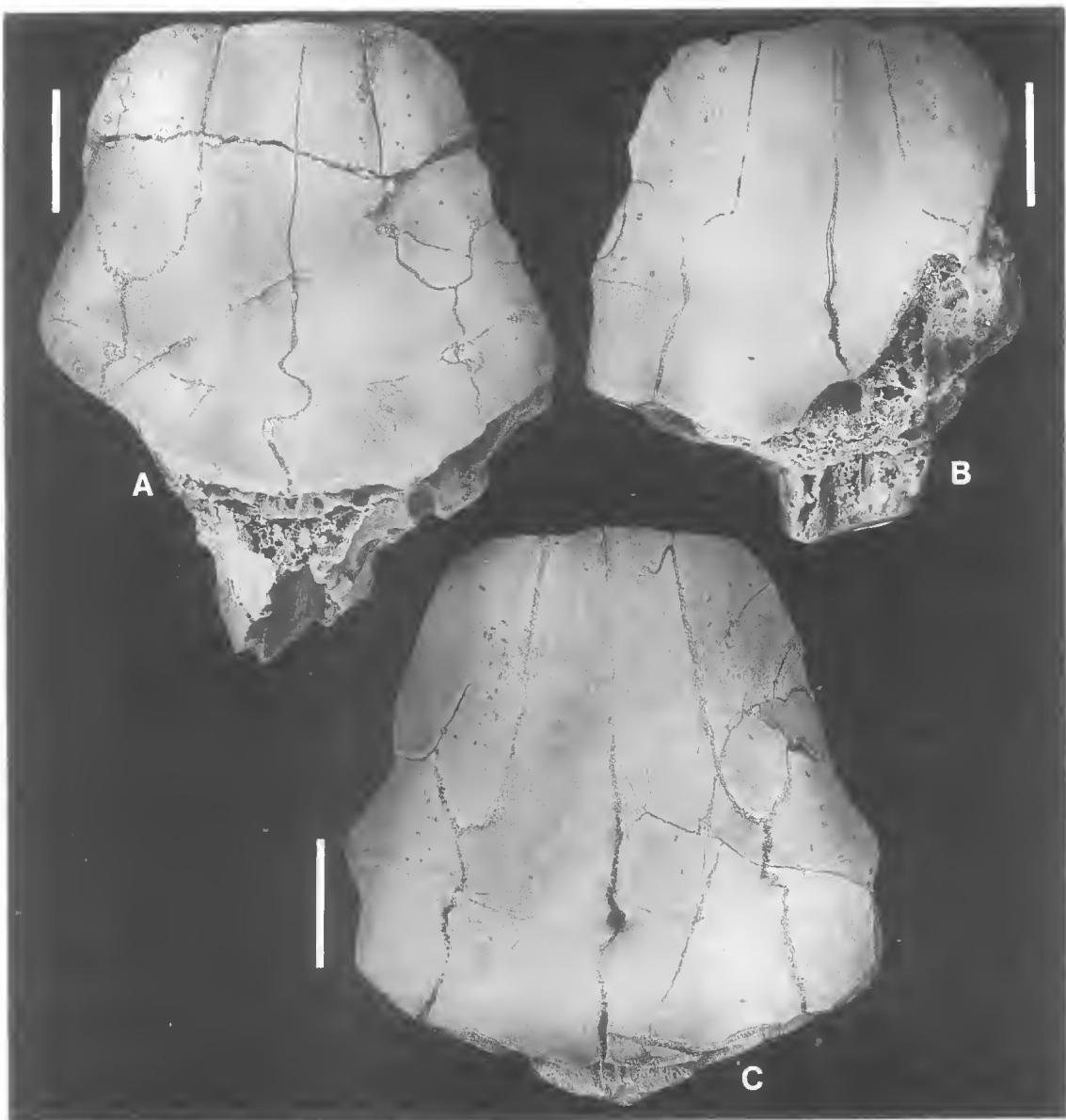


FIG. 9. *Cladarosymblesma narrienense*. Dorsal views of the roofs of three otico-occipital units. A, QMF21085 with highly flexed median suture. Compare with holotype. B, QMF21084 has well-developed cutaneous sensory pore patches on the supratemporals. C, QMF21096 has two peculiar features: the apparent foramen in the mid-line, and sutures in the anterior end of the postparietal and the posterior end of the supratemporal. All of these are indicated on Fig. 10. Scale: 10 mm.

In that figure he shows the infraorbital canal in the lateral rostral, and a more ventrally placed canal in the premaxilla. We consider that one of these canals, probably the one in the premaxilla, is the true infraorbital, and the other one is an offshoot from it. The lateral line in the premaxilla opens to the external surface via an irregular row of pores just above the edge of the lip. Internally,

it opens behind the teeth in a row of pores; these may be large (Fig. 20A), a mixture of large and small (Fig. 21A,C), or small throughout (Fig. 27A,C). Even the largest pores have edges of finished bone, so their size is not a consequence of the etching process. Pores in this position would scarcely have carried seismosensory neuromasts, nor are they effectively placed to house

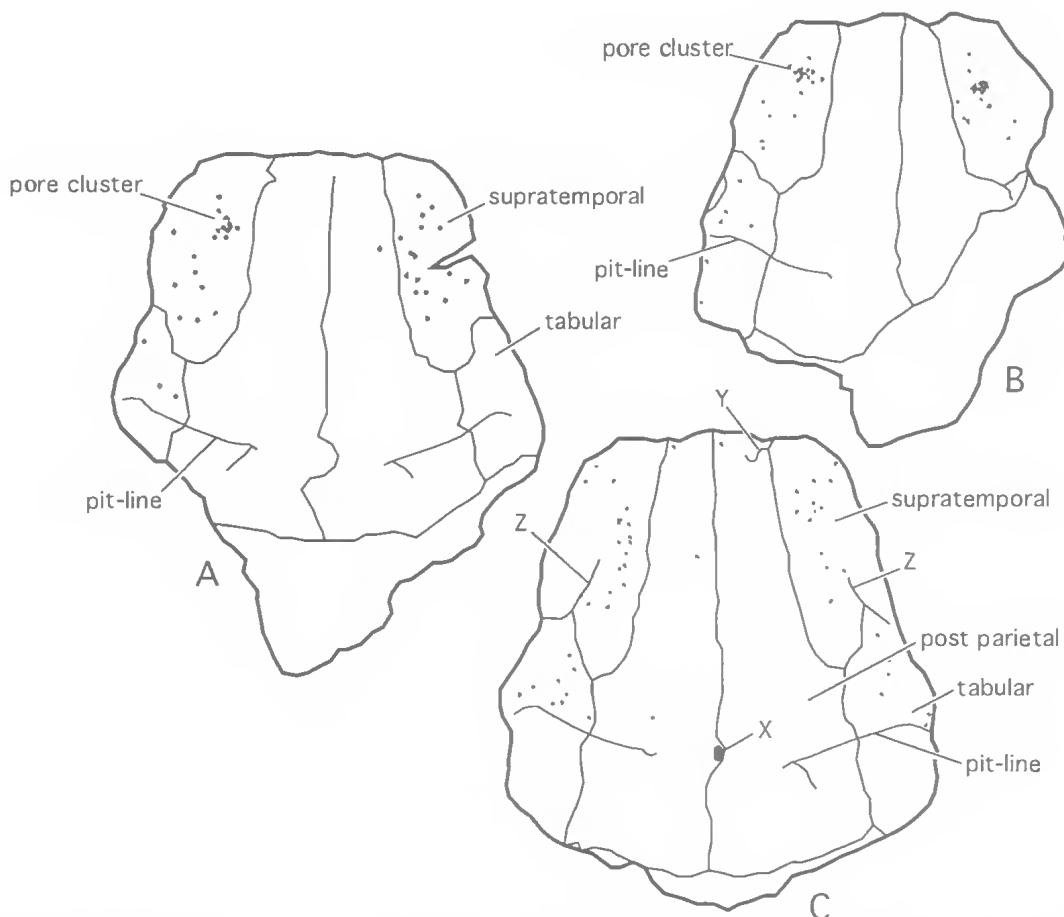


FIG. 10. Outline drawings of the same specimens as Fig. 9. X is an anomalous foramen, and Y and Z are anomalous sutures.

electrosensory receptors. On the other hand, they would be well situated to serve a chemosensory function. We conclude that the lateral line canal in this region carried a variety of nerve fibres.

There is no groove between the premaxilla and the adjacent parts of the circumnarial bones as Westoll (1937, 1940) claimed for *Eusthenopteron* and other osteolepidids (but cf. Panchen, 1967: 394). The lateral line canal in *Cladaroptychus* passes more ventrally, from the premaxilla to the lachrymal; it does not enter the circumnarial bones. This may be considered to raise a question about our identification of the lateral rostral, which is usually thought to carry the infraorbital canal in its anterolateral projection (Jarvik, 1966: fig. 14). We are of the opinion that the presence of the canal in the lateral rostral has not been established in all megalichthyids, and await fur-

ther data on this matter before considering the issue seriously.

QMF21111 shows a second sensory system in the snout. Internally, subjacent to the premaxilla, the median postrostral and intervening bones, an array of ossified tubules passes through the vesicular endocranial bone (Fig. 27C). These tubules are clearly not of dermal origin, and follow a different course from the lateral line canals in the overlying bones, as can be seen by superimposing Figs 27C and D. A branch of the main tubule trunk runs across the front of the median postrostral and turns back in the midline to meet its antimere. The main trunk runs anteromesially beneath the nasals and postrosturals and subdivides to form a ramifying series of tubules. Along the edge of the endocranum, where it is sutured against the palatal lamina of the premaxilla, these tubules open into foramina and then into the front

wall of the nasal capsules. They also communicate in some places *via* short cross-tubules with the lateral line canals. In QMF21110, an ethmoid fragment that has had the palatal region eroded away exposing the mid-levels of the endocranum (Fig. 21C), the tubules do not occur more deeply in the vesicular endocranial bone. Although we have no specimen that offers unequivocal information, the tubules probably connect posteriorly with foramina in the antorbital wall, interpreted as carrying branches of the profundus superficialis V or ophthalmicus superficialis VII or both. The restriction of the tubules to the region immediately underlying the dermal bones suggests that they were not part of a blood vascular system supplying tissues in the snout generally.

These tubules are not approximately straight, do not bifurcate in the same way, and are fewer in number than the ramifying tubules in the snouts of Devonian diploans (Campbell & Barwick, 1982, 1984, 1987; Cheng, 1989), in *Diabolepis* (Chang & Smith, 1992) and in *Youngolepis* (Chang, 1982, 1991). We are not convinced that the tubules in the two groups are homologous. (See Functional Interpretations: Tubules in the Snout, for further discussion.)

Groups or patches of pores that lie in slight depressions have been observed on all ethmoid units, although their distribution is not symmetrical on all individuals and they do not occur on all specimens in the same places. Jarvik (1966: fig. 15) referred to these as 'special cutaneous sensory organs'. The patches contain any number of pores from 4 to 45. The individual pores are generally separate, but on some individuals two or more are enclosed within a rim that is usually bent and may even be U-shaped (Fig. 7A-C). The most common dispositions of the pore patches are as follows: one on each posterior nasal; one just above the lip in the angle between the supraorbital and the commissural canals; one or two mesial to the external narial opening; and one posteromesial to the external narial opening. Each patch is close to a lateral line canal if not actually in a lateral line bone, but we have not been able to establish a connection between the pores and the lateral lines. On the contrary, QMF21111 shows pores on the inner surface of a bone that has a patch of pores externally, suggesting that they open directly to the internal surface. Other patches show no evidence of such openings internally, nor any connection with the lateral line canals.

Because of cosmine cover, only QMF21097 and 21110 show evidence of a suture between the lateral rostral and the anterior tectal dorsal to the

narial opening, although these bones are clearly sutured ventral to the opening on several specimens. The two bones are normally distinguishable on the internal surface, and are approximately the same size. The pattern of circumnarial bones is more similar to that of *Ectosteorhachis nitidus* (Thomson, 1964a) than *Megalichthys hibberti* (Borgen, MS).

Surprisingly well-preserved circumnarial bones bear fine denticles arising from the surfaces lining the narial opening (Fig. 28B,C). These are usually isolated and bear a single pointed cusp, but some are bi-cuspid or even tri-cuspid (e.g., QMF21108, 21110, 21111). Denticles occur on all specimens in which this region is well preserved, so there is no doubt about their reality. They occur on both dorsal and ventral surfaces of the circumnarial bones, and although they vary in extent between different individuals, no part of the rim seems consistently free of them, and on QMF21108 they are densely distributed around the entire rim (Fig. 28C). Apparently such structures have not previously been described in other osteolepiforms. Borgen (MS) has noted abraded tubercles (or minute foramina) in a similar position in his new megalichthyid from Norway. It seems likely that the denticles are so small that they could not be exposed in their entirety by the mechanical preparation of his specimens. Distribution of these denticles puts constraints on the reconstruction of soft tissue structures such as glands, hypothesised for *Eusthenopteron* and *Megalichthys* (Jarvik, 1966, 1980). It is highly improbable that glandular tissue would have been situated on the surfaces described.

When viewed through the ventral opening of the nasal capsule of better preserved specimens, much of the dorsolateral wall of the capsule is made of lateral rostral and anterior tectal bones, their inner surfaces crossed by more or less concentric striations (Fig. 28A-C). The nature of these striations is not obvious, but it is probable that the cartilage of the wall of the nasal capsule was applied to this surface. The surfaces and edges of these bones are finished, showing no signs of breakage, and the endocranum laps on to their sides making a clear sutural contact. We have carefully examined the edges of these bones in view of the importance that has been attached to the existence of the 'processus dermintermedius' and the 'processus tectalis' by Jarvik. In some individuals, (QMF21108 and possibly QMF21111), much of the internal rim projects inwards beyond the adjacent parts of the capsule lateral wall. However, this projection

constitutes the rim itself and seems never to form a thin flange that arises from the rim as in *Eusthenopteron foordi* (Jarvik, 1942, 1966, 1980) and *Gogonodus* (Long 1985a, 1988). The projecting part of the rim in *Cladarosymblema* has both lateral rostral and anterior tectal components; that is, it includes parts of the rim that could give rise to 'dermintermedius' and 'tectalis' processes. QMF21083, our best preserved specimen, shows that the rim does not project far enough to occlude any part of the fenestra endochoanalis beneath, as Rosen et al. (1981:191) claimed for *Eusthenopteron*; nor does the processus dermintermedius or tectalis occlude any part of the fenestra endochoanalis in the holotype of *Gogonodus* (ANU21885). No endocranial tissue, such as in Jarvik's (1966) 'processus intermedius', takes part in the formation of the ventral rim or flange; nor is there a 'processus palatinus' or passage for an infraorbital sensory canal, as in *Megalichthys* (Jarvik, 1966:73). Jarvik (1966) illustrated a depression in the posterior part of the 'dermintermedius' and thought that this may have housed a lateral nasal gland (see caption for his fig.12). Our specimens show no discrete depression in that position, although QMF21083 has a slight embayment in the outline of the flange in the appropriate position (Fig. 28B,C). In that specimen, the embayment is in the tectal rather than the 'dermintermedius', and we consider it to be without anatomical significance. As already noted, the distribution of denticles across all of these surfaces precludes their association with glands in any case. In sum, we see no evidence that the nasal capsule in *Cladarosymblema* was subdivided in the way Jarvik has reported in *Eusthenopteron* and *Megalichthys*.

Otico-occipital Unit. We have five well-preserved (QMF21056, 21084, 21085, 21086 and 21094) and several fragmentary examples of the roof of this unit. Our specimens retain only the postparietals, the supratemporals and the tabulars (Figs 9-10).

The postparietals are the largest bones in the entire roof, and in our view their posterior edge forms the anatomical limit of the skull roof (Romer, 1941). From their anterior extremities, the postparietals widen gradually to the level of the posterior edge of the supratemporals where they abruptly expand; thereafter they continue to expand gradually to the rear of the shield. Consequently, the bone has a distinctive outline. The postparietals extend more posteriorly than the tabulars and have only a very faint notch at the median suture. This median suture is straight

anteriorly, but is mildly to strongly zigzag on the posterior third in different individuals (compare Fig. 9A,C). The supratemporals are widest just behind their midlength, having a small facet anteriorly for the intertemporal and a thickened edge for the articulation of the postorbital extending almost the entire length of the bone. At the posterolateral corner of the supratemporal there is always a notch for the spiracular fenestra, which seems to have extended back onto the flanks of the tabular (Figs 9; 29). A distinct facet on the posterolateral edge of the tabular was for the articulation of the extratemporal. That bone is not preserved on any of our specimens. In its overall pattern, the otico-occipital shield closely resembles that of *Megalichthys laticeps*, as described by Bjerring (1972).

For the articulation of the ethmoid unit, the anterior edge of the supratemporal has a device that is similar to that in *Megalichthys laticeps* (Bjerring, 1972). A flat supratemporal process (fronto-dermosphenotic of Bjerring) on the supratemporal extends forwards beneath the intertemporal; this process has a deeply grooved ventral surface (Fig. 29A,B). Dorsal to the process is a transverse socket that articulated with the reciprocal edge of the intertemporal. On its inner edge, this socket is continuous with a deep posteriorly directed groove that runs along the side of the braincase.

Well-preserved posterior edges of skull tables (Figs 9A,C; 38A,B) show that the tabular and the outer part of the postparietal have a slit in the edge of the bone, the lip below the slit extending posteriorly to form a shelf for the articulation of the lateral extrascapulars. Mesially the situation is quite different. Under the mesial part of the postparietals, the endocranum is tightly appressed to the dermal bone and extends posteriorly beyond its edge to make a platform for the articulation of the median extrascapular; no slit occurs in the edge of the dermal bone.

The course of the lateral line canals has been observed by tracing the pores on the surface, by the position of openings on broken bone surfaces, and by X-radiographs (Fig. 30). The canal enters the skull table at the posterolateral corner of the tabular and runs forward through the length of the supratemporal to emerge just lateral to the supratemporal process. A branch, which seems to be represented by more than one ramus, runs from the tabular into the postulated extratemporal. Unlike *Megalichthys laticeps*, *Cladarosymblema* has no branch of the lateral line canal from the

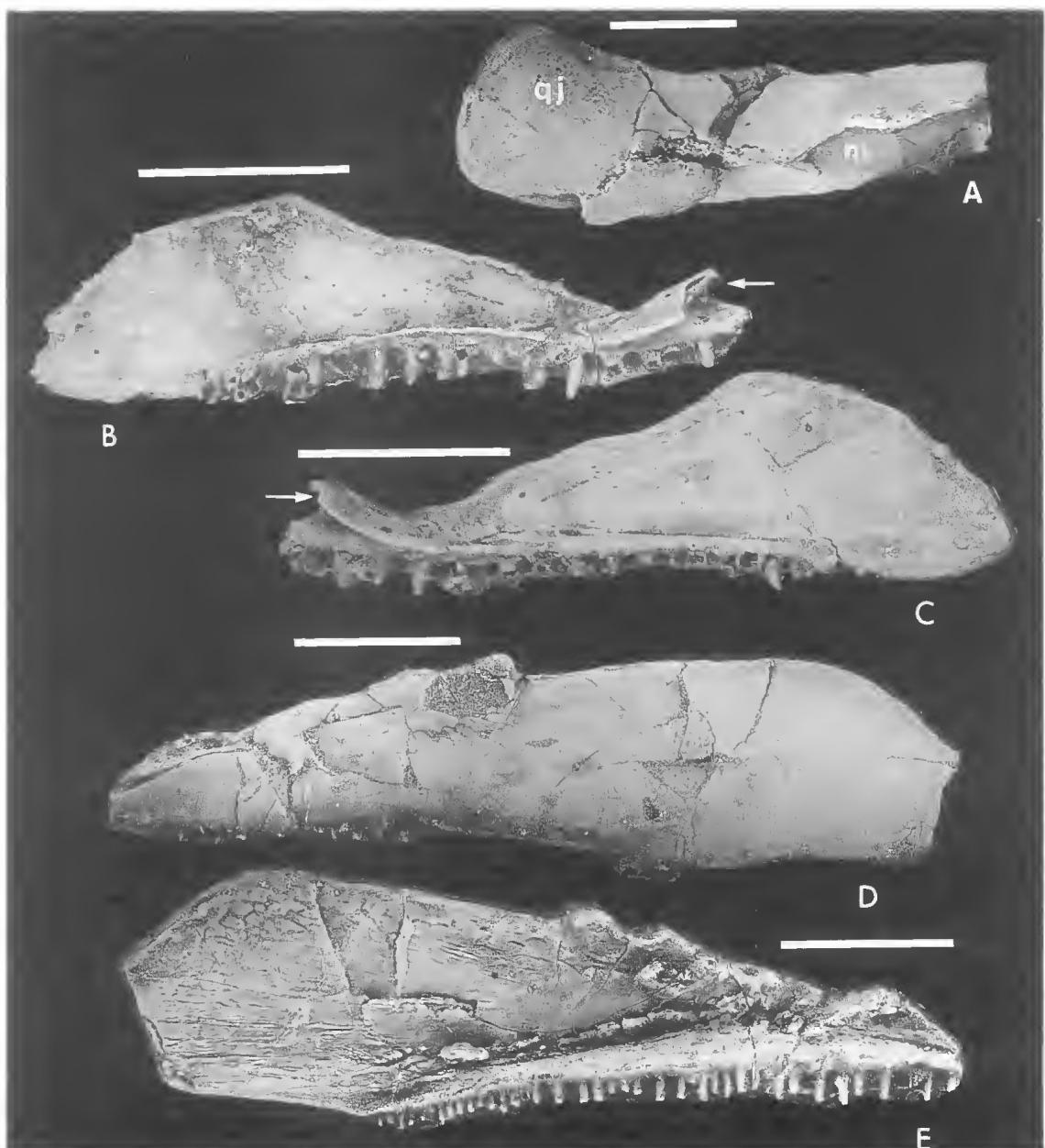


FIG. 11. A, lateral view of right quadratojugal (qj) and the posterior part of maxilla (m) of the holotype of *Cladarosymblema narrienense*, QMF21082. B,C, internal views of left and right maxillae of *Gogoniasus andrewsae*, ANU49259, showing ridge dorsal to the tooth bases and extending forwards into a flange (arrow) that forms the posterior edge of the choana. D,E, external and internal views of an almost complete left maxilla of *Cladarosymblema narrienense*, QMF26551. Note the posterior edge is not quite complete, the true shape of this part of the bone shown on Figs 11A and 14B. The anterior end is also slightly incomplete, but the posterior edge of the choana is partly represented. Scale: 10mm.

supratemporal into the postparietal, and the postparietals have no pores on their surfaces.

Pit-lines are not deeply inscribed, but they can be distinguished on five specimens (QMF21056,

21084, 21085, 21086 and 21098). The longer one runs from the postparietal anterolaterally across the tabular and is slightly deflected posteriorly, before terminating just inside its lateral margin

(Fig. 10A,C). A shorter branch, restricted to the postparietal, runs posterolaterally from the inner end of this line.

A reconstruction of the whole roof of the species is given in Fig. 14A.

Maxilla and Cheek. No complete cheek is available, but its main features can be reconstructed from the maxilla, quadratojugal, squamosal, jugal and postorbital. The posterior position of the maximum height of the maxilla, the large quadratojugal, the almost equidimensional outline of the squamosal, the relationship of the lachrymal to the maxilla, and the shape of the anterior edge of the opercular, enable us to say that the cheek was relatively shorter than in other osteolepiforms, and that the vertical axis of the preopercular was almost at right angles to the line forming the ventral edge of the maxilla (Fig. 14B).

Three maxillae are known, two broken ones in position on the holotype, and a third without its posterior tip that was isolated by acid etching (Fig. 11D,E). Its height/length ratio is 0.28. Its highest point is towards the rear, adjacent to the quadratojugal. At its anterior end, QMF26551 has a peculiar disruption of the cosmine, giving the appearance of being a composite structure. However, we can see no evidence of two centres of ossification in the X-radiographs. Anteriorly, adjacent to the disrupted cosmine, is a patch of special cutaneous sensory pores similar to those on the skull roof. Jarvik (1966: fig. 15A) showed a similarly placed patch in *Megalichthys*. Unlike that of *Megalichthys*, however, the maxilla of *Cladarosymblema* shows no openings to the infraorbital sensory canal, which was confined to a more dorsal position within the lachrymal.

There has been endless argument about the existence of a choana in osteolepiforms. Rosen et al. (1981) claimed that what had been interpreted as a choana in *Eusthenopteron*, the best known osteolepiform genus, was in fact a pit for the reception of a mandibular tusk. This statement has caused much confusion; the summary of the matter given by Chang Mee-mann (1991) still expressed reservations about the reliability of the

data. In the light of this, the material described herein offers vital support for the existence of a choana in osteolepiforms. On the dorsal side of the anterior tip of the maxilla is a triangular process that articulates, in part, with the lachrymal, while anteriorly the maxilla abutted the premaxilla. In *Gogonasus* this process has an overfolded tip which, when the maxilla is reassembled against the palatine bones and the premaxilla, forms the posterior margin to an ovate opening that is ideally placed to be the choana. The process on the specimen of *Cladarosymblema* is worn and does not show this feature in detail, but what is preserved indicates that it was of the *Gogonasus* type. It is important for the understanding of the osteolepiforms in general to note that the *Gogonasus* structure is also present on the isolated maxilla (Fig. 12C) from the de Bretzel specimen, which is described in the ADDENDUM to this paper. Thus it seems clear that a choana is present in primitive osteolepiforms and, as Long (1988) recognised, there is no evidence that the cavity in the palate of *Gogonasus* is for the reception of a tusk from the upper jaw. Confusion about the presence of a choana in osteolepiforms is now dispelled.

More posteriorly on the maxilla two protuberances, both of which carry cosmine, break the dorsal outline. The overlapped edge behind these protuberances is short and narrow for articulation with the lachrymal, whereas the posterodorsal edge behind the maximum height is finished and bevelled, and is gently convex in outline. The posterior extremity of this specimen is broken off, but its outline can be inferred from the shape of the anteroventral edge of the quadratojugal against which it would have fitted. This shows that the maxilla was produced to a posteroventral point, which is unlike the bone in any other osteolepiform genus with which we are familiar apart from *Megalichthys hibberti* (Borgen, MS). The internal surface of the maxilla is generally smooth, but close to its ventral edge it has a thickened ridge, highest anteriorly and gradually decreasing in thickness and height to the posterior end of the tooth row. This ridge is quite different

overleaf on p. 124

FIG. 12. *Cladarosymblema* sp. Illustrations of specimens isolated from a limestone block collected from the roadside, and are described in the ADDENDUM. A,B, external and internal views of an isolated right lachrymal, QMF26522E, showing the posterior overlap and the dorsal articulatory process and groove. C, internal view of isolated right maxilla, QMF26522A, with posterior end and extreme anterior tip broken off. Note the flange (arrow) bordering the choana as in *Gogonasus*, Fig. 11B. D, isolated left lateral extrascapular, QMF26522H; anterior to the left. E, roof of an incomplete ethmoidal unit, QMF26522. Print electronically retouched. Note the large median postrostral and the pore cluster on the posterior nasal. Scale: 10 mm.

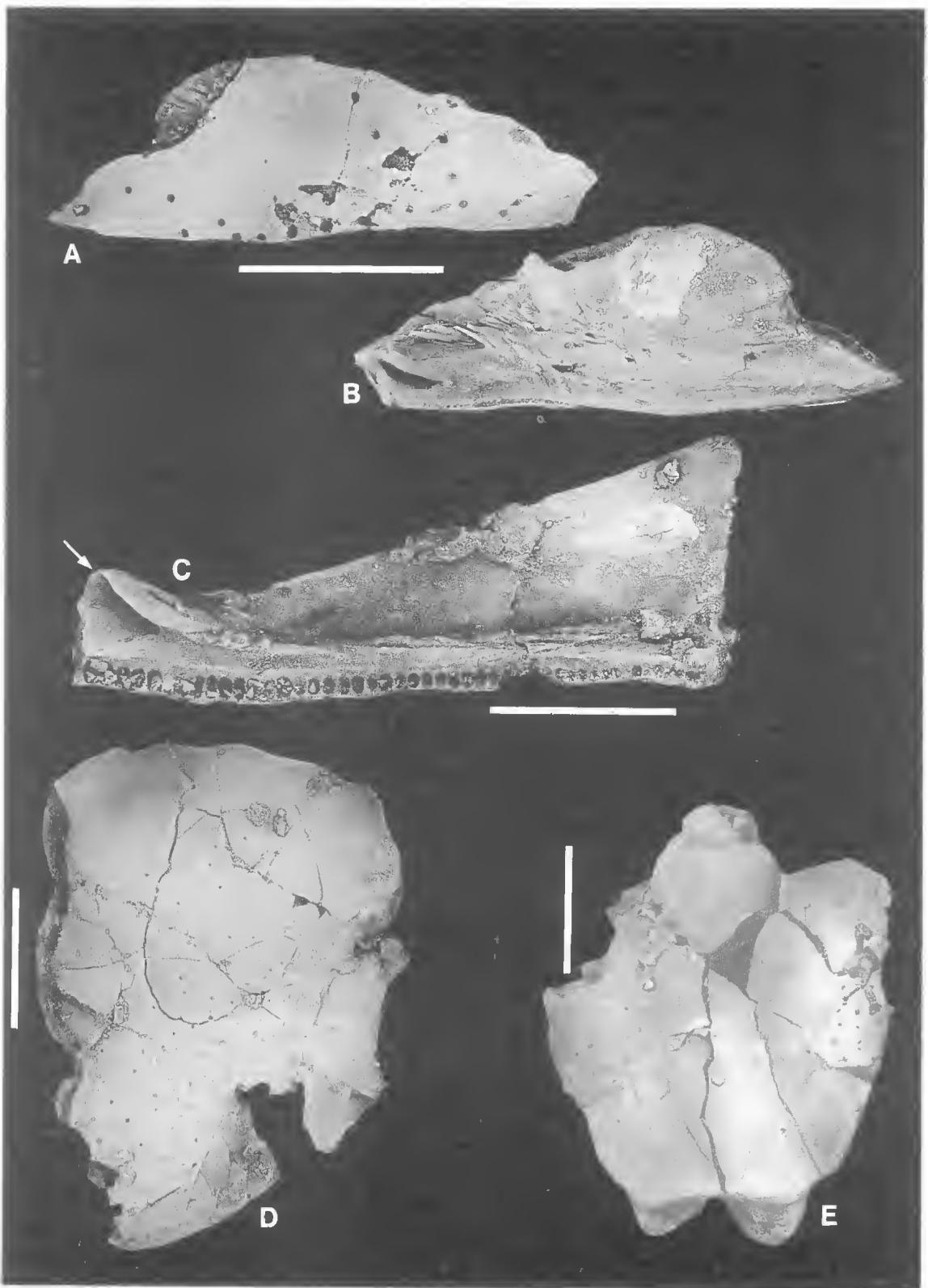


FIG. 12.

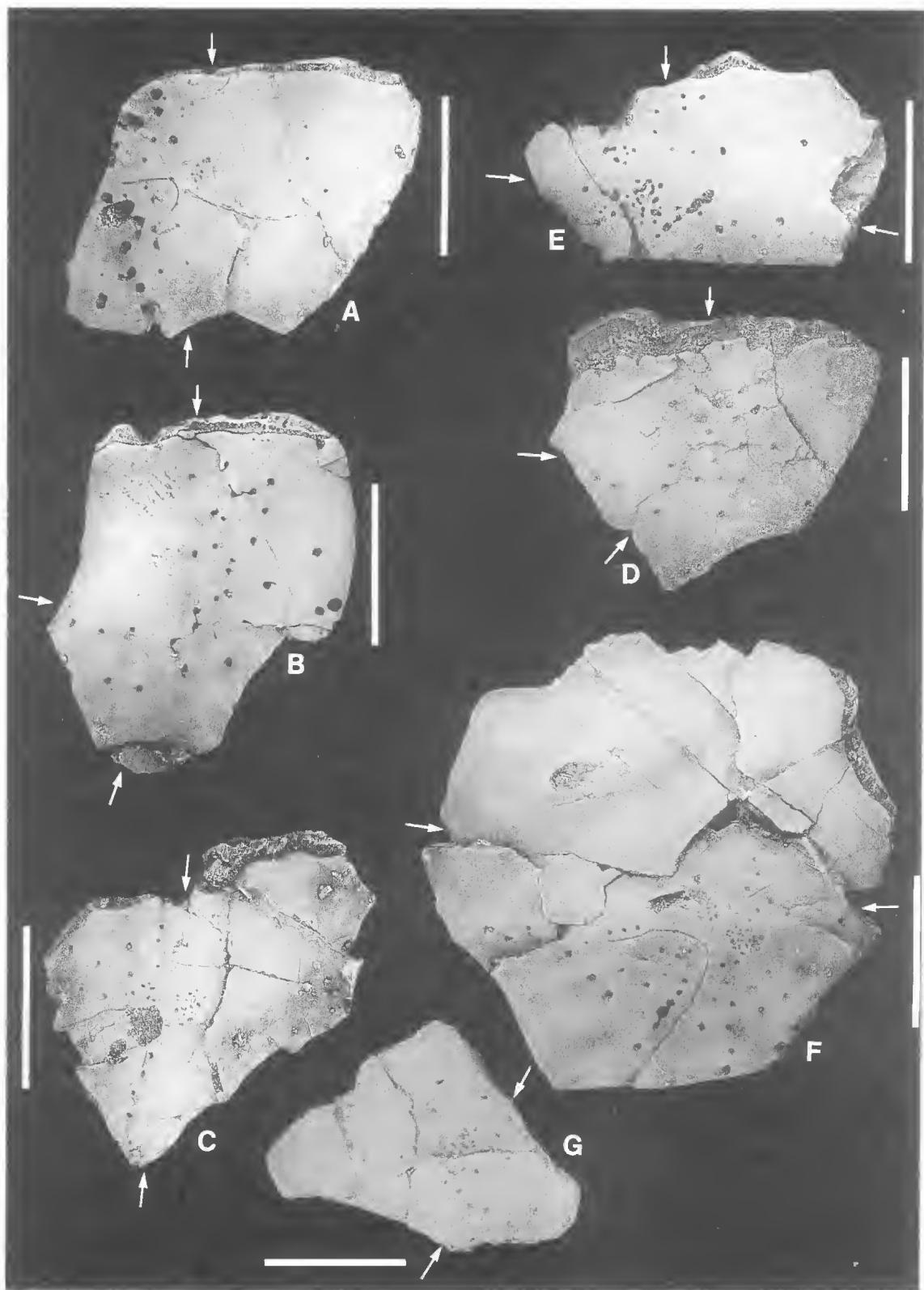


FIG. 13.

in shape from the one in *Megalichthys hibberti* (Borgen, MS).

The quadratojugal is present on both sides of the holotype. Its height is c.0.6 of its length, and its shape is distinctive, having a strong dorsal embayment with an overlapped edge for the squamosal, and a sigmoid outline anteriorly for the maxilla; these intersect to produce an acute angle at its anterodorsal edge (Fig. 11A). The posterior edge of the bone is broadly convex. A vertical pit-line is present at its anterior third. We have been unable to distinguish lateral line pores on its surface; these would be expected if the bone carried the preopercular canal. We conclude that the preopercular bone carrying its canal passed posterior to the quadratojugal. This interpretation is in accord with the posterior outline of the quadratojugal, which swings forwards dorsally in an unusual way for an osteolepiform, to make a pronounced posterodorsal angle.

A fractured almost complete right squamosal (Fig. 13F) with its posterior and dorsal edges broken was identified by the slight overlap on its anterior and anteroventral edges; the lateral line passing along its length; and the long highly arcuate pit-line, which is flexed posteriorly at its dorsal end and joins with the quadratojugal pit-line at its ventral end. Its outline has been reconstructed from X-radiographs and the preserved edges. Contact with the maxilla is short to vanishingly small. Along the edge with the postorbital is a marked underlap, and a much narrower one along the edge with the jugal. Pores from the lateral line occur over the lower half of the surface. The pit-line is formed as a single row of pits spaced 7 per mm. Two patches of small sensory pores occur anteroventrally, opening among the pores of the lateral line.

An almost complete jugal (Fig. 13E) is longer than high, and has a finished ventral edge where it overlapped the maxilla. The dorsal edge changes character along its length; anterodorsally there is a bevelled orbital margin, behind which there is a short prominent overlapped flange; posterior to this, the edge is grooved for the reception of the postorbital. The anterior edge of

the jugal is largely overlapped by the lachrymal, whereas its posterior edge is incomplete. The lateral line canals are strong, the jugal branch being close to the ventral margin as it enters from the lachrymal, and it diverges from the ventral edge posteriorly. The canal is slightly flexed where it joins the infraorbital canal. A large patch of sensory pores lies near the junction of the two canals and a smaller patch just dorsal to it.

One isolated almost complete plate, QMF33057, is interpreted as a postorbital because it carries an undivided lateral line canal, has an overlapped edge against what would be the jugal, and an edge which could be an orbital margin. The evidence is not conclusive. The bone is illustrated in Fig. 13G. As will be apparent from the reconstruction given in Fig. 14, it is difficult to fit the plate precisely into the space left between the surrounding bones, but we assume that individual variation accounts for the main part of the problem. The preserved bone is sub-triangular in shape. The points of emergence of the canal are clear, and a small patch of cutaneous sensory pits occurs over the canal in a similar position to the patch in *Osteolepis* (Jarvik, 1948: fig. 36A).

By matching the pit-line on the quadratojugal of the holotype with that on the isolated squamosal, it is possible to orient these two bones convincingly. Their posterior edges then stand almost normal to the ventral edge of the quadratojugal. Knowing these features and the shape of the anterior edge of the opercular, we estimate that the preopercular was a high, short, vertically-oriented bone, with a gently convex posterior edge. A reconstruction of the cheek of *Cladarosymblema* is given in Fig. 14B.

The cheeks of *M. hibberti* and *E. nitidus* are poorly known. Thomson (1964a: fig. 2A,B) produced schematic reconstructions of the cheeks of both species, but without supporting evidence. We have no means of assessing their validity, and hence have to ignore them in assessing similarities with *Cladarosymblema*. Borgen (MS) presented drawings of a specimen of *M. hibberti* that is too crushed to permit a reconstruction, but it is clear that the jugal is short and the quadratojugal

previous page

FIG. 13. *Cladarosymblema narrienense*. A,C, left post-temporals, QMF31873 and 26537. A small piece has been broken out of the posterior edge to the right of the lateral line in A; otherwise its margins are entire. Note the pit-line and the pore cluster on each figure. B,D, lateral extrascapulars, QMF31871 and 31876. B has most of the anterior margin and a small part of the extreme posterior margin preserved. C has a complete anterior margin, but all other margins are broken. E, isolated right jugal, QMF31874. The orbital margin is on the upper right. F, isolated right squamosal, QMF 26575. G, an isolated left postorbital, QMF33057. In all figures, arrows indicate emergent points of lateral lines. Scale: 10mm.

high; he also produced information on the shape of the maxilla of *M. hibberti* and his new genus from Norway. We conclude that the high posterior point of the maxilla, the relatively short squamosal and the high quadratojugal, make a community of characters that differentiate this group of species from members of the Osteolepididae. Hence we consider that the cheek shape is probably of familial significance.

Gulars and Submandibulars. These are known from the holotype and several isolated gulars, QMF26543, 26544, 26549, 26561, 26562 and 31880 (Figs 6; 16B-D). The principal gular on the holotype is a large bone the width of which is c.40% of its length. The entire lateral edge shows overlap for articulation with the submandibulars, but the posterior third shows deeper embayments for the more posterior submandibulars and the subopercular 2 (Figs 6; 16B). Isolated plates show an anteromedial embayment for the overlapping median gular, and overlapped areas laterally for the submandibulars, the width of the overlap increasing posteriorly in Fig. 16D and on the unillustrated QMF26549. The overlap is broken off posteriorly in Fig. 16C. The left principal gular slightly overlaps the right, at least anteriorly. The only posteromedial edge preserved intact suggests that if there were any overlap it was very small. It seems most likely that the two principal gulars lay almost edge to edge. The surface is cosmine-covered, but the anterior half shows variable resorption patterns. The holotype shows a small patch of resorption rings on its anterior half (Fig. 16B), but QMF31880 has a remarkable pattern (Fig. 16D). This consists of a series of narrow, irregular, resorption channels that isolate patches of cosmine with highly irregular sizes and shapes, a pattern that is nothing like the standard Westoll-line resorption pattern found in most diploans. At the

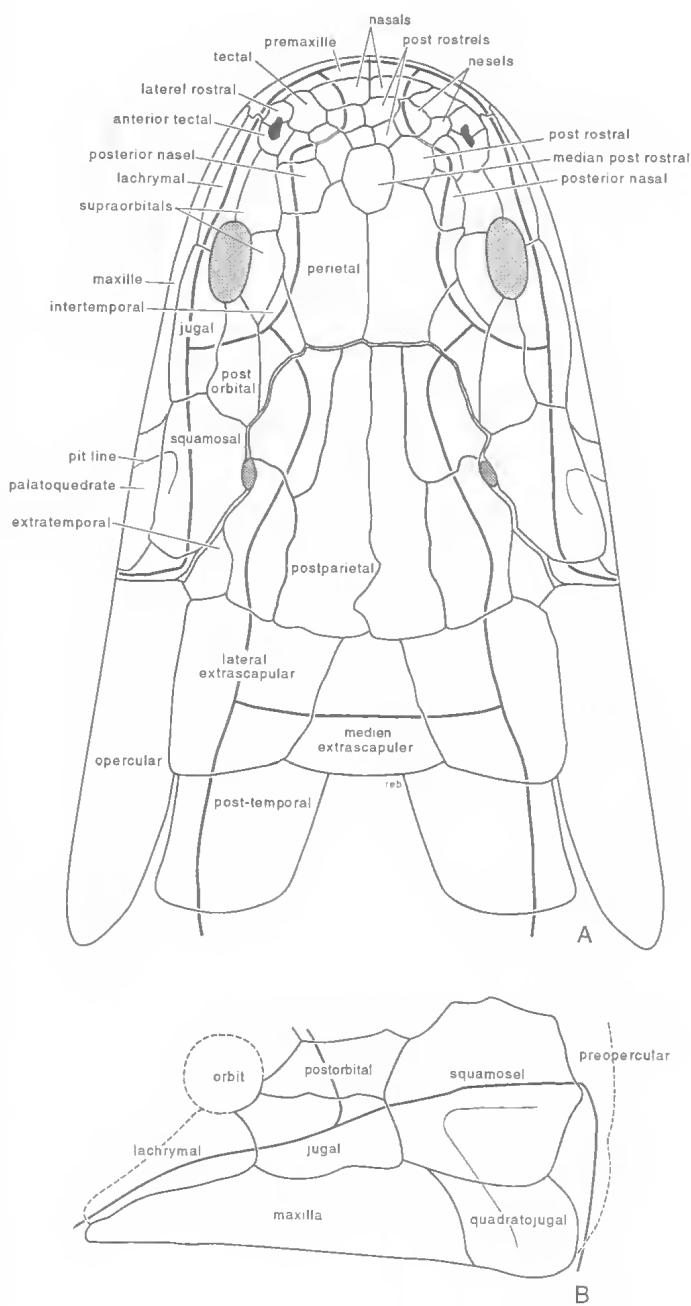


FIG. 14. *Cladarosymblema narrienense*. A, Reconstruction of skull roof based on all available data. B, Reconstruction of the cheek using the holotype for the relationship of the maxilla to the quadratojugal, and isolated jugal and squamosal plates. The lachrymal and the preopercular are based on the positions of the adjacent bones, and hence have dotted outlines.

centre of these resorption rings is a patch of newly formed cosmine with entire margins, and on the outer side of the rings is an irregular edge formed by resorption that was actively resorbing at the time of death. This is exactly like the pattern observed on some scales, and in our view represents the standard mode of cosmine replacement for the genus.

The median gular (Figs 6; 16B) is large compared with that of *Megalichthys hibberti*, but approximately the same relative size as that of the new genus from Norway (Borgen, MS). It is c.30% the length of the principal gulars. We cannot discern a pit line on it. Its anterolateral edges are embayed to receive the anterior submandibulars, producing a median point. Posterolaterally, it overlaps the principal gular on each side.

The number of submandibulars is six on one side, and six or possibly seven on the other (Figs 6; 16B). The most anterior one is very long and thin, and extends around the anterior end of the median gular to meet its antimere. We see no evidence of a median bone in the series. Instead the median gular has an anterolateral embayment on each side to take the first submandibular, thus giving its anterior edge a pointed outline. The second submandibular is of similar proportions to the first, but the more posterior plates are progressively shorter. On the right, the most posterior plate is much wider than long; on the left, length and width are approximately equal. As noted above, the submandibulars of *E. nitidus* are smaller and more numerous than those of *C. narrienense*. A specimen of *M. hibberti* numbered G8.50 in the Hancock Museum, Newcastle-upon-Tyne, figured by Birks (1916: pl. 13) and examined by us, shows a similar number of submandibulars to *C. narrienense*, although the lateral ones are not as elongated as in that species.

Operculars. Both operculars are present on the holotype, but they are broken. Six other isolated specimens, QMF21092, 21093, 21103, 26538, 26545 and 26550, are better preserved (Fig. 15D,E). The operculars are large bones, about 60% the length of the two skull units together, and their height is only a little less than their length. The anterior and anterodorsal edges are almost straight, and the posterior is broadly convex. The anterior edge shows a distinct projection anterodorsally, interpreted as an articulation; the remainder of this edge is bevelled and slightly roughened where it was overlapped by the preopercular. The anterior half of the dorsal edge has a lenticular overlapped surface for the lateral

extrascapular, but posterior to that the edge is finished and curves around to the posterior margin. This implies that as the post-temporal has no overlapped lateral edge, these two bones must have abutted edge-to-edge or were separated by a slight gap.

Running across the surface posteroventrally from the articular process is a broadly rounded ridge, marking a flexure in the bone that gradually diminishes in prominence posteriorly. This presumably reflects the cross-section of the body of the animal. In anterior profile, dorsal to this ridge the opercular is inflected at c.55° to the main surface of the bone. Apart from the anterior and anterodorsal edges, the entire external surface is cosmine-covered.

Towards the anterodorsal corner of all observed operculars, the external surface shows a patch of special cutaneous sensory pores of the kind seen elsewhere on the skull. These are in the same position as the pores on the opercular of *M. hibberti* figured by Moy-Thomas (1935: fig. 2). The number of pores in a patch varies from 19 to c.80. No connection between these pore patches and any underlying structure has been established. Obviously, no lateral line canal occurs in the opercular, but on the inner surface of QMF21105 is a groove that does not extend to the edge of the bone. This could be regarded as evidence of the presence of a nerve beneath the appropriate part of the opercular to innervate the pore group, but the fact that it is seen on only one of the available specimens suggests that it is probably only an individual variant of no significance.

The internal surfaces of the operculars are not well preserved, but anterodorsally in the depression formed by the bone flexure, QMF21093 shows two slight scars which were probably for the attachment of ligaments from the hyomandibular. QMF21103 has a slight scar in the same region, but this has been emphasized by weathering and its significance is in doubt.

Subopercular 1, which is only 85% of the length of the opercular in the holotype, is overlapped dorsally by the opercular. In addition, an incomplete individual, QMF26553 (Fig. 15F,G), is confidently identified as a first subopercular. Cosmine covers its entire external surface except for the dorsal and anterior edges, which have a deep band of rough tissue indicating overlap by adjacent bones. The dorsal overlap is highest anteriorly where it has a distinct dorsal projection, and it decreases in height gradually posteriorly. Its anterior edge has a protrusion in line with

the flexure mentioned below, and the anterior overlapped area becomes smaller ventrally, disappearing completely at the ventral edge of the bone. The bone has a pronounced, subangular longitudinal flexure about 5-6mm below the dorsal cosmine margin. In the anterodorsal corner of the bone is another group of special sensory pores like those on the opercular.

Subopercular 2 is smaller, being 66% of the length of the first in the holotype; it too is cosmine-covered. One almost complete isolated subopercular 2, QMF33056, has been recovered; only its posterodorsal margin is missing (Fig. 15H,I). The bone tapers posteriorly. The dorsal edge has a deeply overlapped surface for subopercular 1, but its extent cannot be determined. Anteriorly a narrower edge was overlapped by the posterior submandibular and the principal gular; the bone is thickest where this edge joins the cosmine-covered part. A large group of sensory pores lies in the cosmine towards its anterodorsal edge. This group contains a high proportion of two or more pores that lie surrounded by ridges containing flask chambers (Fig. 15I), but it has not been possible to remove the sediment to observe the number of pores forming these subgroups. On the inner surface of the bone beneath the pore-covered patch, a number of openings occur, but without destroying the specimen it is not possible to determine if they open through to the outer surface. Judging from its similarity to the second subopercular of *Gogonasmus*, a single isolated fragment, QMF26552, represents the anterior third of this bone. The two suboperculars meet behind the last submandibular (Figs 6; 16B), making a pattern like that of *Megalichthys hibberti*.

The reconstruction of *M. hibberti* by Miall (1885) shows only two suboperculars, but Moy-Thomas (1935) figured four bones in this position on the lectotype, which was chosen and figured by Agassiz, and refigured by Andrews (1982: fig. 8j). It seems to have only two suboperculars, but

the drawing leaves room for doubt. A well-preserved specimen, G8.80 from the Hancock Museum, was illustrated by Birks (1916), and his figure is consistent with Miall's interpretation. We have examined this specimen, and conclude that, at least in this respect, Birks was correct. It is clear that two suboperculars are present in this species as in *C. narrienense* and the new genus from Norway (Borgen, MS).

We note that other osteolepiforms, such as *Eusthenopteron foordi*, have only one bone that is normally identified as a subopercular, but also that there is a second plate lying at the posterior end of the submandibular series, called the submandibulo-branchiostegal plate by Jarvik (1944). This is undoubtedly homologous with our second subopercular. We prefer our terminology for this bone because the first subopercular extends down into the line of the submandibulars and the plate in question continues the line of the operculars. In addition, although the overlaps in *Cladaroptychus* are not completely clear, those in *Gogonasmus* are quite unambiguous (Figs 15A-C). In that genus, the second subopercular is clearly overlapped by the first subopercular, and its anterodorsal corner has a projection like the other subopercular. In other words, its relationships are such that it lies in the opercular series and is morphologically like an opercular rather than a submandibular.

Extrascapulars and Post-temporals. The lateral extrascapular is well represented by two isolated specimens, QMF31871 and 31876 (Fig. 13B,D). It is subtriangular in outline, but with all edges slightly curved. The anterior margin bears a narrow overlapped surface; its lateral edge, the shape of which is also known from the overlapped dorsal edge of the opercular, is finished. Its mesial edge is not well enough preserved to describe. The specimens are readily recognised by the junction of the main lateral line and the occipital commissure.

overleaf on p. 130

FIG. 15. Opercular and subopercular bones of *Gogonasmus andrewsae* Long, and *C. narrienense*. A-C, opercular, and suboperculars 1 and 2 from the left side of *G. andrewsae*, ANU49259. Note distinctive overlaps as described in the text. D-E, two isolated right operculars of *C. narrienense*, QMF21092 and 21103. Note cutaneous sensory pore clusters (arrows) towards the anterodorsal corners, small on D, much larger on E, and the large erosion hole in the centre of D. F-G, two isolated fragments of the left subopercular 1 of *C. narrienense*, QMF26553 and 26550. Note similarity in shape to the subopercular 1 of *G. andrewsae* illustrated in B, and cutaneous sensory pore clusters (arrows) of different sizes in the anterodorsal corners. H, an almost complete subopercular 2, QMF33056, missing only its posterodorsal edge. Arrow shows cutaneous sensory pore cluster. I, enlargement of ventral part of sensory pore cluster from the anterodorsal corner of the same specimen. Scale: 10mm; except I : 1mm.

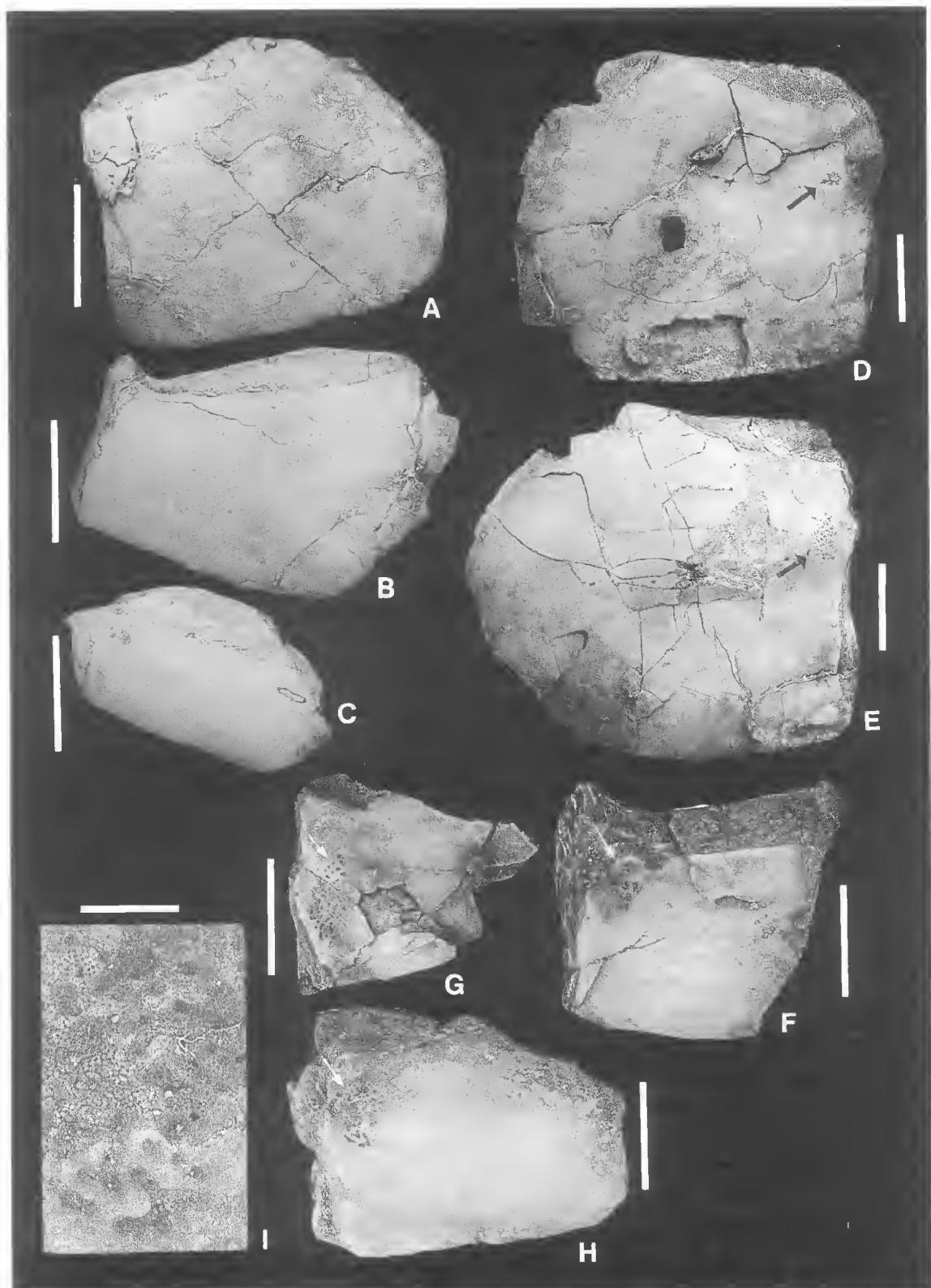


FIG. 15

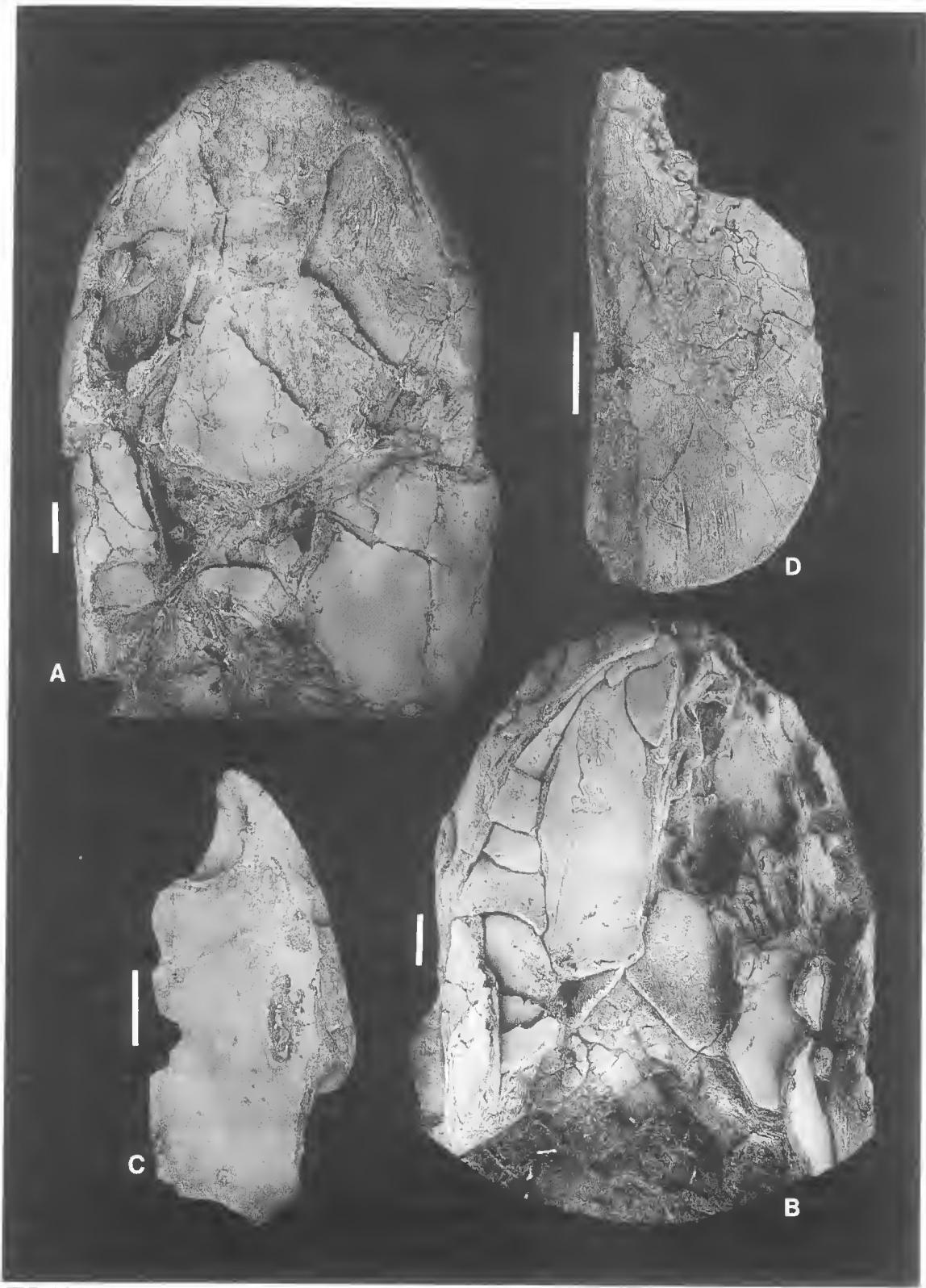


FIG. 16

On the holotype an incomplete fragment of bone lies between the operculars on the dorsal surface. This fragment could represent the only median extrascapular in the collection. Space requirements and the shape of the lateral extrascapulars show that the median extrascapular must have been narrow anteriorly and rapidly expanded posteriorly, its lateral margins bearing overlapped surfaces. Two left post-temporals, QMF31873 and 26537, are known (Fig. 13A,C). The former specimen is the more complete. It is cosmine-covered, sub-rhombic in outline, but the anterior edge is slightly wider than the posterior. The anterior edge bears a slight overlap which is divided into two parts, representing contact with the median and lateral extrascapulars. All other edges are finished, and bevelled on the inner surface, indicating that they overlapped adjacent bones. The lateral line is in the left half of the bone, and seems to run a straight course. A mainly transverse hook-shaped pit-line is present on the lateral half also, and a patch of sensory pores lies mesial to the bend in the hook. This bone is large in comparison with those of *Eusthenopteron* and other osteolepidids, and its anterior overlap is small. The fact that it is almost completely covered with cosmine is also unusual, but we note the presence of patches of cosmine on both the anocleithrum and the supracleithrum. Although it cannot be demonstrated from the material available, a process of the supracleithrum probably extended between the opercular and the post-temporal (Fig. 14A).

PALATAL BONES.

The bones of the palate of *Cladarosymblema* are not well known.

Vomers. The vomers are represented by four isolated incomplete specimens, each of which has a large tusk and associated pit, and a high wall around the anterior edge that carries up to 20 denticles along its crest (Figs 18;19). The anterior crest apparently diminished in height abruptly mesial to the more mesially placed tusk, or its replacement pit. The denticles along the crest are not all of the one size, nor are they confined to a single row. As all the specimens in Fig. 18 show, the largest denticles are restricted to the anteromesial side of the mesial tusk or its replacement pit. Smaller denticles lie in a row in front of

these larger ones, but this row is not continued laterally in front of the lateral tusk on two of the three available specimens. On the third, QMF26558 (Fig. 18D,E), the row is also continued around the lateral tusk.

The front wall of the vomer is high and almost vertical. Its surface is smooth except for a patch of horizontal ridges (Fig. 18F) that would have articulated with the similar ridges on the premaxilla.

The holotype has the crushed left vomer exposed by excavation. It seems to have the median process almost complete, but it is so fractured that interpretation of its features is difficult. No median process is preserved on any of the isolated specimens, but the broken end of the process is shown on Fig. 18G,H. The extent of this median process can be judged from the attachment areas for the vomers on the endocranum (Fig. 20A; 21A); these are very transverse and have mesial extensions that meet or almost meet in the midline (see description of these surfaces below). We conclude that a depressed median process was present, but was broken off the isolated specimens. The vomers, therefore, are comparable with those of *M. hibberti*.

QMF26556, in which the lateral side of the vomer is almost complete, shows a notch that may mark the passage of the maxillary branch of cranial nerve V to the nasal capsule, as Thomson (1964b:328) has hypothesised for *Ectosteorrhachis* and Jarvik (1942: fig. 61) for *Eusthenopteron*.

Pterygoid. Despite continued attempts, no pterygoids or other palatal bones have been recovered by etching. Excavation of the holotype has exposed part of the endopterygoid, but nothing significant can be said about it.

Parasphenoid*. The parasphenoid is a bone of dermal origin, closely applied as a thin sheet over much of the base of the endocranum. However, owing to deficiencies of preservation, the complete limits of the parasphenoid are impossible to determine in any one specimen of *Cladarosymblema*. However, by careful examination of several specimens on which parts of the parasphenoid are preserved (Fig. 20A,B,D), a reasonably accurate composite picture of the bone can be constructed.

previous page

FIG. 16. *Cladarosymblema narrienense*. A-B, dorsal and ventral views of the skull of the holotype, QMF21082. In B, the left side of the gular and submandibular series has been removed to expose the palate, the clavicle, subopercular 2 and the broken subopercular 1. C-D, right and left principal gular plates, QMF26544 and 31880, showing general form, nature of the overlaps, and peculiar resorption and regrowth pattern of the cosmine. Scale: 10mm.

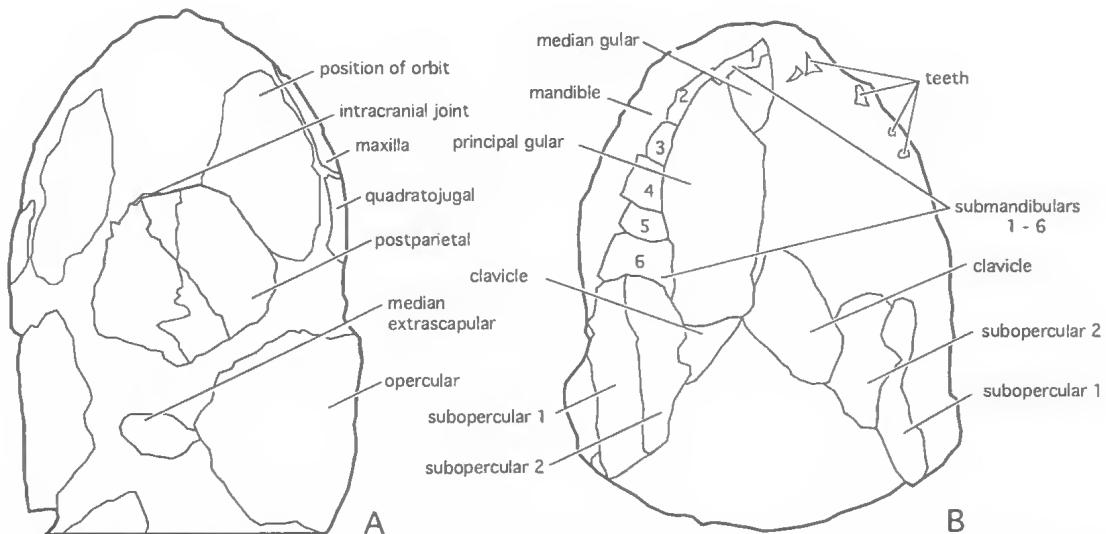


FIG. 17. *Cladarosymblema narrienense*. A-B, labelled outline drawings of views of the head of the holotype as shown in Fig. 16A-B.

The anterior limit of the parasphenoid is clearly shown on QMF21104, where it can be followed along an irregularly transverse line well behind the vomers (Figs 20A; 22); medially a smooth ridge, which is the extension of the denticulated surface, extends forwards of this transverse line. A broad, flat area of endocranial bone is exposed between the vomers and the parasphenoid, in contrast to the condition that Jarvik (1966) has shown in *Megalichthys* and that Thomson (1964a) has described in *Ectosteorhachis* (but see Romer, 1937:19). As noted above, the parasphenoid in *Cladarosymblema* does not border the prenasal fossae nor does it meet the posterior process of the premaxilla along the midline. Posteriorly from its anterior transverse limit, the parasphenoid sheathes the entire width of the palatal exposure of the endocranum between the pterygoquadrate and, as described by Romer (1937) in *Ectosteorhachis*, it sends an 'ascending process' well up the flanks of the basipterygoid process (see QMF21083); it does not, however, ascend the endocranial wall more anteriorly. Anterior to the basipterygoid process, the parasphenoid terminates at the edge of the subocular shelf.

The central part of the parasphenoid is dominated by a raised denticulated surface that, as in *Megalichthys* and *Ectosteorhachis*, is well rounded in posterior outline, but unlike in those genera it tapers to an acute anterior termination; it is bordered by a shelf-like expansion of the bone laterally. The depth of the denticulated sur-

face below the lateral expansion is greatest posteriorly and diminishes regularly towards the front. The central part of the denticulated surface is somewhat depressed (Fig. 20B,D) and has relatively few teeth (see QMF21105, 26547). Posteriorly the denticulated surface is bounded by a narrow rim of dense periosteal bone. The denticles, when completely preserved, are sharp cones, but in the specimens at hand, most are broken off or worn, leaving a basal annulus of enamel and dentine enclosing a central pulp canal. The buccohypophysial foramen, which is conspicuous in our specimens, is encircled by a ring of smaller denticles. Posterior to the denticulated surface, the parasphenoid forms a thin layer closely appressed to the endocranum as far back as the edge of the notochordal pit (Figs 20B,D; 21A; 22; 25D).

ETHMOIDAL ENDOCRANUM

The endocranum of the ethmoid unit is known in some detail from five specimens, none of which is complete (Figs 20-27). Of these specimens, QMF21083 is the best preserved, QMF21104 has lost the dermal roof and part of the endocranum, QMF21110 has lost all of the endocranum except that immediately under the skull roof, QMF21108 has only the right side preserved, and QMF21105 retains only the ventral surface of the palate that is well preserved. Consequently, it is not possible to give a complete description of the ethmoid unit, although more

detailed information is available than for most other described osteolepiforms.

Prenasal Fossae. (See Terminology.) These fossae are well exposed on three specimens, QMF21083, 21104 and 21110, and are mesial and partly anterior to the nasal capsules (Figs 20A; 21A,C; 22; 25D). On QMF21110, the endocranial ridge is worn through to expose a mass of vesicular tissue, thereby demonstrating its endochondral origin (Fig. 21C). Anteriorly, the ventral edge of the endocranum is overlapped by a concave flange of the premaxilla (see below), which continues laterally to the articulation with the vomer; Jarvik (1966: fig. 17) referred to this structure in *Megalichthys* as the palatal lamina of the ethmoid shield. It lies directly on the endocranum, which in turn forms the roof and walls of the prenasal fossa. The posterior wall of the fossa is steep and terminates beneath the vomer. There is no suture in the endocranial bone of this wall as was shown by Jarvik (1966: figs 17A; 19D) for *Megalichthys*.

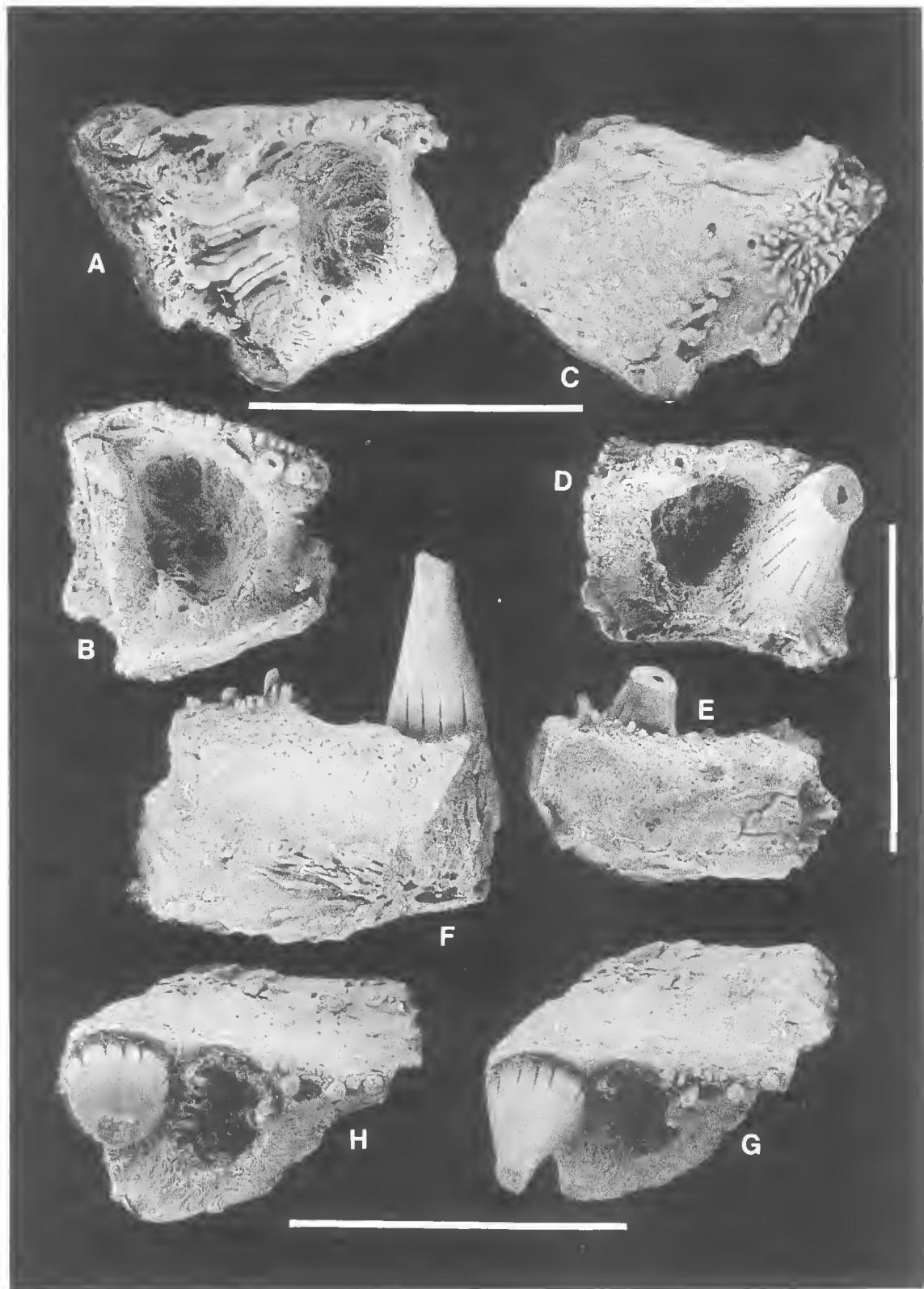
Several specimens of *Cladarosymblema* are well enough preserved to show that the prenasal fossa is in direct communication with the nasal capsule lateral to it. In QMF21104, a wide nasobasal canal (see below) penetrates the bony wall between the two, from the lateral extremity of the fossa to the base of the mesial wall of the capsule (Figs 20A; 22; 24; 25D); thereafter, the canal is continued part way across the ossified part of the floor of the capsule as a groove. In QMF21083, the canal has not been cleared of matrix, but foramina mark its course; however, these are substantially smaller, and the canal presumably narrower, than in QMF21104. Across the roof of the prenasal fossa in QMF21104 and 21110, a deep groove extends mesially from the lateral foramen and opens into two or more foramina that in turn open into the vesicular tissue making up the substance of the endocranum (Figs 20A; 21C). QMF21083 shows a much shallower groove on the left side and even less on the right, but several small foramina penetrate the bone here, as well. In the posteromesial corner of the prenasal fossa on QMF21104, there are two more foramina opening posteriorly into the vesicular tissue of the endocranum. We see no evi-

dence that these small foramina are interconnected or that their pattern is constant.

In *Megalichthys* and *Eusthenopteron*, the passage between the prenasal fossa and the nasal capsule was named the ventral branch of the nasobasal canal by Jarvik (1966: 86 & fig. 17). He believed it carried the medial branch of the profundus nerve, which then anastomosed with the palatine nerve. We can see no evidence that reflects the pattern of these nerves in this region in *Cladarosymblema*, and note that the basis for his interpretation is the presence of such an arrangement in the anuran *Rana esculenta*. Thomson (1964b: 326-7 & 345) has discussed this matter and has concluded that the nasobasal canal carried the ramus medialis narium of the profundus nerve. As noted above, the groove in the nasal capsule entering the nasobasal canal in *Cladarosymblema* runs below the olfactory bulb, whereas the profundus nerve passes above it (see below). Therefore, we accept the conclusions of neither Jarvik nor Thomson. Instead, we believe that a vein draining the prenasal fossa entered the corner of the nasal capsule and ran across its floor, an inference that is consistent with the marked individual variation that the channel and foramina show in the specimens of *Cladarosymblema*.

Jarvik (1966) claimed that the prenasal pit (presumably the deepest part of the prenasal fossa in our terminology) in *Megalichthys* contained an intermaxillary gland. From the vessels or nerves entering these spaces it may be inferred that some soft tissue was present, but we have no evidence to indicate what its dimensions or homologies might have been. Thomson (1964b:332) and Jarvik (1966: 83-84) have also suggested that in *M. hibberti* the anterior tusks of the dentary fitted into the prenasal fossae, but we have mandibles that are from animals of the same size as our ethmoid units, and these show that the tusks in question entered the fossae only shallowly and only on their anterior edges; most of the opening of the fossae would then have been opposed by the mandibular parasymphysial plate. However, during elevation of the lower jaw to full occlusion, the parasymphysial plate remained in too ventral a position to have entered the fossa, and its posterior (toothed) edge moved past the ante-

FIG. 18. *Cladarosymblema narrienense*. A-C, oblique, buccal and visceral views of incomplete right vomer, QMF26559. In A, note the lateral tusk is broken vertically to expose the labyrinthine structure. C shows the intricate modelling of the surface of attachment to the endocranum. D,E, buccal and anterior views of a broken left vomer, QMF26558. F-H, anterior and variously tilted buccal views of a right vomer, QMF26560. In F, note rugosities on the anterior face where the vomer fitted against the similarly patterned face of the premaxilla (see Fig. 25D). All specimens have the mesial projection broken off. Scale: 10mm.



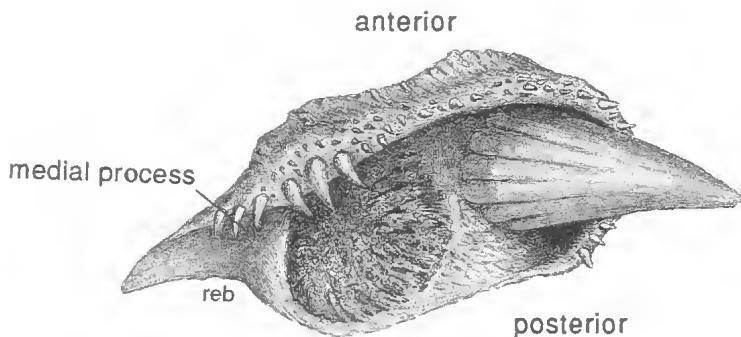


FIG. 19. *Cladarosymblema narriense*. Reconstruction drawing of a vomer in oblique anteroventral view, based primarily on Fig. 18F,G, with the continuation of the denticles around the lateral crest is based on Fig. 18D,E.

rior (toothed) edge of the vomer. The suggestion that the fossae contained soft bodies of considerable size cannot be ruled out on that account.

Nasal Capsule. The nasal capsules are well preserved on two specimens (QMF21083, 21104) and less completely preserved on three others (QMF21105, 21108, 21110) (Figs 20A, B; 21A,C; 22; 23B; 24B; 25C,D). As is usual in osteolepiforms, the capsules are open ventrally through a large unossified solum nasi, the original borders of which can be reconstructed from the specimens at hand. The rim of this opening is not all in the one plane, but rises to form a notch lateral to the autopalatine articulation, and a more profound notch at the lateral extremity of the solum nasi (Figs. 21A; 25C,D). In life, as discussed above, the vomers would have extended laterally at least to a level below part of the bony capsules as preserved in these specimens, but almost certainly there was a vertical gap between the upper surface of the vomer and the opposing capsule rim. However, in *Cladarosymblema*, the floor of the nasal capsule, the solum nasi, was not ossified, although in our best preserved specimen (QMF21083), endocranial bone does complete the lateral wall of the nasal capsule beneath the circumnarial bones. Further ventrally in the capsule, however, the lateral wall is not preserved and we do not know the full extent of ossification beyond the limits shown on this specimen.

The external naris opens into the wall of the nasal capsule anterolaterally; beneath the naris, the lateral wall of the capsule is swollen out beyond the plane of the naris, carrying the capsule laterally well past the limits of the vomer beneath, unlike Thomson's reconstructions of *Ectosteorhachis* and *Megalichthys* (Thomson,

1964a: fig. 3). This has important implications for the position of the choana, which, as we have discussed in relation to the anterior shape of the maxilla, must have been posterolateral to the vomer and anterior to the maxilla. The premaxilla and the bones around the external naris are firmly fixed to the neurocranium, and although the maxilla and the lachrymal abut against, and are not fused to the bones ante-

rior and dorsal to them, we see no evidence that the snout was kinetic on the cheek (cf. Rosen et al., 1981:191, 234).

Apart from the foramen for the nasobasal canal, which has been dealt with under *Prenasal Fossae* above, several large foramina can be seen in the mesial and posterior walls of the nasal capsule (Figs 23B; 24B). The largest is for the olfactory tract, and it opens high on the posteromedial wall just under the dermal bones. The second largest foramen, which is only about one quarter the size of the olfactory opening on whose dorsolateral side it lies, opens posteriorly into a short tube that emerges through the antorbital wall into the orbital chamber. On our best preserved specimen, QMF21083, this foramen joins a groove that runs across the roof of the nasal capsule and enters a foramen in its mesial wall; this latter foramen can be seen in turn to divide into two channels more deeply. A second specimen, QMF21104 (Figs 23A; 24A) in which the roof had been eroded away before burial, shows a foramen on each side of the capsule in the same place, but the course of the canal across the roof has been lost. However, a foramen in the mesial wall is preserved in QMF21104 and this shows that it enters a ramifying set of deeply buried tubes that run forward and downward toward the premaxilla (see above). Although we have been unable to establish the connection, it seems likely that these tubes opened into those described above, for example in QMF21111, running beneath the lateral line system and carrying fibres for ophthalmicus profundus V to innervate the snout as in *Gogonasus* (Long, 1985a: fig. 5). This is an unlikely course for a nasolachrymal duct, a point we

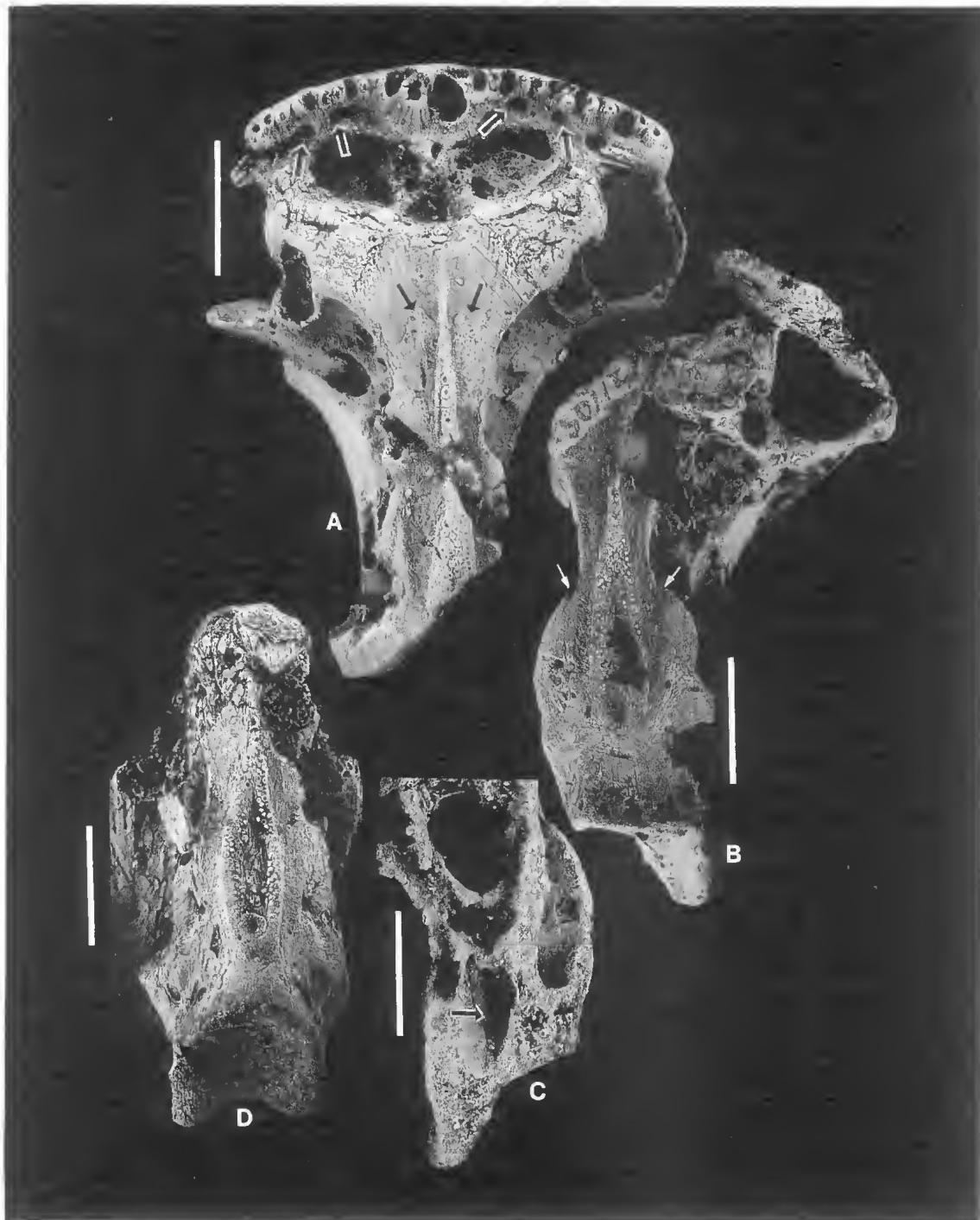


FIG. 20. *Cladarosymblema narrienense*. A, B, D, ventral views of three incomplete ethmoid units with paraspheoids attached, QMF21104, 21105 and 26547. In A, black arrows indicate anterior edge of paraspheoid; white bordered arrows indicate openings into the transverse (rostral) commissure of the lateral line canal. In B, arrows indicate position of notch. C, dorsal view of posterior part of the specimen in B showing hypophysial pouch (arrow). Scale: 10mm.

make because Jarvik considered that a large foramen in the ventrolateral part of the posterior wall of the nasal capsule in *Eusthenopteron*, carried a nasolachrymal duct. No foramen corresponding with this foramen of Jarvik occurs in *Cladarosymblema*, nor indeed in *Gogonasus*.

Other foramina enter the mesial wall of the nasal capsule in *Cladarosymblema*. In QMF21104, a groove passes up from the edge of the solum nasi ventrolateral to the olfactory foramen, curves around the ventral edge of that foramen, and leaves the capsule through a foramen (fmi in Fig. 24B) in the mesial wall just in front of the olfactory foramen. We do not know the function of this groove. Other minor foramina are present in this wall, but they are not consistently developed on even the two sides of a single specimen; nor are they constant between specimens. We consider these to be nutrient foramina. Specimen QMF21104 shows a small foramen in the posterolateral wall on both sides of the specimen, although it is largely eroded on the left. This enters a canal that opens high on the lateral extremity of the antorbital wall. No other specimen has this part of the animal preserved so that we cannot assess its significance. Its size and position suggest that it is more likely to have transmitted a nerve than a vessel, but apart from that comment we cannot offer any useful suggestion.

On QMF21083, a second large foramen penetrates the antorbital wall posterodorsal to the ophthalmicus profundus V foramen (Figs 21A; 22; 25D), but it does not open into the nasal capsule. Rather it opens into a tube that cannot be traced with clarity; however, what is clear is that it does not open into the same canal as the ophthalmicus profundus V. It runs mesially, and probably ramifies in the vesicular tissue between the olfactory canals. Such an orientation suggests the ramus ophthalmicus superficialis VII nerve. The foramen in question has been lost by erosion in QMF21104.

On QMF21083 and 21105 a smaller foramen occurs in the antorbital wall lateral to the foramen for the ophthalmicus profundus V (Figs 21A; 22). From it a tube passes through into the posterolateral corner of the nasal capsule where there is a conspicuous foramen. On QMF21083, a shallow groove runs up across the roof of the capsule parallel with the inner margin of the striated bone forming the inner surface of the bones surrounding the external naris. It passes over the top of the olfactory foramen and joins the same foramen in the mesial wall of the capsule as the ophthalmicus

profundus V. This groove is present on QMF21105 also, but the roof of the capsule has not been preserved so its course cannot be traced throughout. What occupied these foramina and groove? Thomson (1964b: fig. 3) considered that in *Ectosteorhachis* a lateral nasal vein exited the nasal capsule posteriorly in approximately the same position as the structure under discussion, but the more anterior course of the lateral nasal vein is around the flank of the capsule rather than over the roof and into the internasal septum as in *Cladarosymblema*. Hence, this is not an adequate interpretation. A second possibility is that it carried a ramus of nerve V, either the maxillaris or infraorbitalis (Jarvik, 1942: 477; Thomson, 1964b: 328). We prefer this interpretation because the groove across the roof of the capsule reaches the foramen we have interpreted as carrying the ramus profundus V. We have labelled it maxillaris N V in Fig. 22.

We have not dealt with the drainage of blood from the nasal capsule, because no foramina likely to have carried veins have been observed. It seems most likely that a vein passed out of the capsule into the lateral head vein through the notch near the autopatine articulation.

Olfactory Canals. The olfactory canals are well exposed on QMF21104, in which the dermal roof has been eroded away (Fig. 23A); their disposition can also be inferred from QMF21083 (see also Fig. 28B). The separate canals arise towards the posterior end of the unit, much further posteriorly than in *Eusthenopteron* (e.g., see Jarvik, 1980: fig. 89), but are comparable in their pattern with those in *Ectosteorhachis* (see Romer, 1937: figs. 8, 9). A short distance along their course, the canal for the optic nerve is given off in an anteroventrolateral direction (Figs 23A; 24A). This peculiar arrangement is matched by that in *Ectosteorhachis* as figured by Romer (1937: figs 8, 9). Further forward are several foramina of varying aperture in the floor of the olfactory canal (Figs 23A; 24A). These seem to connect with tubules that traverse the spongy tissue between the canals, but they seem not to exit the bone at any identifiable points more ventrally. Presumably they carried sensory nerves or vessels of some kind. Thomson (1964b: 321) has commented that cutaneous and ethmoid arteries passed through foramina in the walls of the olfactory tract; we are unable to comment further on the basis of our material. It is not uncommon to find such tubules in other osteolepiforms or in diploean specimens that are sufficiently well preserved to show them.



FIG. 21. *Cladarosymblema narrienense*. A-B, ventral and posterior views of QMF21083. The black arrows on the left side of Fig. A indicate (from left to right) the foramina for the maxillaris V, the ophthalmicus profundus V, and the ophthalmicus facialis VII. C, ventral view of incomplete ethmoid unit, QMF21110, showing spongiform tissue between the olfactory canals, openings into the transverse commissure of the lateral line canal (arrows), and the roof of the left nasal capsule. Scale: 10mm.

Inner Wall of the Orbital Chamber. The endocranial surfaces forming the inner wall of the orbital chamber are well preserved on QMF21083 and 21104, although on neither specimen are these surfaces complete. The wall stands

vertically under the roof, is swollen where it covers the olfactory canals, and is deeply concave more ventrally, forming a broad sub-olfactory recess (Figs 21A; 22) and meeting the lateral edge of the subocular shelf (=suborbital ledge of

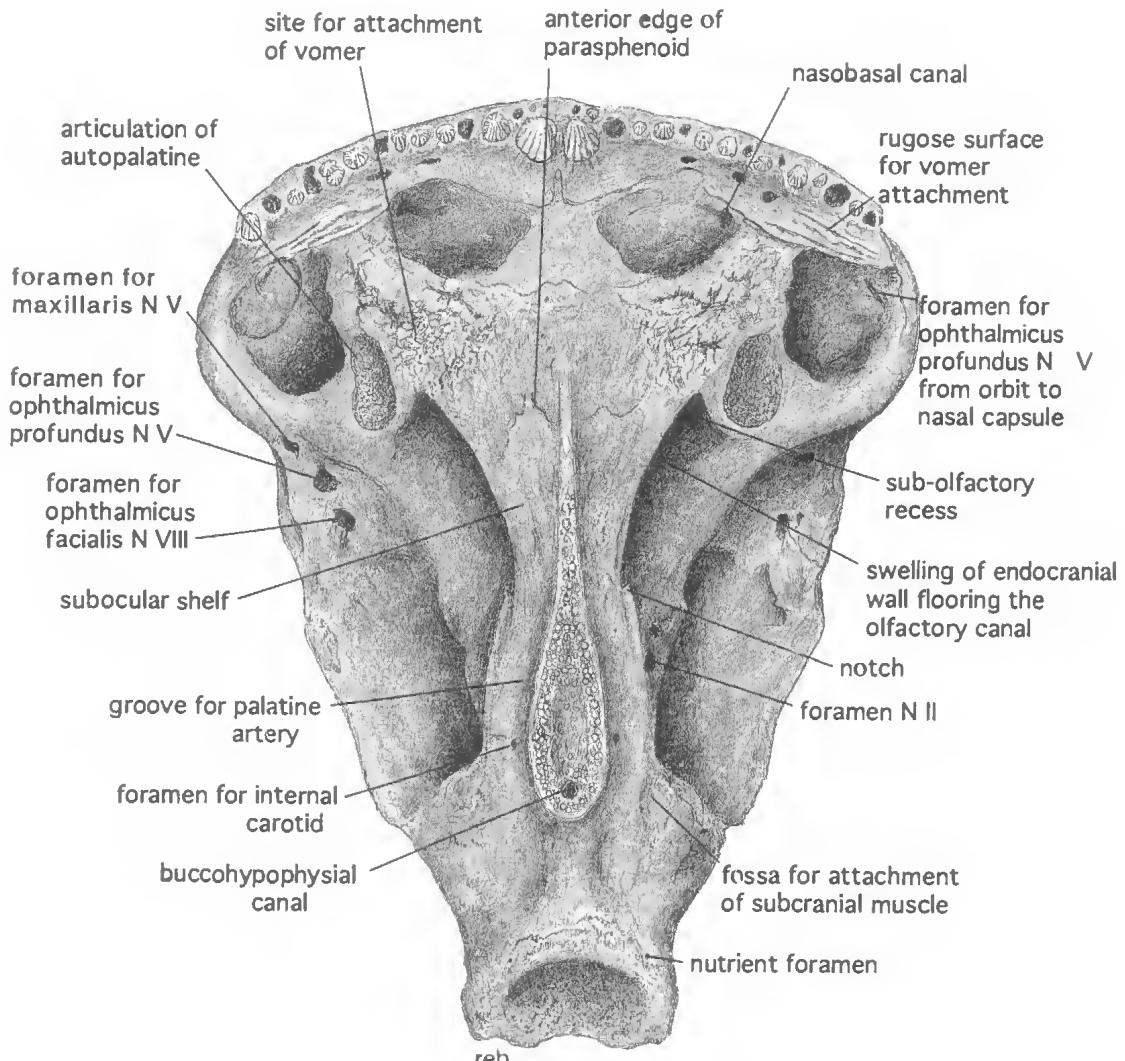


FIG. 22. *Cladarosymblema narrienense*. Reconstruction of the ethmoid unit without vomers, based on QMF21083 and 21104.

Jarvik, 1980: fig. 86A) along a sharp keel; the ventromesial edge of the pterygoquadrate articulated in this recess.

Anteriorly, and immediately below the nasal capsule, is a deeply concave facet of vesicular bone (Figs 20A; 21A; 22; 25D) that received the anteromedial process (pars autopatina) of the palatoquadrate. This facet extends far enough ventrally to border upon the horizontal attachment surface for the vomer, and it terminates

posterodorsally at the base of the antorbital wall. This articulating surface is twisted, with its anteromesial extremity directed laterally and its posterior extremity facing ventrally. In life, presumably, it was lined with cartilage, and the complexity of its surface is probably related to limiting the range of possible movement of the pterygoquadrate on the endocranum.

Posteriorly from the autopatina facet, the subolfactory recess is the dominant feature of the

lower parts of the endocranial wall, and this recess becomes progressively deeper posteriorly; its surfaces are marked by irregular processes, ridges and depressions that reflect the connective tissue attachments of the pterygoquadrate to the endocranial wall. The recess terminates at a laterally robust process (Figs 20A-C; 21A; 22) that is mostly formed by endocranial bone but is sheathed superficially by the parasphenoid (see below). This structure is the basipterygoid process, the site of the second, and perhaps the most important moveable joint between the pterygoquadrate and the endocranum. In *Cladarosymblema*, the basipterygoid attachment is C-shaped in lateral aspect, with the ventral arm of the 'C' prolonged anteriorly. The articulatory surface of the process consists of vesicular bone that lacks a perichondral covering. Most posteriorly, where the process is especially robust, this surface is nearly vertical and faces anteriorly. As it continues ventrally and then anteriorly, along the ventral arm of the 'C', the articulatory surface comes to face increasingly laterally. Directly above the basipterygoid process, just beneath the skull roof on QMF21083, is a small patch of unfinished bone that may represent the suprapterygoid process, the third site of attachment of the pterygoid on the endocranum. Jarvik (1980: fig. 8) has illustrated a suprapterygoid process in this position in *Eusthenopteron* and Long (1985a: fig. 3) in *Gogonasus*.

Anteriorly, the basipterygoid process encloses a pit (Fig. 25A, black arrow), deep within the confines of the 'C'; this pit in *Eusthenopteron* was interpreted by Jarvik (1980: fig. 85) as being for the retractor bulbi muscle, a muscle found in tetrapods and used for pulling the eye deeper into its socket. The evidence for this is not clear. On the other hand it would be appropriately placed with respect to the line of muscle action and the position of nerve III to be the myodome for the posterior rectus eye muscle in a fish. Long (1985a: fig. 3B) reached the same conclusion with respect to *Gogonasus andrewsae*. At the base of the pit is a foramen for the exit of the pituitary vein; the vein must then have continued dorsally to join with the jugular vein; the passage posteriorly of the latter is marked by a shallow groove (Fig. 25A) above the basipterygoid process (QMF21008, 26547). The scars for the attachment of the other eye muscles have not been positively identified.

In *Cladarosymblema*, the optic nerve foramen is a major landmark on the orbital wall (Fig. 25A-D). It opens on the olfactory ridge a short

distance anterior to the basipterygoid process. It is large and ovate, and the optic canal for passage of the nerve from the endocranum is oriented anteroventrally and leaves the olfactory tube near its base (see above). Nerve III exited from the endocranum via a small foramen posterodorsally adjacent to the optic foramen (Fig. 25A), as shown in QMF21083, 21104, and 26547, a position similar to that in *Eusthenopteron* (Jarvik, 1980: fig. 86) and *Gogonasus* (Long, 1985a: fig. 3). Romer (1937) and Thomson (1967) were unable to recognize the foramina for nerve III and IV in *Ectosteorhachis*; and we have been unable to recognize the foramen for nerve IV in *Cladarosymblema*.

Immediately anterior to the optic nerve foramen on both sides of QMF21104 is a small subcircular scar about 1mm in diameter that has a slightly raised periosteal rim (Fig. 25B,C; asterisk). A similar scar occurs in *Gogonasus* (ANU 49259) as well; consequently, there can be no doubt about its anatomical reality. Obviously, soft tissue of restricted extent was attached to it. The only possible eye muscles to attach at such a point would be the obliques, but in our view the scar is unlike a muscle attachment and is not appropriately placed to be so interpreted (Goodrich, 1958: fig. 244). An alternative explanation would be that this structure represents an eye stalk such as occurs in elasmobranchs and placoderms. According to Young (1986: 15), however, the eye stalk is 'similarly positioned in both groups, behind the optic nerve and beneath the oculomotor foramen'. In our material the scar is clearly anterior to the optic nerve, and hence this option is also ruled out. Furthermore, as far as we are aware, an optic stalk has not been previously recorded in osteolepiforms, nor in any other sarcopterygians.

Above the optic foramen in *Cladarosymblema*, the endocranial wall appears to have been depressed mesially, forming an elongate fossa beneath the skull roof. The exact dimensions of the fossa cannot be determined owing to breakage and erosion. Long (1985a) identified a fossa in this position in *Gogonasus* as serving as the attachment area for arcus palatini muscles. A similar interpretation for the area is warranted in *Cladarosymblema*.

Base of the Endocranum. Posterior to the prenasal fossae, the endocranial surface is broad and flat, and is marked by an irregular pattern of ridges and furrows, the sites of attachment of the vomers. These sites are broad and extend laterally over the endocranial surfaces that encroach on the



FIG. 23. *Cladarosymblesma narrienense*. A, dorsal view of a fragment of ethmoid unit, QMF21104, with most of the roof eroded away exposing olfactory tracts and nasal capsules. Anterior parts of lateral line canals excavated to show their great depth of burial. B, anterolateral view into the right nasal cavity of the same specimen. Large opening is the olfactory tract. For interpretation see Fig. 24B. C, posterodorsal view of QMF26547 showing parietals and large median postrostral. Posterior part of the roof has been eroded to allow a view into the hypophysial pouch (arrow). Scale: 10mm.

outline of the nasal capsule (Figs 20A; 21A; 22). Mesially, the markings fade and on QMF21083, they are quite obscure. They include a complex network of vascular elements that may have supplied the vomers and the connective tissues that held the vomers in place. On QMF21104, the rugosities are sufficiently clear to show that the vomers extended to, or almost to, the midline.

Posterior to the vomerine attachment surfaces, the base of the endocranum narrows to a level

just anterior to the vertical plane containing the optic foramen, behind which it widens posteriorly to the basipterygoid attachment. Ventrally, QMF21105 shows a notch (Figs 20B; 22: notch) on both edges of the parasphenoid, about midway along the length of the subocular shelf; a short groove leads to the notch from the posterior. This specimen is the only one in our collection that is undamaged in this area, but QMF26547 shows evidence that it had similar structures. As far as

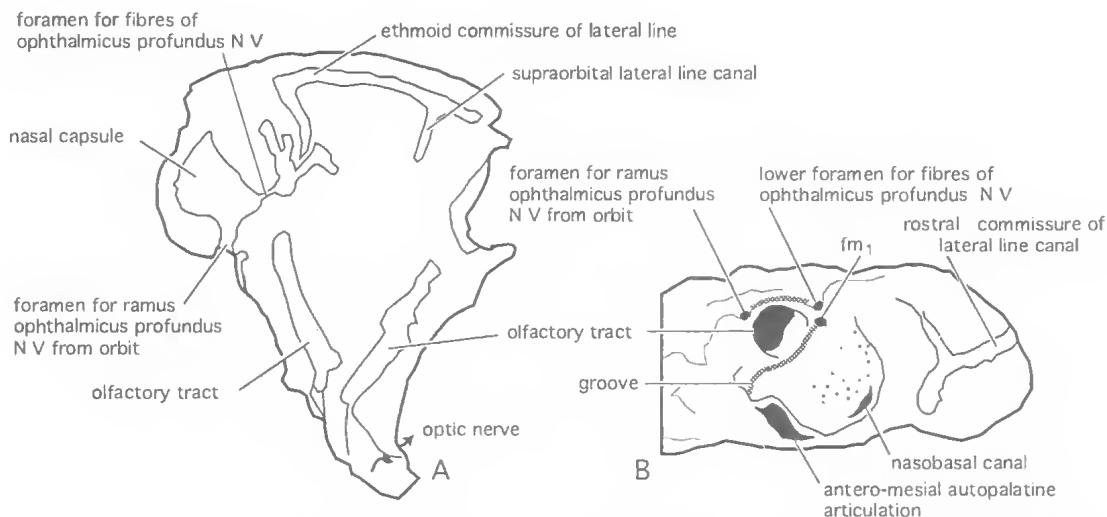


FIG. 24. Labelled outline drawings of Fig. 23A,B.

we are aware, no structure resembling this notch has been reported in other osteolepiforms, but a comparable structure occurs in the specimen of *Megalichthys* used by Jarvik (1966: fig. 17A & pl. 3), and in *Gogonasus* (ANU49259), in which it is much closer to the foramen for the palatal artery. The notch marks the passage of a nerve or vessel dorsally, to a level above the lateral flange of the parasphenoid, and then on to tissues between the endocranial wall and the opposing surface of the pterygoquadrate. Although it cannot be proved, it seems likely that the notch would have carried a branch of the palatine artery. (See below for a discussion of this vessel.)

Posterior Part of the Endocranum of the Ethmoid Unit. As is shown particularly well by QMF26547, on either side of the denticulated surface of the parasphenoid anterolateral to the buccohypophyseal foramen, the internal carotid artery enters the basicranium through a moderate-sized foramen (Fig. 22). Posterior to this foramen is a shallow groove that runs from near the base of the basipterygoid attachment, where it disappears from the surface of the bone. It marks the course of the internal carotid artery. Closely associated with the internal carotid foramen is a slit-like furrow for the palatine artery, which leaves the basicranium to continue further anteriorly in a shallow groove. This slit-like furrow is partly concealed on the right side of QMF26547 by a small ventral shelf, but this is probably of little consequence as it is not present on the left side. Thomson (1964b: fig. 7) has figured a similar arrangement of the internal carotid and pa-

tine arteries for *Ectosteorhachis* and Jarvik (1966) has noted it for *Megalichthys*. The only other specimen sufficiently well preserved to show this area is QMF21105, but it has not preserved these foramina. On the other hand, QMF21083 and 21104 show short vertical openings in this position, apparently reaching up into the base of the hypophysial pouch, as would be expected if this were the position of the internal carotid.

On each side of the same specimen, near the base of the basipterygoid process, is a foramen in approximately the same position as the one regarded by Romer (1937: fig. 4) as carrying the internal carotid in *E. nitidus*. Each is entered from a posterolateral direction by a short groove. We agree with Jarvik (1966: 91-92) that these foramina have been incorrectly identified by Romer, and are nutritive foramina associated with the attachment of the subcranial muscles. The scars for these muscles are well preserved on QMF21083 and 36547 (Figs 20D; 22). The posterior part of the endocranum of the ethmoid unit is constructed in its entirety of robust but finely vesicular endochondral bone covered by a well-developed perichondral layer.

The anterior end of the notochord fitted within a shallow, rounded pit (Figs 21A,B; 22), as in *Ectosteorhachis* and *Megalichthys* (see, e.g., Romer, 1937; Jarvik, 1966). In *Cladaro symblema*, this pit has a sharply defined rim around its ventral and lateral sides (see QMF21083, 26547), although the ventral edge has been eroded in QMF21083. Poster-odorsally to the edge of the notochordal pit are the scars of the processus connectens, marking the ventral

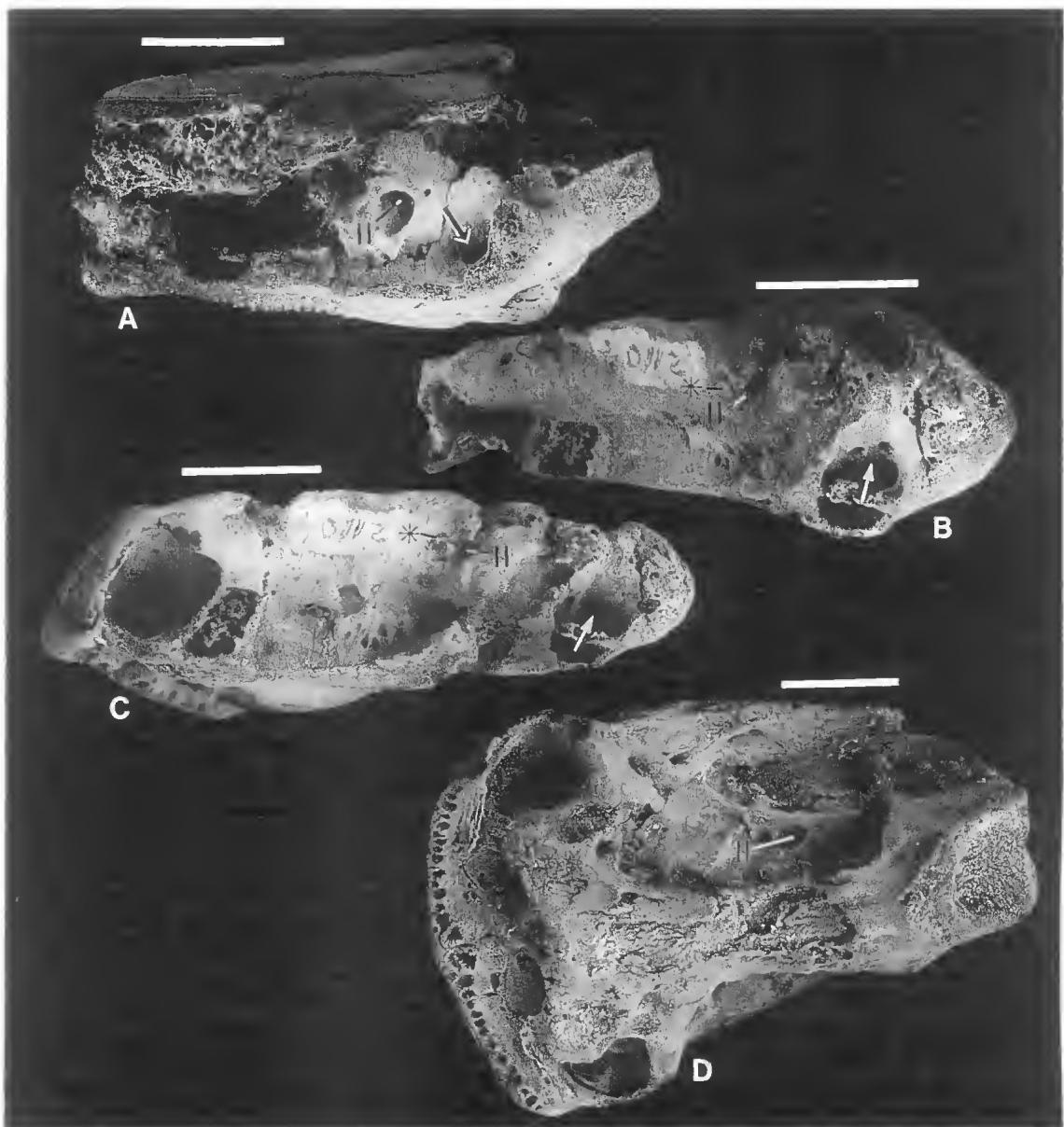


FIG. 25. *Cladarosymblema narrienense*. All figures are of ethmoid units. A, lateral view of QMF26547 showing large foramen for the optic nerve II, small foramen for the oculomotor nerve III posterodorsal to it, and a large myodome with foramen for the pituitary vein posteroventral to it (arrow). Spongiform tissue occupies the anteromesial space between olfactory tracts. B,C, two lateral views of QMF21104 with specimen tilted at different angles to show details of the hypophysial fossa (white arrows), and foramina opening into its anterior and lateral walls. Note the gap between the base of the hypophysial pouch and the buccal surface of the parasphenoid, and the foramina in the walls of the pouch described in the text (see Fig. 26). Asterisk indicates scar for a stalk of unknown function. D, oblique ventral view of incomplete ethmoid unit, QMF21083. Optic nerve foramen labelled II. Scale: 10mm.

articulation of the endocranum of the ethmoidal unit with that of the otico-occipital unit. The anterior ascending process of the parasphenoid

(see Jarvik, 1980: 172) covers the side of this bone, and is depressed relative to the most lateral extent of the processus connectens, but we see no

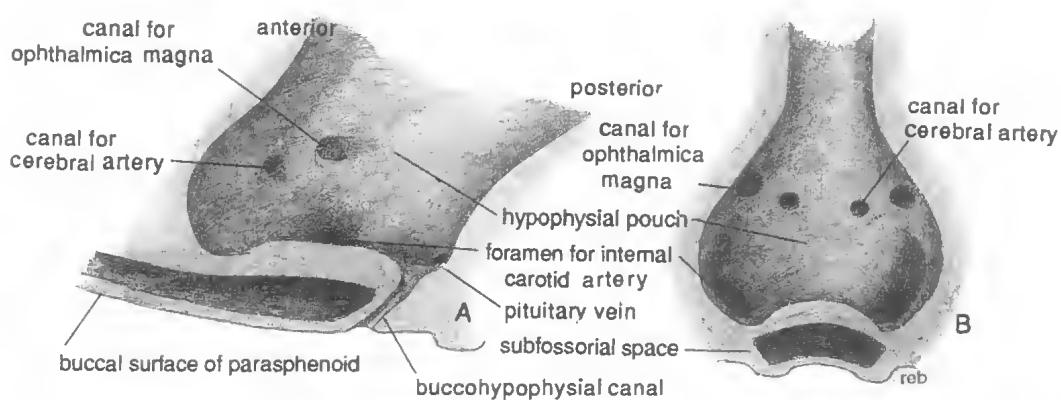


FIG. 26. *Cladarosymblema narrienense*. Reconstruction drawing of the hypophysial pouch and its foramina, based on the specimen in Fig. 25 B,C.

anatomically distinct structure here reflecting what Jarvik (1980: 172) has identified as the prespiracular groove in *Eusthenopteron*.

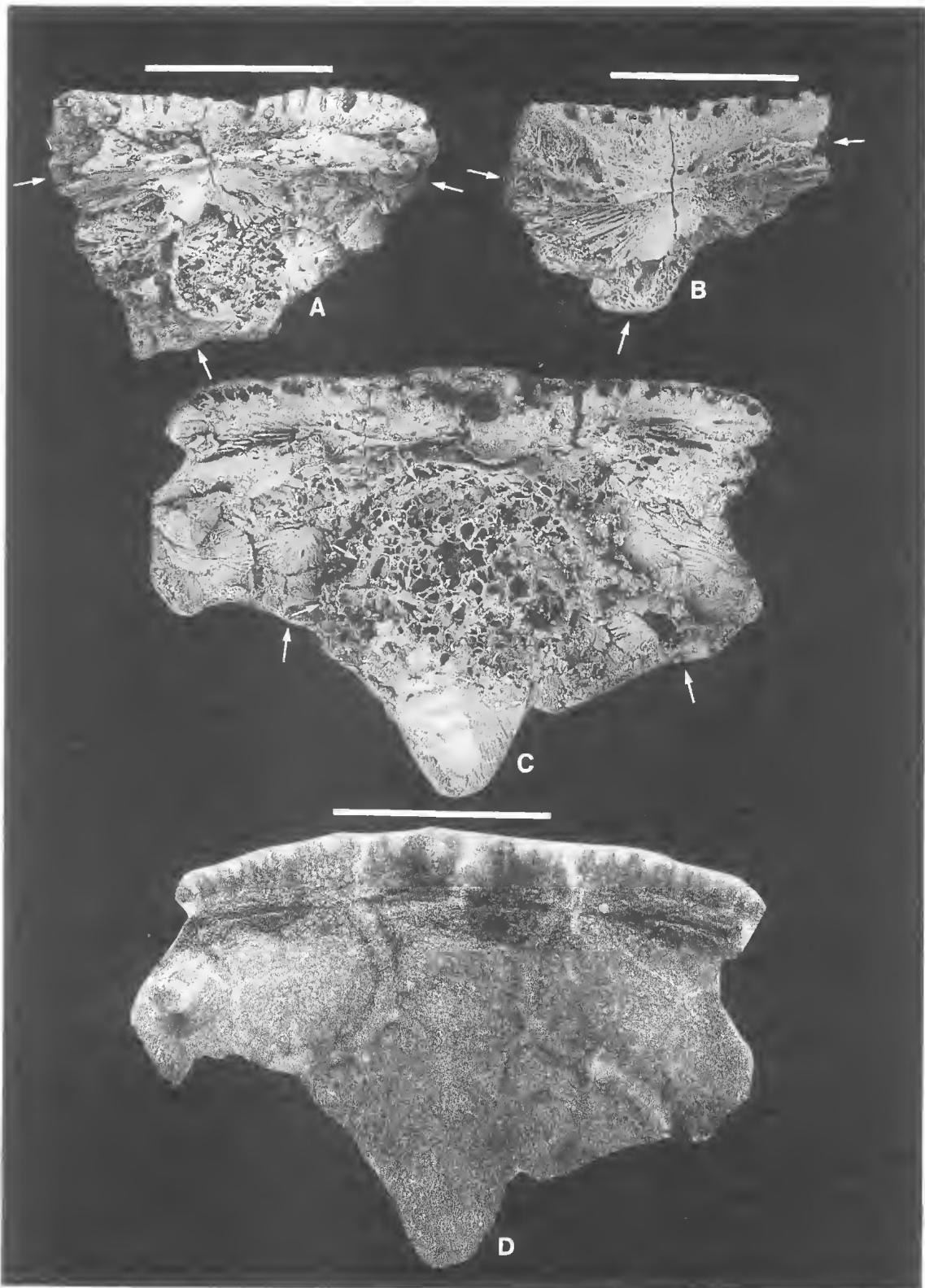
Above the notochordal pit is the cavity for the brain stem; it has a thick floor and lateral walls. Ventrally, the posterior edges of these walls, which face the posterior unit, are vertical, but more dorsally they are inclined anteriorly at a steep angle. The external surfaces of the bone here have been damaged on even our best-preserved specimens, but they retain evidence of ligaments that extended between the two units and held them together. At their dorsal ends, the posterior braincase walls flare laterally and are fused to the ventral surface of the parietals (Fig. 21B). Along their outer edges, immediately beneath the parietals, they contain deep vertically striated pits for the articulation of the supratemporal process (the fronto-dermosphenotic process of Bjerring, 1972). Below these is the small patch of vesicular bone forming the suprapterygoid process for the distal articulation of the pterygoquadrate. This is well-preserved only on QMF21083.

Hypophysial Fossa. The best specimen for examining the hypophysial fossa is QMF21104 (Fig. 25B,C), which exposes the right side and most of the front wall. The fossa and the buccohypophysial opening (see above) are preserved on QMF21105 and 26547, but do not expose as much detail. Putting together the data from all these specimens (Fig. 26), it is clear that the fossa emerges from the floor of the cranial cavity near the posterior end of the paraspheoid. The dorsal part of the fossa is elongate and narrow (Fig. 20C), and it passes down into a large flat-bottomed chamber that is subtriangular in trans-

verse section. The anterior wall of the chamber is planar and its lateral wall concave. The internal carotid artery joins the fossa at its anterolateral corner through a passage that runs posteromedially from its external opening on the palate. A pair of foramina opens half way up the anterior wall of the fossa, one on each side of the midline. A second foramen opens in the anterolateral angle of the chamber dorsolateral to the one previously mentioned. These mark canals that appear to run anteriorly and anterolaterally from the fossa. In *Gogonasus* (ANU49259), a foramen opens externally a short distance anteriorly from the hypophysial fossa in the appropriate position for the exit of this laterally placed canal, and we assume a similar arrangement in *Cladarosymblema*, although the specimen is not well enough preserved to show the external foramen. In *Eusthenopteron*, Jarvik (1980: 118) has interpreted a tube in this position as having carried the ophthalmica magna artery supplying the soft tissues dorsal to the palate. The more mesially placed canal is likely to have transmitted the cerebral artery. Posteriorly, on the broken lateral wall of the fossa in QMF21104 (Fig. 25B) is the incomplete rim of a foramen that marks the exit of the pituitary vein.

QMF21105 and 26547 show the buccohypophysial canal best among the specimens at hand (Fig. 20B,D). It leaves the floor of the fossa a short distance behind the anterior wall and runs in an anteroventral direction to open about 1 mm in front of the posteriormost edge of the denticulated area of the paraspheoid.

The pattern of the whole hypophysial fossa seems very different from that of *Eusthenopteron* (Jarvik, 1980: fig. 196B), which genus should not be taken as representative of the condition in



osteolepiforms. The structure seems to be highly variable within the group. It is also very different from that of the porolepiform *Glyptolepis* figured by Jarvik (1980: fig. 196A).

OTICO-OCCIPITAL ENDOCRANUM

Occipital Region. No specimen having this part of the skull preserved is uncrushed or otherwise undamaged, but we nevertheless have five specimens that yield important information (QMF21084, 21085, 21094, 21096, 21109); of these, QMF21085 and 21094 are the most useful. In those specimens, the occiput extends well behind the postparietals and the endocranum is well-ossified in this region. It forms a flat platform (the occipital shelf) that continues backwards from the posterior edge of the postparietals and that supported the anterior parts of the extrascapular series (Figs 38A,B; 39A,B). This shelf narrows laterally and does not extend fully to the lateral extremity of the postparietals. At its lateral limit, a separate shelf of dermal bone is developed by the tabular. It is separated from the neurocranial shelf by a notch (Fig. 38B) that is situated beneath the most lateral extent of the postparietal.

On either side of the midline beneath the occipital shelf in QMF21094, a shallow but well-defined fossa lined with pitted and ridged bone is developed. This fossa appears to have been the area of origin for muscles and ligaments extending to the anterior vertebrae (Figs 38B; 39B). Anterior and lateral to this fossa is a much deeper depression that presumably also provided the origin for axial muscles and ligaments. The roof of this latter depression is penetrated by a large foramen that opens to the dorsal surface of the occipital shelf. This foramen opens into a vertical tube that is continuous with a broad groove that runs anterolaterally and turns beneath the postparietals, through foramina including several minor ones laterally (Figs 38A,B; 39A,B). These grooves and foramina seem most likely to have been associated with blood vessels. In *Eusthenopteron*, Jarvik (e.g., 1980) has identified a system of grooves in this region as carrying the

occipital artery and its branches forward across the endocranial roof of the otico-occipital unit. We have observed similar grooves in two large fragments of *Cladarosymblerma* (Fig. 31A,B), but these are not sufficiently well exposed to enable us to outline their disposition. They were probably vascular in function, and probably connected with the occipital artery.

Mesial to the large foramina that penetrate the occipital shelf in *Cladarosymblerma* is a pair of much smaller openings that clearly run forward into the endocranial cavity, well seen in QMF21094 and 21085 (Figs 38A,B; 39A,B); these openings represent the emergence of the endolymphatic duct from the skull (see below for evidence of the course of these ducts within the endocranial cavity). In *Latimeria*, the endolymphatic duct leaves the skull roof posteriorly and terminates beneath the extrascapulars (Millot & Anthony, 1958) and perhaps the duct had a similar configuration in *Cladarosymblerma*, as would be indicated by QMF21094. Other specimens, however, have a somewhat different structure. In QMF21056, a smaller specimen than QMF21094, the occipital shelf is narrower and the posteriormost parts of the postparietals conceal the foramina for the occipital vessels and the endolymphatic ducts from dorsal view, making it even more unlikely that the ducts reached the body surface. In any case, these differences in proportions most probably are age-related and have no taxonomic significance.

In QMF21094 and 21085, a deep median pit passes forward between the openings for the endolymphatic ducts immediately beneath the dermal roof (Figs 38A,B; 39A,B). This pit corresponds to the attachment of the supraneurial ligament in *Eusthenopteron*, as identified by Jarvik (1980: fig. 86).

The outer edge of the occiput in QMF21085, the best preserved of our specimens in this part of the skull, is bounded by a rounded ridge that encloses the posterior vertical semicircular canal; this ridge also forms the inner rim of the entrance to the fossa Bridgei, the major cavity in the skull for the origin of axial musculature. Just mesial to

FIG. 27. *Cladarosymblerma narrienense*. A, a left premaxilla in ventral view, QMF26540, with some tectals attached, all showing distinct radiation centres. Arrows show transverse (rostral) commissure and anterior end of supraorbital lateral line. B, isolated left premaxilla, QMF31877, in ventral view; arrows show entry points of lateral line canals. C, Paired premaxillae and attached small polygonal roofing bones on each side, QMF21111, identified by their distinct radiation centres and in some instances by their sutural boundaries. Arrows show lateral line entry points. Note tubules embedded in spongiform tissue (inner white arrows). D, X-radiograph of the specimen shown in C. (This and subsequent X-radiographs have been made by printing X-ray negatives on hard photographic paper.) Scale: 10mm.

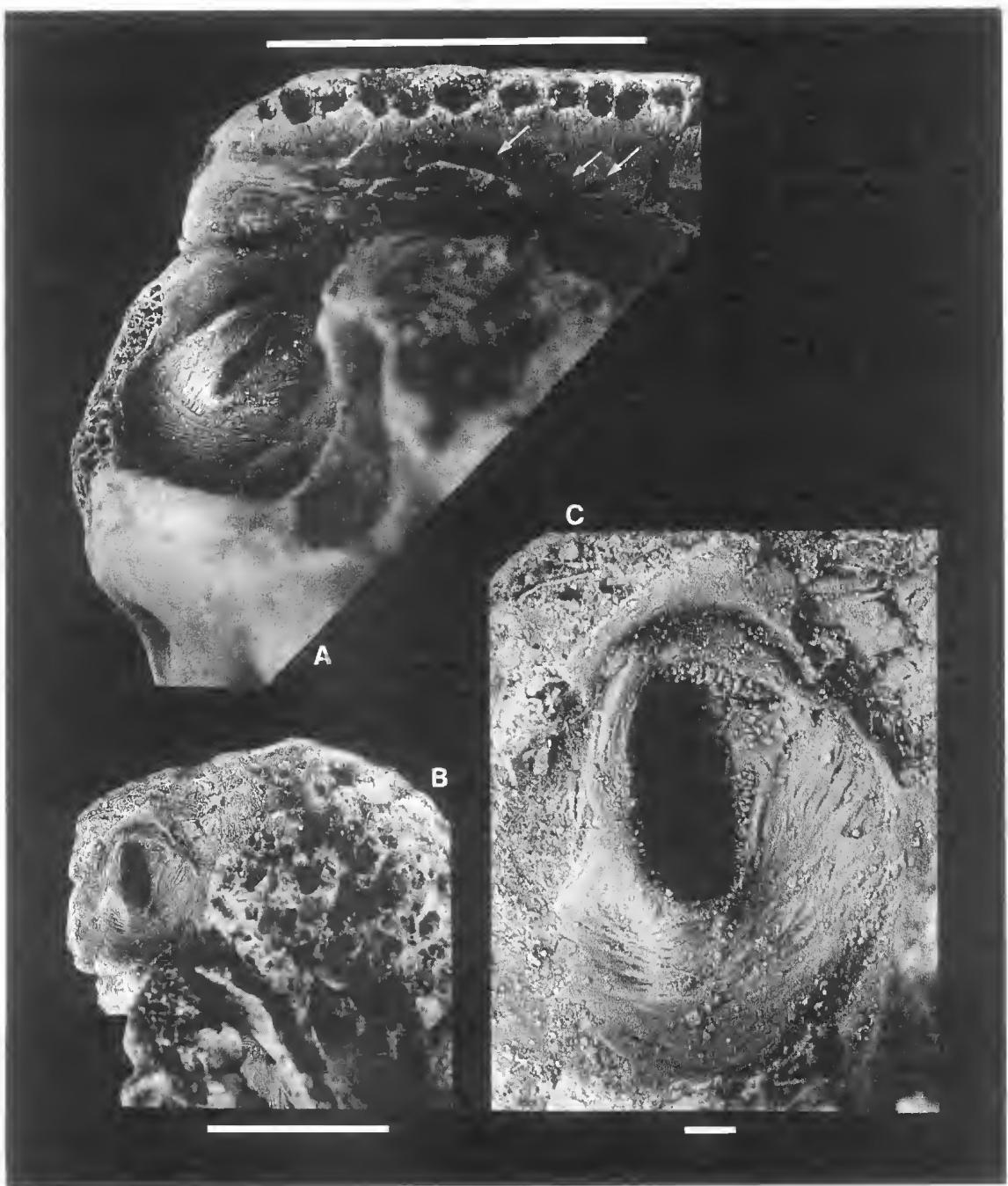


FIG. 28. *Cladarosymblesma narrienense*. Ventral views into the nasal capsules of two specimens. A, right nasal capsule, QMF21083, showing the bones with characteristic texture forming the roof of the capsule, the eroded lateral edge of the capsule formed from thick vesicular endocranial bone, and a thin outer rim of dermal bone (see also Fig. 21A). Note behind the teeth in the premaxilla several pores that open into the transverse (rostral) commissure of the lateral line canal (white arrows). B, ventral view of right nasal capsule of an eroded specimen, QMF21108, showing the relationship of the capsule to the olfactory canal. C, enlargement of the roof of the nasal capsule in B. Note the mass of small denticles around the edge of the narial opening; especially well developed in the embayment on the mesial side. Scales: A, B, 10mm; C, 1mm.

the base of this ridge are two large foramina, one above the other, and separated by a slightly protruding lip (Figs 34A; 35A; 38A; 39A). They open externally at or near the junction between the occipital ossification and the auditory capsule. These foramina lead into short canals that pass through the braincase wall just posterior to the sacculus; within the wall, the canals join and open to the cranial cavity by a single foramen. From comparison with *Ectosteorhachis* (Romer, 1937:14), the lower foramen transmitted nerve X, and the upper, the posterior lateral line nerve. These two nerves are also closely associated, for example, in *Neoceratodus* (Northcutt, 1987), and have been reconstructed according to this same pattern in *Eusthenopteron* (Jarvik, 1980, fig. 86C). In *Gognasus* (ANU49259), a fissure that incorporates the separate foramina opens here, and each foramen is subdivided at least once, indicating the exit of several at least partially separated trunks of these nerves.

Immediately below and slightly in advance of the vagus foramen in QMF21085, a subcircular depressed area is developed in which vesicular bone is exposed (Fig. 38A). This corresponds in position to the postotic process or facet for the attachment of the first suprapharyngeal branchial arch in *Eusthenopteron* (Jarvik, 1980: fig. 86) and in *Ectosteorhachis* (MCZ6499) (Thomson, 1967:229). In *Gognasus* (ANU49259), a blunt process occupies this position; its surface lacks periosteal bone and probably articulated with the suprapharyngeal branchial, as well. In *Eusthenopteron*, the opening for cranial nerve IX is found below this facet. In none of our specimens of *Cladarosymblema* is this part of the skull well preserved, but QMF21085 retains what may be part of the rim of the foramen for nerve IX; nerve IX opens at this position in *Gognasus*. In both QMF21085 and ANU49259, a system of ridges runs anteroventrally from the suprapharyngeal branchial articulation; their significance is unknown, but they possibly mark the attachment of various muscles, including the hyomandibular adductor, protractors of the first branchial arch, and a protractor and adductor of the opercular, as in *Ectosteorhachis* (Thomson, 1967: 229).

Fossa Bridgei. The fossa Bridgei in QMF21085 is a more or less pear-shaped space in cross-section, with its apex directed laterally and dorsal side flattened. In *Ectosteorhachis* (MCZ6499, Fig. 42A), the posterior entrance to the fossa is more nearly rectangular than in *Cladarosymblema* (Fig. 38A), with the lower rim subparallel to the upper. The mesial wall of the



FIG. 29. *Cladarosymblema narrienense*. A,B, ventral views of the roofs of two otico-occipital units with most of the endocranum removed, QMF21086 and 21096. Note centres of radiation of the supratemporals and tabulars; transverse attachments of the endocranum to the postparietals, the tabulars, and the posterior extremity of the supratemporals; the longitudinal attachment of the endocranial walls to the postparietals; the almost complete restriction of the crista parotica to the ventral surface of the tabulars. Articulatory processes on the supratemporals have deep grooving (white arrows) and a slot on their dorsal edges for the articulation of the edge of ethmoid unit. The foramen for the occipital artery connecting the fossa Bridgei with the trigemino-facialis chamber indicated by black arrows. Scale: 10mm.

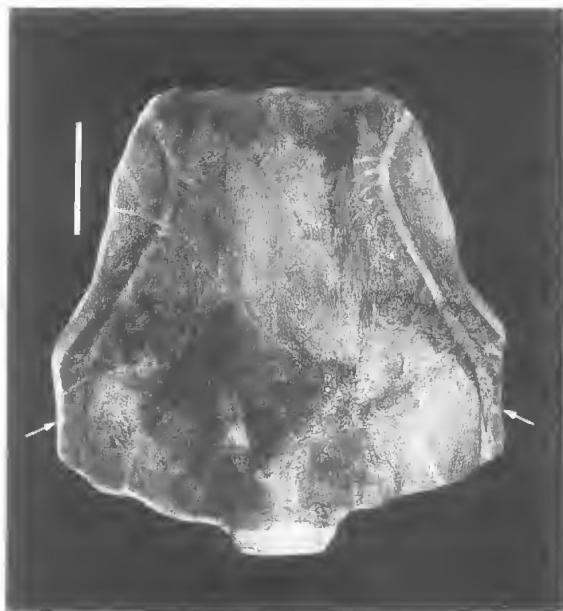


FIG. 30. *Cladarosymblema narrienense*. Roof of an otico-occipital unit, QMF21096 (see also Fig. 29B). Note lateral line canals, the absence of branches into the postparietal, the faint canals branching off into pores in the supratemporal, and the thick branch (arrows) on both sides into the putative extratemporal. Scale: 10mm.

fossa in our specimens consists partly of a continuous sheet, and partly of a meshwork of finely reticulated endocranial bone (Fig. 32C). Most of the roof of the fossa Bridgei, however, is of dermal bone, provided by the undersurface of the tabular and the most lateral extent of the postparietal, particularly well shown in QMF21086 and 21096 (Fig. 29A,B). At its anterior end, the fossa is nearly completely walled off by the endocranial bone that encloses the anterior vertical semicircular canal. However, in QMF21085, two foramina, one above the other, penetrate this wall, connecting it with the trigemino-facialis chamber anteriorly (Fig. 32A; arrows). In QMF21096 most of the endocranum has been removed, but the two foramina are still preserved on the left side, the more dorsal one being depressed (Fig. 29B). In QMF21084, there is only one large foramen at that location. The function of these foramina is uncertain. Romer (1937, fig. 5) showed a single large foramen (dorsomesial to a smaller foramen for nerve VII) in this position in *Ectosteorhachis*, and merely indicated that it communicated between the 'temporal' (= trigemino/facialis) and 'supraotic' (= fossa Bridgei) chambers. Passive communica-

tion between the chambers seems to us to be an unlikely function of these foramina and, as discussed below, we suspect that they carried blood vessels.

In QMF21084, a groove runs forward down the medial wall of the trigemino/facialis chamber from the larger of the foramina that pierce the anterior wall of the fossa Bridgei; a comparable groove is seen in the skull of *Gogonasus* (ANU 49259), in which the foramen is single. Further, in ANU49259, a second groove runs forward from this foramen, along the mesial wall of the chamber, just beneath the dermal roof. In turn, this splits into two channels, one continuing further along the wall, and the other associated with a system of grooves on the undersurface of the supratemporal, adjacent to the spiracular notch. All this suggests that two structures passed through the anterior wall of the fossa Bridgei and ran forwards along the lateral wall of the braincase. The nature of these two structures is clarified by reference to features at the posteroventral edge of the fossa Bridgei in both *Cladarosymblema* and *Gogonasus*, as described below.

On the occiput of the *Gogonasus* skull (ANU49259), a groove enters the posterior edge of the fossa Bridgei from a ventromesial direction. From its position well posterior to both the foramen for nerves IX and X and the hyomandibular (see below), we believe that this groove carried a branch of the occipital artery, and not a dorsally coursing artery such as the orbital artery, which is normally in an anatomically more anterior position, and which always leaves the lateral aorta close to the hyoid arch (Goodrich, 1958: fig. 284). Once over the lip of the fossa Bridgei, the artery crossed the floor of the fossa, exiting anteriorly and giving rise to temporalis and supraorbital arteries of the trigemino/facialis chamber. A similar pattern can be seen in *Cladarosymblema* (Figs 29; 35), in some specimens of which the split evidently occurred before the passage through the anterior wall of the fossa Bridgei; in those specimens two foramina are seen here; in other specimens the split occurred after the wall was penetrated, and only one foramen is present. In QMF21084 a well-defined groove crosses the floor of the fossa and leads to the foramina. As noted above, specimens of *Cladarosymblema* show both patterns, which represent individual variation with no taxonomic significance.

This pattern of the occipital artery differs from that which Jarvik (1980: fig. 131) has shown in *Eusthenopteron*, in which the channels for the oc-

cipital artery are contained within the endocranial roof. As mentioned above, the space between the dermal roof and the endocranum in *Cladarosymblerma* contains an anastomosing set of fine tubules (Fig. 31A,B) which we consider are connected with the vertically rising occipital artery. These tubules are much too fine to have carried the entire blood supply for the supraorbital, infraorbital and mandibularis arteries as shown by Jarvik (1980: fig. 131) for *Eusthenopteron*.

In *Cladarosymblerma*, the crista parotica, which forms the outer wall of the fossa Bridgei and is best seen on QMF21085, is heavily ossified and firmly attached to the lateral edge of the tabular; it stands almost vertically. *Ectosteorhachis* (MCZ6499) is closely similar. About half of this vertical face on QMF21085 is occupied by a subcircular depression lined with vesicular bone that lacks a perichondral lining (Figs 32B; 33); this fossa received the dorsal head or process of the hyoman-dibular (see below). Immediately ventral to this surface, the bone on QMF21085 has been eroded away and reveals the jugular canal, which passes forward into the trigemino-facialis chamber. In QMF21085, the posteriormost parts of the canal begin to turn ventrally, an orientation matching that shown to better advantage on the more extensively preserved skull of *Gogonasus* (ANU49259). The floor of the jugular canal in QMF21085 is penetrated by a large foramen, carrying the hyomandibularis branch of nerve VII (Figs. 32B; 33). The nerve ran dorsally and posterolaterally, in front of the auditory capsule in its passage from the cranial cavity, as in primitive gnathostomes generally (deBeer, 1937). It is likely as well that the orbital artery left the lateral aorta at this level and passed dorsally, as Romer (1937: 12; 1941: fig. 2) has supposed in *Ectosteorhachis*, but the ventral parts of the skull that would document its passage in *Cladarosymblerma* are not preserved in the specimens that we have available.

Smithson & Thomson (1982), in their discussion of the hyomandibular in *Eusthenopteron*, hypothesized that the jugular canal carried the orbital artery through part of its anterior course, and such may well have been the case here. In fishes, the artery in the canal is well ventral to the floor of the fossa Bridgei, additional evidence that the orbital artery did not pass through the fossa. Furthermore, *Gogonasus* shows a distinct notch on the ventral rim of the facet for the ventral hyomandibular process; perhaps this notch marks the ascent of the orbital artery, in which case the vessel passed anterior to the hyomandibular and

did not enter the jugular canal. Jarvik (1980: figs 78, 86) shows the orbital artery in a position anterior to the hyomandibular in *Eusthenopteron*, but passing through foramina that we believe were occupied by branches of nerve VII alone (see below). Below the jugular canal on QMF21085, the uppermost parts of the ventral articulation for the hyomandibular are lined with vesicular bone like that in the upper facet. Both facets are comparable in position to those in *Ectosteorhachis* (MCZ6499), but the canal in *Cladarosymblerma* seems to have been substantially larger in diameter and located in a more ventral position. Given the limitations of the sample, the meaning of these differences is not known.

Ventral Surface. The ventral side of the endocranum of the otico-occipital unit is not well preserved in any of our specimens, but some useful information about its features is available. The notochordal chamber has robust walls, the internal surfaces of which show strong annular markings. Similar markings are seen in *Gogonasus*, and presumably reflect the pattern of organization of the connective tissue sheath that surrounded the notochord. Enough of our material is preserved to show that a median space was originally present anteroventrally in the endocranum of the otico-occipital unit such that the walls of the notochordal canal did not meet to enclose the notochord anteroventrally (Figs 36B; 40). In life, an arcual plate presumably covered this space, as Jarvik (1980) has shown in *Eusthenopteron*. The more posterolateral region, around the vestibular fontanelle, is not preserved in any of our specimens. The skull of *Gogonasus* shows that the bone is very thin here and, hence, would be easily destroyed, either prior to burial or in preparation. However, our comparative material of *Ectosteorhachis* (MCZ6499) shows no development of the vestibular fontanelle whatever; the area in this specimen is completely sheathed in bone, and the structure in *Cladarosymblerma* may well have been the same. *Ectosteorhachis* shows no sign of a fenestra ovalis such as Jarvik (1980: 118, 126) has reconstructed as adjacent to the ventral surface of the articulation for the hyomandibular in *Eusthenopteron*.

A broad triangular surface of bone that served for the attachment of the basicranial muscles (Figs 36B; 40) forms the floor of the otic region. This continuous plate, which is best preserved in QMF21084, is composed of thick vesicular bone and is strongly attached to the equally thick walls

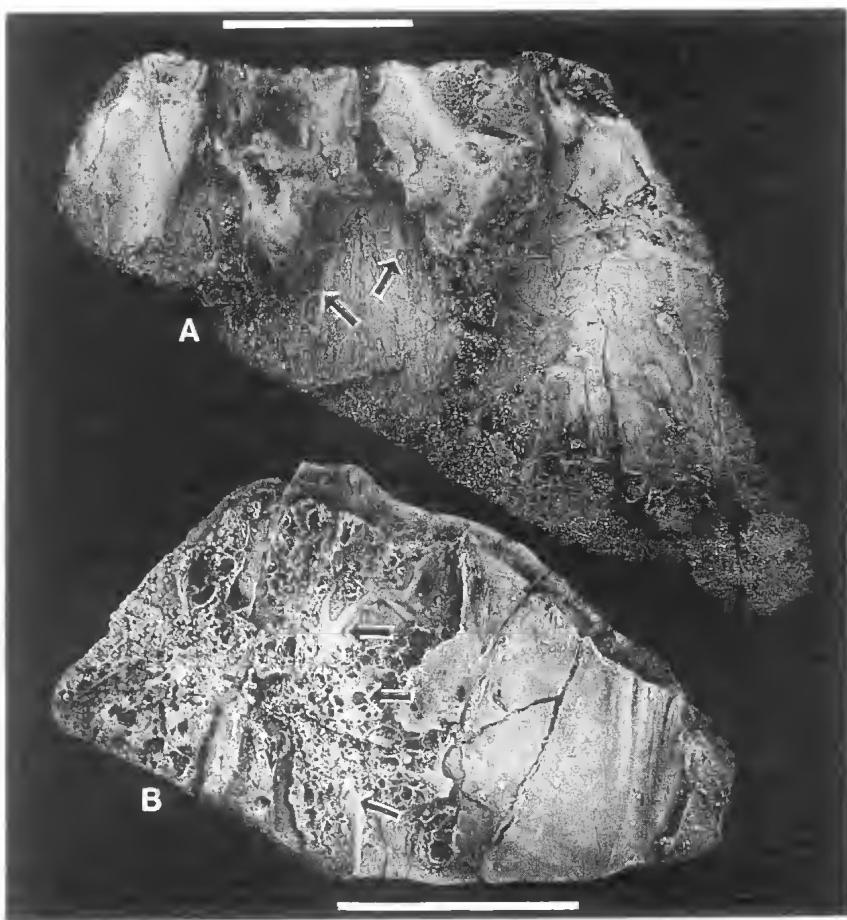


FIG. 31. *Cladarosymblema narrienense*. A,B, ventral views of incomplete otico-occipital shields, QMF26567 and 31863, with most of the endocranum removed to show reticulation of tubules between the roofing bones and the endocranum (arrows). Scale: 10mm.

of the notochordal chamber. Posterolaterally on this plate, a conspicuous foramen opening anteroventrally carried the palatal branch of nerve VII as it left the endocranum (Figs 36A,B; 37); a similar foramen occurs in *Ectosteorhachis* (MCZ6499) (see Romer, 1937: fig. 4) and is referred to by Jarvik (1980: fig. 78) as carrying the orbital artery as well as the nerve. Further anteriorly on QMF21085, and less well shown on QMF21084, on the dorsal side of the plate and lateral to the groove holding the jugular vein, a second foramen opens (Fig. 32B: white arrow); this foramen leads into a posteroventrally inclined tube which, although its posterior end is not exposed, seems to join with the canal for the hyomandibularis nerve. It must therefore be a branch of nerve VII. Romer (1937: fig. 2) labelled an opening in this position in *Ectosteorhachis* as

the hypotic branch of nerve VII. A foramen occurs in the same position in *Gogonanus* as well.

Perichondral Covering of the Braincase. The posterior part of the braincase enclosing the brain stem is narrow, domed and with a floor that is distinctly arched from side to side. Posteriorly three to five foramina exit ventrolaterally on each side (Fig. 35). Presumably, these carried small vessels and spino-occipital nerves, including perhaps fibres of nerve XII. They undoubtedly connect with at least some of the several small foramina that open externally on the occiput on either side of the foramen magnum. Anteriorly, the roof of the braincase is composed of gently wrinkled perichondral bone forming a shallowly inclined surface that extends back posteriorly to the supra-otic cavity (Figs 32A; 36A,B; 37).

As QMF21085 shows, at the level of this cavity the roof of the braincase rises abruptly and steeply, enclosing a deep pocket subdivided at the midline by a low ridge but no bony median septum. Although insufficient exposure of the region makes description difficult, it must have contained high pouches for the superior sinuses of the otic cavity and the endolymphatic sacs. Those of the two sides must have been in contact medially. Posteriorly from each of the pocket subdivisions, the foramen identified above as pertaining to the endolymphatic duct opens to the dorsal surface of the occipital shelf (Figs 38A,B; 39A,B). These spaces for the supra-otic cavities, the superior sinuses and the endolymphatic sacs, are very different in position and shape from those figured by Romer (1937) for *Ectosteorhachis nitidus*, and

we have no means of comparing them with *Megalichthys hibberti*.

Adjacent to the intracranial joint, the most anterior part of the roof of the braincase in the otico-occipital unit is marked by a distinct subcircular depression, sometimes partly encircled by a horseshoe-shaped groove (Figs 32A; 36A; 37) (see QMF21084, 21085, 21109); two larger, shallower, and less distinct depressions are located posterolaterally to this. According to Jarvik (1980: fig. 89B) these depressions in *Eusthenopteron* probably reflect the position of the optic lobes in the roof of the brain. We see no reason to dispute this interpretation.

Three conspicuous foramina mark the passage of major nerves and a vein through the braincase wall into the trigemino/facialis chamber. Of the three, the anteriomost foramen is the largest and penetrates the wall more dorsally than the others (Figs 32B,C; 33; 41). It is the opening for the maxillary and mandibular branches of nerve V, corresponding in position to the same foramen in *Ectosteorhachis* (Romer, 1937: fig. 2; Thomson, 1967: figs. 1, 3). Immediately posterior to this, a second foramen opens at the end of an oblique tube that passes forward through the braincase wall. This foramen is well shown on QMF21085, and it carried the anterior lateralis branch of nerve VII in Romer's (1937) terminology, and the opthalmicus superficialis ramus of VII in Thomson's terminology (1967); we prefer Thomson's terminology. Posteriorly from that point our specimens are damaged, and the surface where the oticus branch of nerve VII would be expected to have left the chamber wall has been impaired (Romer, 1937; Thomson, 1967). We have not been able to identify its foramen. Below and slightly posterior to the exterior ophthalmicus superficialis foramen, on QMF21085, a third, large foramen is present (Figs 32B,C; 33). Its ventral edge is not preserved in this specimen, but its dorsal rim is ventral to a thick horizontal ridge that in turn is ventral to the previously described nerve foramina. This opening marks the exit of the middle cerebral vein immediately prior to its junction with the jugular vein as the latter passed posteriorly in the jugular groove (see Romer, 1941: 153-154). The middle cerebral vein is a major drainage vessel of the endocranial cavity, and the size of this foramen in *Cladarosymblema* is in accord with its significance.

By contrast, in *Gogonasus*, there are only two major foramina anteriorly in the wall of the trigemino/facialis chamber, an anterior large one, for the mandibular and maxillary branches of

nerve V, and a smaller posterior one, for the anterior lateralis VII. Both are at the same level in the braincase wall, as in *Cladarosymblema*. Also as in *Cladarosymblema*, they are situated dorsal to a longitudinal ridge that extends along the inner wall of the braincase. The more extensive preservation of *Gogonasus* shows, however, that this ridge is simply the dorsal edge of a broad groove that ran along the internal surfaces of the cranial cavity near its floor. We suggest that this groove marks the limits of a lateral venous sinus, and that the middle cerebral vein drained from this sinus through the foramen in QMF21085, below the level of the foramina for the rami of nerve V and VII. In *Gogonasus*, however, there is no foramen here for the middle cerebral vein. Instead, there is a conspicuous notch lined with periochondral bone further forward at the anterior edge of the braincase wall; this notch also terminates the ventral groove. We suggest that these relations indicate that in *Gogonasus* the middle cerebral vein exited anteriorly, to join with the jugular vein within the soft tissues of the intracranial joint, anterior to its position in *Cladarosymblema*, *Ectosteorhachis* and, by implication, other megalichthyids.

Romer (1937) and Thomson (1967) indicated that the profundus branch of the trigeminus (nerve V₁) left the braincase in *E. nitidus* through soft tissue between the two units, and we have no evidence to indicate that the nerve followed a different course in *Cladarosymblema*. Dorsal to the level of the nerve foramina, the braincase wall of QMF21085 is marked by a series of parallel, irregularly vertical ridges (Fig. 32C). These probably reflect the attachment of palatal levator muscles.

In *Eusthenopteron*, Jarvik (1980) has identified a depression on the posterior wall of the trigemino/facialis chamber, adjacent to the spiracular notch in the dermal roofing bones, as indicating the position of the spiracular diverticulum; Thomson (1967: fig. 1) shows the spiracular diverticulum in the same position in *Ectosteorhachis*. One of our specimens of *Cladarosymblema*, QMF21085, has a shallow depression here bordered by two pairs of blunt, knob-like processes, one above the depression, the other below; none of our other specimens is preserved in this region. In *Gogonasus*, a shallow depression occurs in a somewhat more mesial position on the posterior wall of the chamber, beneath the foramen for the occipital artery or its branches. In keeping with Jarvik (1980) and Thomson (1965, 1967), we suggest that this depression marks the position of the spiracular di-

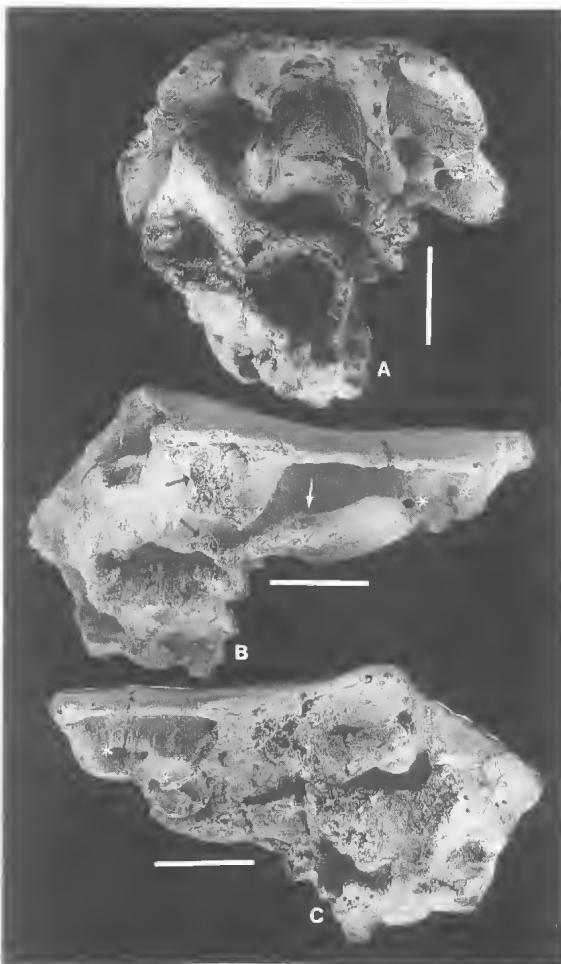


FIG. 32. *Cladarosymblema narrienense*. A-C, anteroventral, and right and left lateral views of incomplete otico-occipital unit, QMF21085. In A, white arrows indicate foramina for the occipital artery in the anterior wall of the fossa Bridgei. In B, black arrows indicate the dorsal and upper part of the ventral hyomandibular attachments. White arrow indicates position of hypotic branch of nerve VII as it exits the endocranum. Parts of both the left and right walls of the braincase have been broken away so that the foramina on the left side of the braincase are more clearly exposed than those on the right. The photographs have been made to show these to advantage. Asterisks indicate positions of nerves and vessels on the left side of the braincase, viewed from inside the braincase in B and from outside in C. (See Fig. 33 for interpretation.) Scales: 10mm.

verticulum in both *Cladarosymblema* and *Gogonasus*.

In our specimens of *Cladarosymblema*, the saccular region of the otic capsule is not well-preserved and we are unable to determine the

configuration of the sacculus, utriculus and the relevant nerves. However, in QMF21084 it is possible to infer that the sacculus is not as extensive laterally as the sacculus illustrated by Romer (1937: figs 8, 9) for *Ectosteorhachis*, because it has to fit within the confines of the surrounding bones. Only a fragment of the utriculus is represented on the same specimen, and it must have been only a slight swelling. The horizontal and posterior vertical semicircular canals are best shown on QMF21085 (Fig. 34A), but they cannot be seen in their entirety. The vertical canal must have been more depressed than semicircular to fit beneath the roofing bones.

HYOID SERIES

Hyomandibular. One well-preserved right hyomandibular, QMF21107, is known from *Cladarosymblema*. It resembles that of *Eusthenopteron* in general but differs significantly from all available descriptions and figures of that element in several ways. Among the more important of these is its display of features that Jarvik (1954) described for the *Eusthenopteron* hyomandibular, but which Smithson & Thomson (1982) had not found during their more recent review. Despite its importance for the study of the origin of tetrapods, the bone is poorly known in osteolepiforms, with extensive descriptions only for *Eusthenopteron* and *Ectosteorhachis* (Eaton, 1939; Romer, 1941; Westoll, 1943).

The hyomandibular of *Cladarosymblema* is deeper relative to its length than that of *Eusthenopteron* (compare our Figs 43 & 44 with Jarvik, 1980: fig. 107) but, as in the older genus, it is narrow mesiolaterally; that of *Ectosteorhachis* is more rod-like. Although relatively large when compared with the tetrapod stapes, the hyomandibular appears to have been constructed of delicate vesicular bone covered by a thin, dense layer of perichondral bone on all its external surfaces except the anteroventral extremity. This light construction of the hyomandibular contrasts with the much denser bone of the lateral walls of the braincase in the area of articulation of the hyomandibular to the side of the skull. In that sense, the hyomandibular of *Cladarosymblema* is not a massive bone at all (see Romer, 1941: 150).

At its proximal end, QMF21107 shows two vertically ovoid facets of unfinished bone, the dorsal and ventral processes; the dorsal process is slightly deeper and anteroposteriorly narrower than the ventral process. Between the two processes is a thin lamina of perichondral bone (Fig.

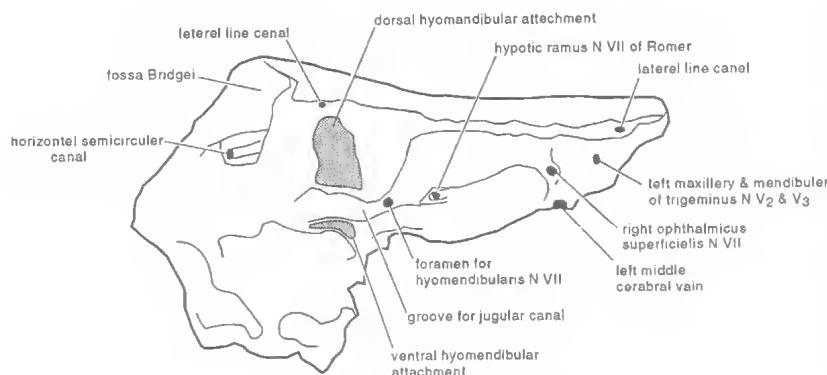


FIG. 33. Outline drawing of the view shown in Fig. 32B.

43H), much as described by Romer (1941) for *Ectosteorhachis*, and Smithson & Thomson (1982) for *Eusthenopteron*.

Only one specimen in our collection, QMF 21085, clearly preserves the articulating surfaces of the skull that supported the hyomandibular (Fig. 32B; 33). The large dorsal facet lies on the lateral wall of the fossa Bridgei and extends from just beneath the skull roof to the dorsal margin of the jugular canal. The lower facet borders the jugular canal ventrally, but only the dorsalmost extent of this facet is preserved on our specimen. Nonetheless, it is evident from QMF21085 that in *Cladarosymblema* much of the jugular canal between these facets was open laterally, with the lateral commissure being limited to a more anterior position. In this respect, *Cladarosymblema* closely resembles both *Ectosteorhachis* (MCZ6499) and *Gogonasus* (ANU49259), in which the lateral commissure is limited to a thin strip of bone entirely anterior to the hyomandibular; in both these genera also, the jugular canal is open laterally at the level of the hyomandibular.

The dorsal margin of the hyomandibular of *Cladarosymblema* continues distally in a nearly horizontal direction for slightly more than half of the total length of the bone (Figs 43E,G; 44A,C). This margin is crossed by a well-developed dorsal groove that obliquely traverses the hyomandibular, and then continues down on to its anterolateral side (Figs 43E,F; 44A-C). The perichondral bone that lines this groove is more dense than that of the adjacent surfaces, which appear somewhat spalled on this specimen, and this feature, combined with the geometry of the groove itself, can leave no doubt that this structure was real, and that it has anatomical significance. As final confirmation, the groove has its obvious counterpart in *Gogonasus* (Fig. 45A,B,E), where it has the

same orientation as in *Cladarosymblema*.

Jarvik (1954) described a groove comparable with this in the hyomandibular of *Eusthenopteron*; he believed the groove carried the ramus hyoideus of the hyomandibular trunk of nerve VII. In the *Eusthenopteron* hyomandibulars available to them, however, Smithson & Thomson (1982) found the dorsal

groove to be variable in its occurrence, not recognized at all on one individual (the 'Gosselin' skull), but 'reasonably distinct' on the right side of ROM1234, a braincase with associated hyomandibulars. Smithson & Thomson (1982) concluded that the groove Jarvik had described was of no significance. They argued that its more medial parts were an artifact of preservation, the lateral parts were variable in occurrence (as already noted), and that in no living fishes does the hyoid ramus loop dorsally over the hyomandibular. However, our specimens indicate that Jarvik was correct, at least in his determination that the dorsal groove is an anatomically real feature of the hyomandibular in osteolepiforms. Indeed, the hyomandibular of *Gogonasus* shows that not only is the dorsal groove present, but that it continues down on to the anterolateral face of the bone, towards a conspicuous depression (see below) adjacent to the distal opening of the hyomandibular canal (Fig. 45A,B). We have observed that in other parts of the cranial skeleton of *Cladarosymblema*, impressions of nerves and vessels into bone surfaces are highly variable between individuals; we therefore do not accept that the absence of a groove in some specimens of *Eusthenopteron* is valid evidence that no structure crossed the hyomandibular dorsally. The presence of this groove in specimens representing three divergent osteolepiforms, *Eusthenopteron*, *Cladarosymblema* and *Gogonasus*, indicates that it was a feature of primitive osteolepiforms.

But what did it carry? If Jarvik's (1980) argument that it carried the hyoid nerve is to be accepted, one must confront the objection by Smith & Thomson that no modern fish species shows a similar course for this nerve. Alternatively, the groove may have carried a vessel, but

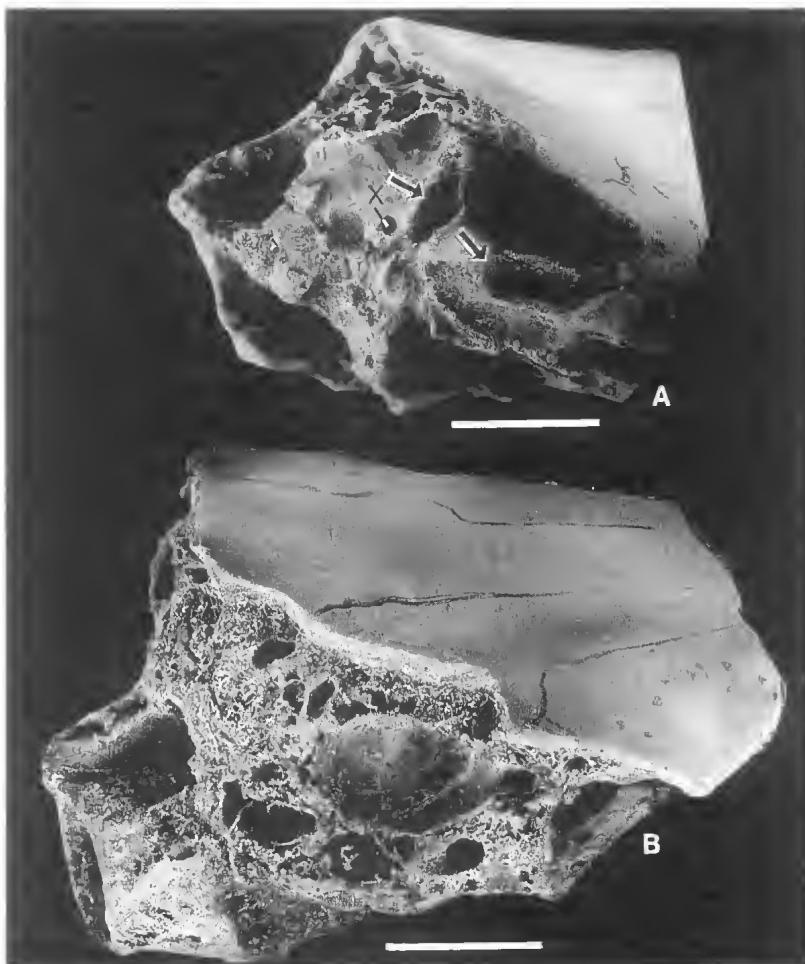


FIG. 34. *Cladarosymblema narrienense*. A, posterolateral view of an otico-occipital unit showing the wall of the endocranum, QMF21085; arrows indicate vertical and horizontal semicircular canals, and X indicates the foramen for the posterior lateral line nerve. (See also Fig. 35.) B, lateral and slightly posterior view of QMF21084, which has an eroded posterolateral wall of the endocranum exposing several otherwise unknown features. For explanation see Fig. 35. Scale: 10mm.

similar impediments apply to this interpretation. The only vessel that suggests itself as relevant is the efferent hyoid artery. In *Eusthenopteron*, according to Jarvik (1980: fig. 107), this artery entered the hyomandibular accompanying the hyomandibular nerve. But if it followed the dorsal groove, the artery arose in a mesial position at its proximal extremity (behind the hyomandibular) coursing to a lateral position distally, in front of the hyomandibular. The skull of *Gogonasus* (see ANU49259; WAM86.9.661) provides additional evidence bearing on this problem. Especially well defined on the right side, is a short,

shallow groove that leaves the posterior opening of the jugular canal dorsally and curves towards the dorsal facet of the hyomandibular. When the hyomandibular is manually articulated to the skull in this specimen, the most proximal part of the hyomandibular groove is brought immediately adjacent to the groove from the jugular canal. Clearly, the two grooves reflect the course of the same structure, either a vessel or a nerve; the available evidence is inadequate to determine which.

Along the dorsal edge of QMF21107, distal to the dorsal groove, is a depression exposing vesicular bone (Figs 43E,F; 44A,B); in life this was probably continued dorsally in cartilage. A low bony process arises in this same position on the hyomandibular of *Gogonasus*, and partially borders the dorsal groove mesially. Beyond this depression in *Cladarosymblema*, the dorsal margin of the hyomandibular abruptly descends obliquely to the most distal extremity of the bone as in *Ectosteorhachis* (Romer, 1941: fig. 1). The dorsal margin is not smoothly curved as is

shown in Smithson & Thomson's (1982) figure of the *Eusthenopteron* hyomandibular. In *Gogonasus*, the descent of the dorsal margin distally is also abrupt, but not at as steep an angle as in *Cladarosymblema*. The most proximal parts of the descending dorsal edge on QMF21107 are widened and enclose an elongate depression of vesicular bone that lacks a perichondral covering. Here, too, this area in life must have been capped or otherwise continued in cartilage. A comparable surface is seen on the hyomandibular of *Gogonasus* (Fig. 45). This depression clearly corresponds to what Romer (1941) has identified

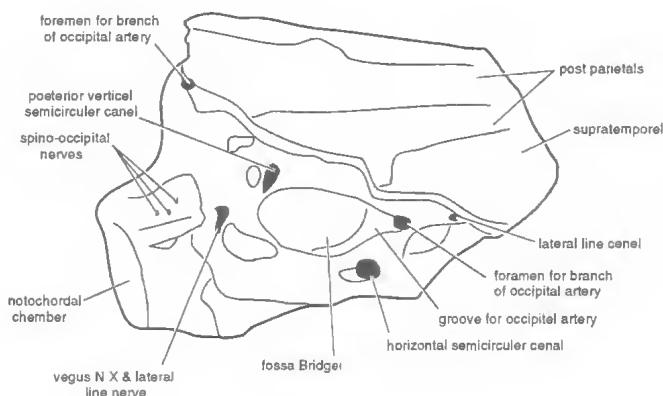


FIG. 35. Key to Fig. 34B.

as the opercular process in the hyomandibular of *Ectosteorrhachis*, and Jarvik (1954) in *Eusthenopteron*. However, Smithson & Thomson, together with Westoll (1943), saw no process or other structure in that position. Its presence in *Cladarosymblema*, *Gogonasus*, and at least some individuals of *Eusthenopteron* (its apparent absence from other individuals may well be an artifact of preservation) implies that a connection between the hyomandibular and opercular is primitive in osteolepiforms. Indeed, the internal surface of the opercular of *Cladarosymblema* appears to have an attachment surface in this position (see below). This is not surprising in view of the accounts of primitive fishes by Lauder (1980a,b; 1985).

Smithson & Thomson (1982) identified a preopercular process on the lateral side of the hyomandibular of *Eusthenopteron*, beneath the distal opening to the hyomandibular canal. Neither *Cladarosymblema* nor *Gogonasus* shows a process, tuberosity, or any other discontinuity of the surface here that might indicate an articulation between the hyomandibular and preopercular. In any case, an attachment between the preopercular and hyomandibular is unexpected on functional grounds. The preopercular is normally a fixed bone, whereas the hyomandibular is an integral component in the kinetic action of the skull, as Thomson (1967) has already shown.

Overall, the anterolateral side of the hyomandibular in *Cladarosymblema* is dorsoventrally convex. However, as mentioned above, it is marked distally by the deep depression that is adjacent to the lower opening of the hyomandibular canal. Similar features are present in the hyomandibular of *Gogonasus*. The

hyomandibular canal opens proximally on the posteromesial side, which is concave, at the end of a short deep groove that begins between the dorsal and ventral processes. When the hyomandibular is manually articulated with the skull in both *Cladarosymblema* and *Gogonasus*, this groove, and hence the hyomandibular canal, is in open continuity with the jugular canal passing mesially to it, with the lateral commissure occupying a more anterior position. This means that there is no bony separation between the two canals, and the hyomandibular nerve could turn directly into the canal at the

base of the hyomandibular. Whereas the posterior opening of the jugular canal appears to occupy this same relationship to the hyomandibular in *Eusthenopteron*, the lateral commissure extends further anteriorly and the fully enclosed parts of the canal are comparatively longer than in either *Cladarosymblema* or *Gogonasus*. All authors appear to agree that the hyomandibular canal carried the rami mandibularis externus and internus (chorda tympani), and we see no reason to conclude otherwise for *Cladarosymblema*.

The posteromesial surface of QMF21107 shows other features of interest, and at least some of these also occur in *Gogonasus*. Distal to the proximal opening of the hyomandibular canal on QMF21107, the more dorsal parts of the posteromesial face are occupied by an elongate depression having a well-defined ventral rim and a surface crossed by several short, irregular ridges (Figs 43G; 44C). A similar depression is seen in *Gogonasus*. This depression probably furnished the attachment area for the adductor hyomandibularis muscle, with its most ventral extent marked by the ventral rim. Romer (1941: fig. 1) believed that this groove in *Ectosteorrhachis* marked the course of the vena capitis lateralis (=jugular vein), but manual articulation of the hyomandibular on the skull of *Gogonasus* shows that the jugular canal is too mesial and curves in too marked a ventral direction opposite the hyomandibular for the groove to reflect the passage of the vein. Also occurring within the adductor depression, but well set off distally from the opening of the hyomandibular canal, is a short oblique groove that leads to a narrow canal. From the angle of the orientation of this groove, the canal probably merged with the hyomandibular



FIG. 36. *Cladarosymblema narriense*. A-B, anterior and ventral views of QMF21084. Note particularly the foramina for the lateral line canals lateral to the articular processes in A (arrows), and the foramina for the palatal branch of nerve VII (arrows) in the flat triangular plate for the attachment of the basicranial muscles, in B. For interpretation see Fig. 37. Scale: 10mm.

canal within the hyomandibular; there is no alternative exit visible externally. The left hyomandibular of *Gogonasus* shows what is undoubtedly the homologous foramen, but in that specimen it is located closely adjacent to the proximal entrance of the hyomandibular canal, being separated from it by only a narrow bridge of bone; this bridge has been broken away on the right hyomandibular of the same specimen. Jarvik (1954) and Smithson & Thomson (1982) illustrated a foramen in this position in *Eusthenopteron*; Jarvik (1954) identified it as a foramen for a vein, and Smithson & Thomson (1982) left it unidentified. Its undoubted occurrence in *Eusthenopteron*, *Cladarosymblema* and

Gogonasus indicates that it is a real feature, a conclusion supported by the groove associated with it in QMF21107. Perhaps as Jarvik (1954) suggested, it carried a vein; but to us it seems more probable that it carried a nerve which, from its position on the mesial side of the hyomandibular, would have been the opercularis ramus of nerve VII. In *Ectosteorhachis*, Romer (1941: fig. 1) illustrated a foramen for the opercularis nerve distally on the side of the hyomandibular; there is no foramen in this position on QMF21107.

On QMF21107 beneath the ridge marking the ventral limit of the adductor hyomandibularis musculature is a long narrow groove that extends from the ventral process to the lateral edge of the bone, beneath the opercular process (Figs 43G; 44C). Romer (1941) identified a groove in this position in *Ectosteorhachis* as indicating the path of the pretrematic branch of the glossopharyngeal (IX) nerve. Smithson & Thomson (1982) reported that this groove is absent in *Eusthenopteron*. It is present and well defined in both *Cladarosymblema* and *Gogonasus*, although it is very nearly straight in *Gogonasus*. No other conspicuous features are present on the mesial face of the hyomandibular in either *Cladarosymblema* or *Gogonasus*.

Smithson & Thomson (1982) identified a distal surface that could mark the attachment of the stylohyal, but neither QMF21107 nor the *Gogonasus* hyomandibulars are well enough preserved in this area to provide any additional information that might confirm this articulation or allow further elaboration of its features.

In the osteolepiform hyomandibular, the hyomandibular canal crosses from its mesial, proximal entrance to a lateral and distal exit, opening in a deep depression (see above) towards the distal end of the bone. Along the dorsal side of this depression in *Cladarosymblema* (Fig. 43E) is a system of short irregular ridges and pits that served as attachment surfaces for the protractor hyomandibularis muscle (Jarvik, 1954; Smithson & Thomson, 1982). In *Gogonasus*, this depression is shallower on the right hyomandibular than on the left, but on both there is a well-developed complex of irregular surfaces consistent with muscle attachment (Fig. 45A,F). The right hyomandibular of the *Gogonasus* specimen has particularly well-preserved surfaces in this area. The specimen clearly shows the dorsal groove continuing down the lateral face of the bone into the distal depression, running proximally and ventrally to the scars for the protractor muscle.

The hyomandibular canal carried the hyomandibular nerve; whether it was divided into external and internal mandibular rami within the canal or only after exiting the canal, is not known. On QMF21107 the canal has been cleared of matrix; direct inspection of its walls gives no indication of a subdivision such as would be expected if the canal carried two major nerve rami within it. More distally, but still within the confines of the hyomandibular, it appears that the nerve split, following the pattern seen in other osteolepiforms: the more dorsal trunk, presumably the ramus internus, left by passing under a small bridge of bone, incomplete on our specimen; the other, the ramus externus, passed over a raised platform or pad of bone distally on the hyomandibular before continuing onward to the lower jaw (Fig. 43E). These features are not preserved on the *Gogoniasus* specimens; Smithson & Thomson (1982) report a distal bridge of bone in the same position as that on QMF21107, but it is complete.

Urohyal*. Laterally compressed bones (QMF26573, 26574 and 26576) that have a short anterior stem and a blade-like posterior section, represent the urohyal of this species (Fig. 43A-D). In making this interpretation we have taken into account that these bones are obviously from the midline of the animal; they are cartilage bones with a thin perichondral layer on the lateral, ventral and dorsal surfaces, and exposed dense endochondral bone at the anterior and posterior ends; the bone texture is very similar to that of a large number of visceral bones found in the same etches; and the bones have a shape similar to that of the urohyal in *Eusthenopteron foordi* (Jarvik, 1980: fig. 112D). The anterior stalk is about half the length of the bone, is elliptical in cross-section with the long axis of the ellipse vertical. The posterior blade is approximately two-thirds as high as long, has a truncated posterior end and a variably shaped anterior end. The posterior edge is truncated, and low on its surface an isthmus of perichondral bone separates a large dorsal and a smaller ventral surface to which other cartilaginous elements were attached. Its posterior end is less angular than that of the urohyal of *E. foordi*. Both the ventral and dorsal surfaces of the blade are distinctly flattened. Jarvik (1980: vol. 2, figs 109; 117) showed the geniohyoideus and hyogenioglossus muscles attached to the blade of the urohyal in *Eusthenopteron*. The blade in *C. narrienense* shows strong concentric ridges that we interpret as reflecting growth stages; they are not interrupted as would be expected if muscles

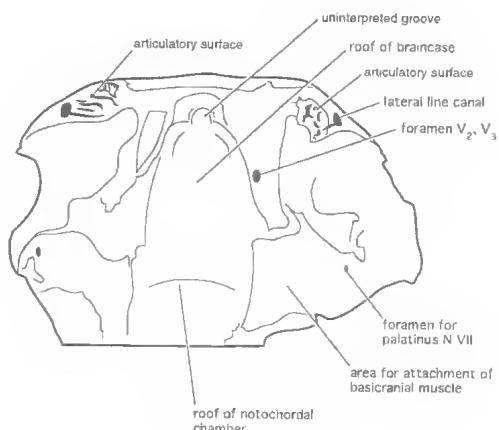


FIG. 37. Labelled key to Fig. 36A.

were attached to these surfaces. So far as we are aware, no other megalichthyid urohyal is known.

MANDIBLE

We have more than 20 mandibular elements, some preserved as more or less complete rami, but the majority fragmentary (Figs 46-51; 54-56; 57A-G). Nine specimens have the posterior end at least partly preserved, and of these eight provide significant information on the glenoid fossae and the foramina and grooves in the vicinity of the articulation. The smallest complete specimen is only about half the size of the largest. The fractured specimens are very valuable because they provide information on the lateral line canals and the grooves in the open spaces within the jaw. One specimen, QMF31861, consists of the external dermal bones from the posterior extremity with part of the articular still attached, and a second one, QMF21100, has the same posterior part preserved and extends a little further anteriorly. These specimens have been particularly useful because they exhibit the courses of the canals from the exterior into the Meckelian space as well as the lateral line entry point. This wealth of material provides the opportunity for a discussion of variation that is unusual for the osteolepiforms.

General Form. In lateral profile (Figs 46A; 48; 49A,D) the mandible varies in height systematically along its length, the minimum height / maximum height ratio being c.0.75. Posteriorly the dorsal edge turns downwards as it does in *Megalichthys*, but unlike some specimens of that genus, the ventral edge invariably turns upwards towards the posterior end of the mandible. The maximum mandibular height is a short distance

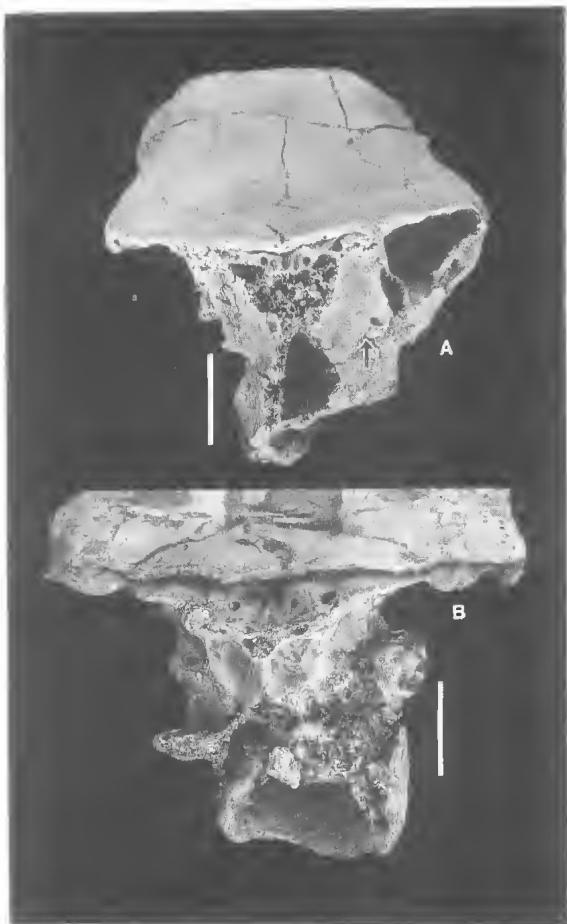


FIG. 38. *Cladarosymblema narrienense*. A, B, posterodorsal views of two otico-occipital units, QMF21084 and 21094. The vagus nerve X foramen, indicated by an arrow, is hidden beneath a ledge of bone. (For lateral view of A see Fig. 34A, and for its interpretation, Fig. 39.) Scale: 10mm.

in front of the glenoid articulation and not near the anterior end of the jaw (cf. the mandible of *Gogonasmus* in Fig. 52A,B). Towards the anterior end, most individuals show an embayment in the ventral edge, its depth varying from specimen to specimen. Presumably it allowed for the articulation of some of the submandibulars, but, as is shown below, it also made space for the passage of a nerve and an artery. In dorsal view, the curvature shows an increase anteriorly (Figs 46C; 47B; 49C).

A submandibular furrow of variable depth lies along the ventral edge of the mandible just inside the external dermal bones. This furrow has two distinct parts, an outer surface on the infradentaries for the articulation of the submandibulars, and

an inner deeply concave surface along which traversed nerves and vessels which are discussed below. The double nature of this furrow is well shown in Figs 46D and 49E.

External Dermal Bones. The external dermal bones are all cosmine-covered and are usually smooth. However, two individuals, QMF21101 and 21090 (Fig. 49A,D, respectively), display areas of resorption. In the former, patches where the cosmine has been removed are obvious; the latter has less continuous areas of resorption, and some of these contain irregular blisters of new cosmine that rise above the general surface. These blisters resemble some of the new-growth cosmine on the scales, the significance of which will be discussed below when dealing with scale morphology.

The sutures between the external dermal bones cannot be recognised consistently on any specimens, irrespective of their size, thereby creating a major problem for us when comparing *Cladarosymblema* with other species. On most specimens, a clear incision is observed approximately in the position one would expect to find the suture that separates the dentary from the infradentaries, but it becomes obscure anteriorly. Within this incision a row of pores of the same kind as those that occur in other pit-lines can be seen, so there is no question that the incision is a pit-line and not a suture. This is in accord with previous work (Watson, 1926; Jarvik, 1942, 1980; Borgen, MS), but the pit-line has been considered by most workers to lie along the suture between the dentary and the infradentaries. However, X-radiographs of three specimens from which the internal bones have been removed, show that most of the ventral edge of the dentary lies dorsal to the pit line and diverges from it (Figs 54-56). Jarvik (1980) recorded that the dentary in *Eusthenopteron* is overlapped by the infradentaries, and it is clear that such an arrangement could cause difficulty in the interpretation of X-radiographs. Broken edges of mandibles of *C. narrienense*, however, show no sign of such an overlap. This implies that the standard interpretation of *Megalichthys* (Watson, 1926; Borgen, MS) needs to be re-examined, a process that can be undertaken only by sectioning or X-radiography.

The sutures between the infradentaries are not obvious on the external surface of any of our specimens, but two, QMF21088 and 21030, show rows of peculiar short oblique *en echelon* markings in the approximate position of the angular/surangular and the postsplenial/angular

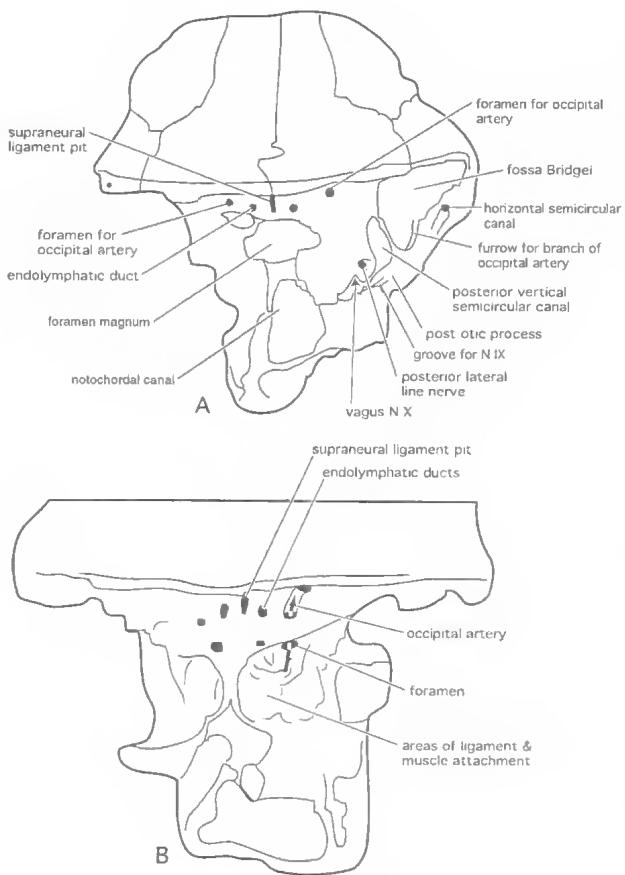


FIG. 39. Labelled key to Fig. 38.

sutures; a third, QMF31867, has what are probably incomplete surangular/angular and angular/postsplenial sutures (Fig. 55A: arrows). The interpretation of these markings is not clear, although on one specimen, QMF21089, they have been observed in line with a definite suture, and might therefore be thought to mark an extension of a suture. However, such a view is untenable, because such markings have also been found on a lateral gular (QMF26543) where they are obviously not related to sutures. X-radiographs show the centres of ossification of the infradentaries, and these can be confirmed on the internal surfaces of some bones; the boundaries between these bones can be defined with some confidence by the joint use of X-rays and radial markings around the centres of ossification on the bone interiors. The very posterior position of the centre of ossification of the surangular is a remarkable

feature, as is the great size of that bone. Note that we have been unable to find the boundary between the splenial and postsplenial. This does not mean that we consider the two bones to be fused, but rather that the suture cannot be seen on any of our material. The most probable reconstruction of the external dermal bones is given in Fig. 48.

The horizontal pit-line is well developed on all specimens. It rises to, or almost to, the dorsal edge of the mandible just posterior to its highest point. From there it turns posteroventrally parallel with the edge of the cosmine, although it shows some minor flexing in some specimens. This line isolates a cosmine-covered strip from which a low naked blade rises up against the anterolateral wall of the articular (Figs 46A; 49A,D). In *M. hibberti*, Watson (1926: fig. 37) and Borgen (MS) record marked deflections of the horizontal pit-line where it meets the sutures between the infradentaries. No such deflections are present in *C. narrienense*, in which the line is straight or only gently flexed.

A vertical pit-line is situated towards the front of the mandible, approximately in the same vertical plane as the anterior coronoid tusk. It is never straight, but stands vertical in its lower course from the ventral edge, bending

forwards to a variable extent towards its upper edge in different specimens (Figs 46A; 48; 49D). The extent of the bending is not correlated with the size of the specimen. On several specimens a group of special sensory pores lies either slightly in front of the vertical pit-line or straddling it. Where this group has not been observed, its absence is probably the result of cracking or abrasion.

Small teeth occur along the dentary from a point just behind the anterior end of the adductor fossa almost to the median symphysis. The crest of the dentary is formed of finished bone with the cosmine turned inwards slightly, and the teeth stand inside this edge at a somewhat lower level. The teeth vary little in size, are turned slightly inwards, and are too poorly preserved to determine their replacement pattern. Inside the tooth row along most of its length, there is only a very narrow shelf against the coronoids. Lateral to the median symphysis, however, the dentary thick-

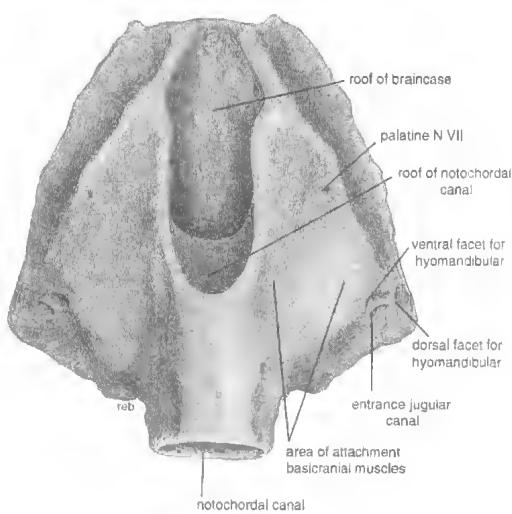


FIG. 40. *Cladarosymblema narrienense*. Reconstruction of the otico-occipital unit in ventral view, based on all available specimens.

ens and widens to form a wider shelf, which carries a tusk and one or two pits (Figs 46C; 47B; 50D,E; 57A-E). As the dentary shelf widens, it carries a distinct groove that continues around the front of the jaw anterior to the parasympathetic plate. The row of small teeth that runs along the dentary is usually absent in front of the tusks, but occasionally the teeth in the row are only reduced in number (Fig. 57A,B,D).

The tusks are strongly folded at their bases, and their replacement pits have radially arranged ridges of bone of attachment. The small marginal

teeth also have folded bases, but the folding is weak. Details of the teeth and tusks are given below.

The lateral line canal enters the mandible posterolaterally to the glenoid fossa, and at first runs anteroventrally. As it approaches the edge of the specimen, near the ossification centre of the angular, it turns through a gentle arc to run parallel with the ventral edge of that bone, from which it is separated by about 2-3 mm. The canal is deeply buried over its entire length. It opens to the exterior via a number of large pores that are scattered on either side of its course, but which occasionally form a single line. As shown on Figs 55C and 56, the arrangement of a second row of pores below the main canal is served by a more-or-less regular set of tubules. The canal and its pores are deflected around the embayment in the ventral edge previously mentioned. Anteriorly the canal joins its fellow below the large symphyseal area of vesicular bone. There is no oral branch of the canal in the surangular, and no sign of a pit-line on that bone. Owing to inadequacy of description and illustration, it is difficult to determine from the literature if this is an unusual feature in osteolepiforms.

The external dermal bones at the median symphysis are not complete, a space being left for a small bone between the ventral edges of the splenials, as in *Megalichthys hibberti*. This bone is always missing on our specimens, indicating that it was not fused into the dermal series. Such a feature is present also on *M. hibberti* (Watson, 1926; Borgen, MS), and we consider that it is a family character.

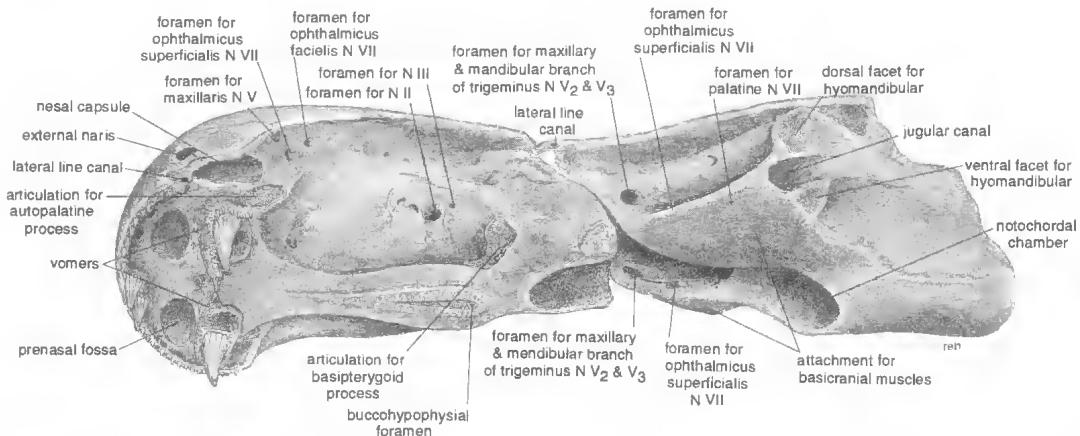


FIG. 41. *Cladarosymblema narrienense*. Labelled reconstruction of the assembled units of the cranium, showing the main features of the skeleton.

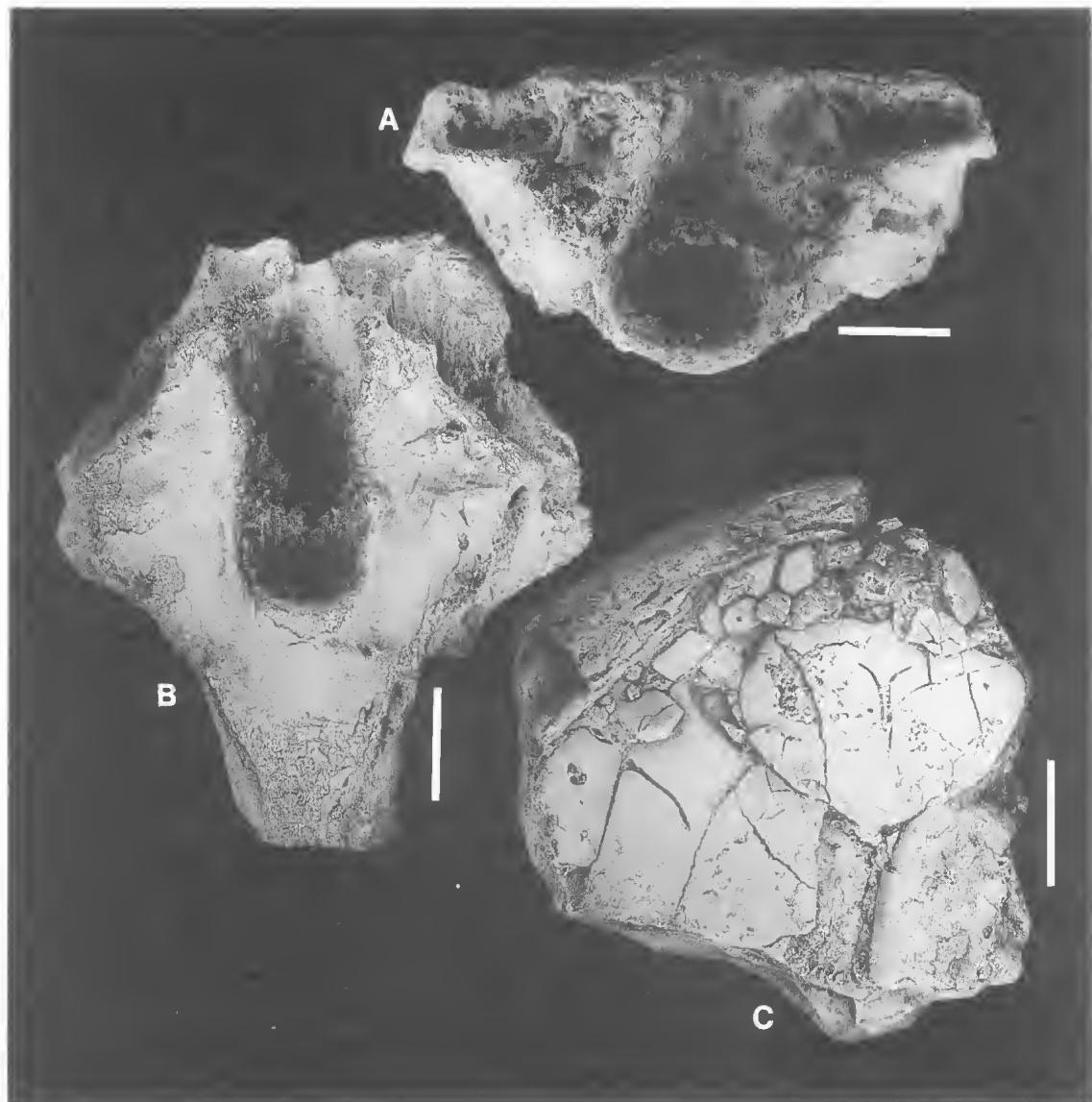


FIG. 42. *Ectosteorhachis nitidus* Cope. A,B, posterior and ventral views of MCZ6499, to show the depressed nature of the roof and the fossa Bridgei. C, ventral view of MCZ6999, part of a cranium showing the small submandibulars and the large median gular with lyre-shaped pit-lines particularly well. The right principal gular shows a very transverse anterior edge and a longitudinal crack. The apparent suture on its right side has not been identified. Scale: 10mm.

Articular and Meckelian Bones. The articular bone is thick and long, forming a sloping posterior surface to the adductor fossa (Figs 46C; 47B; 49C,F). This surface always carries ridges that presumably indicate the positions of attachment of the adductor muscles. The doubled glenoid fossa is hourglass-shaped, the two fossae being in contact (Figs 46B,C; 47B; 49C; 50B; 57F). They are floored by coarse vesicular bone, and must

have been invested with moderately thick cartilage in life. The transverse axis of the whole structure is not set at right angles to the sagittal line; the inner fossa is slightly anteromesial and ventral to the lateral fossa. The significance of this arrangement is discussed in the section on Functional Interpretation below. Ventrally, the articular is exposed between the surangular and the prearticular, its extent being well displayed on

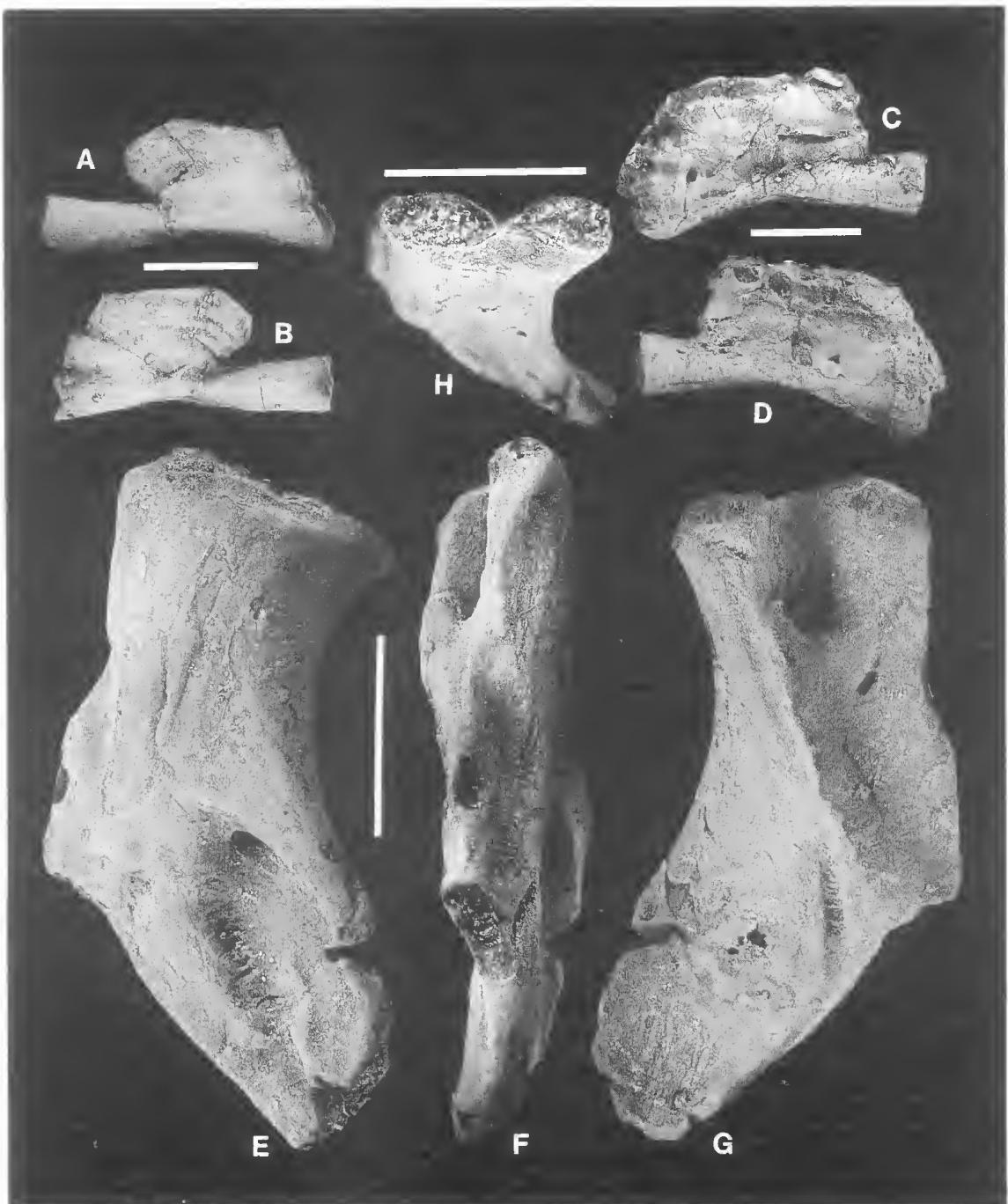


FIG. 43. *Cladarosymblesma narrienense*. A,B, left and right lateral views of urohyal, QMF26574. C,D, right and left lateral views of another urohyal, QMF26573. E, anterolateral. F, dorsal. G, posteromesial. H, anterior and slightly lateral views of right hyomandibular, QMF21107. Scale: 10mm.

QMF21088, 21000 and 21102 (Figs. 46D; 50C). It occupies most of the posteroventral surface of the mandible, and diminishes in width anteriorly,

where it forms the inner wall of the submandibular furrow. Approaching the symphyseal region it becomes more extensive (see below). The extent

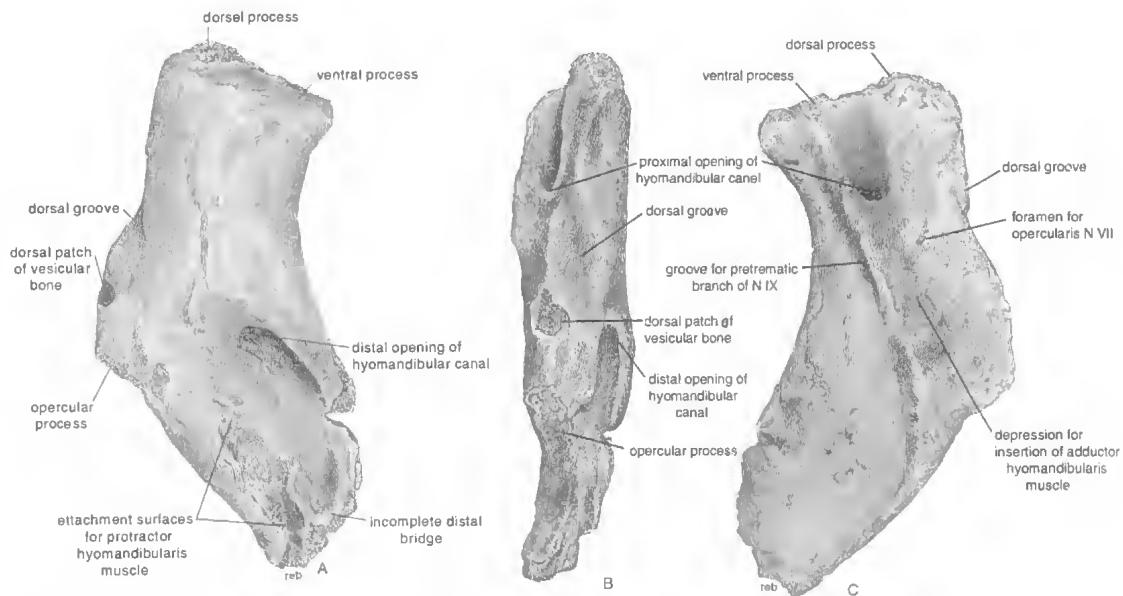


FIG. 44. *Cladarosymblema narrienense*. A-C, labelled reconstructions of the hyomandibular shown in Fig. 43, in anterolateral, dorsal and posteromesial views.

to which the articular is exposed on the posteroventral surface decreases with the age of the individual as the prearticular expands posteroventrally over its surface. A well-preserved mandible of *Gogonasmus* to which we have access, is similar to our material, and has the separate bones more clearly defined. In this specimen a narrow strip of Meckelian bone extends along the entire ventral surface between the prearticular and the infradentaries, expanding again beneath the parasymphysial plate (Fig. 52D). This pattern is very similar to that in QMF21088 and 21102, a well-preserved mandible of *C. narrienense* in which the surface of the Meckelian bone clearly carries signs of the attachment of the posterior intermandibularis muscle (Figs 46D; 50C). This attachment surface is widest posteriorly where it is well-rounded in outline, and it gradually tapers anteriorly.

A pronounced postglenoid process is present behind the outer glenoid fossa. The dorsal surface of the process is usually poorly preserved, but it is covered with slightly roughened perichondral bone in the best-preserved individuals (Figs 49 C,F; 50B). Analogy with *Latimeria* suggests that the anterior mandibulohyoïd ligament was attached to this dorsal face (Millot & Anthony, 1958: fig. 20), but Jarvik (1980: fig. 131) shows the depressor mandibulae muscle in the same position. On the ventral face of the post-glenoid

process two well-preserved specimens, QMF21087 and 31887, show a slightly vesicular surface (Fig. 46E), but many specimens show different amounts of bone removal, most of which is probably post-mortem (Figs 46D; 49B,E; 50C). However, in all specimens this ventral exposed scar-like surface is widest posteriorly and tapers anterolaterally. The scar is separated from the bone in front by a broad, deep and smooth furrow. A similar structure occurs in *Gogonasmus*, although in that form the postglenoid process is not as large, and the furrow in its ventral face is smaller (Fig. 52D). The nature of the tissue attached to this ventral scar is difficult to determine. It could be that the posterior mandibulohyoïd ligament encroached on the ventral face of the process, but this is far from certain and is in need of further research.

Internal Dermal Bones. The dominant dermal bone on the inner face of the jaw is the prearticular, which extends along almost its entire length but stops short of the median symphysis. It forms the internal rim and the mesial part of the anterior rim of the adductor fossa (Fig. 47A). As indicated above, the prearticular expands posteroventrally with increasing age of the specimen. At its anterior end it tapers to an acute angle where it is butted against the splenial and the Meckelian bone. Adjacent to the coronoids, it is slightly turned outwards to form a narrow flange. No-



FIG. 45. *Gogonasus andrewsae*. A-C, anterolateral, dorsal and posteromesial views of the right, and D, E, F, of the left hyomandibular of ANU49259, for comparison with Fig. 43E-G. Scale: 10mm.

where is there a deep gutter between the prearticular and the coronoids as there is in *Gogonasus* (Fig. 52C). Ventrally, the prearticular lies against a narrow band of Meckelian bone which makes a distinctive support for the junction with the infradentaries. In the Meckelian bone, between the prearticular and the infradentaries, lies a deep groove for the articulation of the submandibulars and for the transmission of nerves and arteries (Figs 46D; 47A; 49E; 50C). This groove is shallowest and narrowest posteriorly, and deepest below the posterior end of coronoid 1; more anteriorly it remains broad but its inner edge becomes less well defined.

On all specimens regardless of size, the dorsal edge of the prearticular is embayed in front of coronoid 1 to form a large slightly elongated pit, the anterior mandibular fossa. This fossa has a well-rounded base and is floored by Meckelian bone, whereas variable amounts of coronoid, parasymphysial and infradentary bone make up its walls. Projections of these dermal bones into the outline of the fossa are present in several specimens (Figs 46B; 47A; 50D,E; 51A,B). Presumably the fossa received the vomerine tusk, but that cannot have been its only function because it has a vascular supply suggesting the presence of soft tissues. Such soft tissues could have been either ligaments or muscles that would have served to give stability to the flexible symphysis. Running anterodorsally from below this fossa to a point on the symphysis below the parasymphysial plate is a sharp, prominent flange (Figs 46B; 51A,B), the significance of which is not well understood, although it could have been for muscle attachment.

A second fossa, the intercoronoid fossa, which is shallower and more elongated in outline than the anterior mandibular fossa, also significantly embays the prearticular. It occurs in front of, and below, the tusk and replacement pit on coronoid 2 (Fig. 50D,E), and is lined with relatively smooth prearticular bone.

A broad and deep longitudinal depression occurs along the posterior half of the inner face of the prearticular at about its mid-height. On most specimens this depression or groove is devoid of denticles, and so probably its surface was not exposed in the buccal cavity; it must have been embedded in soft tissue. On QMF31864, however, the groove shallows out rapidly anteriorly and does carry denticles of reduced size (Fig. 50D). On all specimens, above this groove there is a flattened surface that is highest at the rear and tapers gradually to a position below the tusk on

coronoid 2, where it is deflected slightly ventrad before fading away in front of the tusk on coronoid 1. Posteriorly this surface lacks denticles, but about one-third of the distance along the adductor fossa, small denticles appear and rapidly increase in number anteriorly. They normally disappear anteriorly where the flattened surface fades away, but on QMF31864 they continue almost to the anterior end of the bone (Fig. 50D). Along the crest of the surface between the anterior end of the adductor pit and the tusk on coronoid 2 lies a row of slightly enlarged denticles that gradually disappear both anteriorly and posteriorly.

Three tusks (or tusk pairs separated by a replacement pit) and associated pits are present on all specimens, and so it is assumed that three coronoids are the norm for the species. The coronoids are well developed, and although the sutures separating them are not visible on most specimens, they can be approximated on QMF21088, where they are markedly zigzagged (Figs 46B,C; 47B). The boundary with the dentary is indicated on some specimens by a suture that shows as a discontinuous line of elongated pits. Coronoid 3 forms much of the anterolateral rim of the adductor fossa, meeting the prearticular at the mid-width of the rim and curving backwards to form a strip attached along the lateral wall of the fossa. The surface of each coronoid is highest laterally, falls away medially and, in adults, carries longitudinal ridges, particularly on coronoid 2. The lateral edge of each bone forms a low crest of variable height, and this normally lacks a row of denticles. It is deflected around the tusks, but on one specimen (QMF21099), a cluster of 6-7 teeth, some of which reach the size of the smallest dentary teeth, surmount this deflected edge on the posterior side of coronoid 1, and on QMF21089 three or four similar teeth lie adjacent to coronoid tusks 2 and 3. These structures are referred to as teeth rather than denticles, because at least some of them on QMF21089 have folded bases.

The floors of the pits immediately adjacent to the tusks all show radial ridges, indicating that they have been the sites of former tusks which have been shed. The radial ridges conform with the folding of the labyrinthine structure of the tusks and represent bone of attachment, as is shown by the sections dealt with in Histology (below).

Apart from the tusks and the few clusters of small teeth described above, the coronoids on most specimens do not carry any dental tissue.

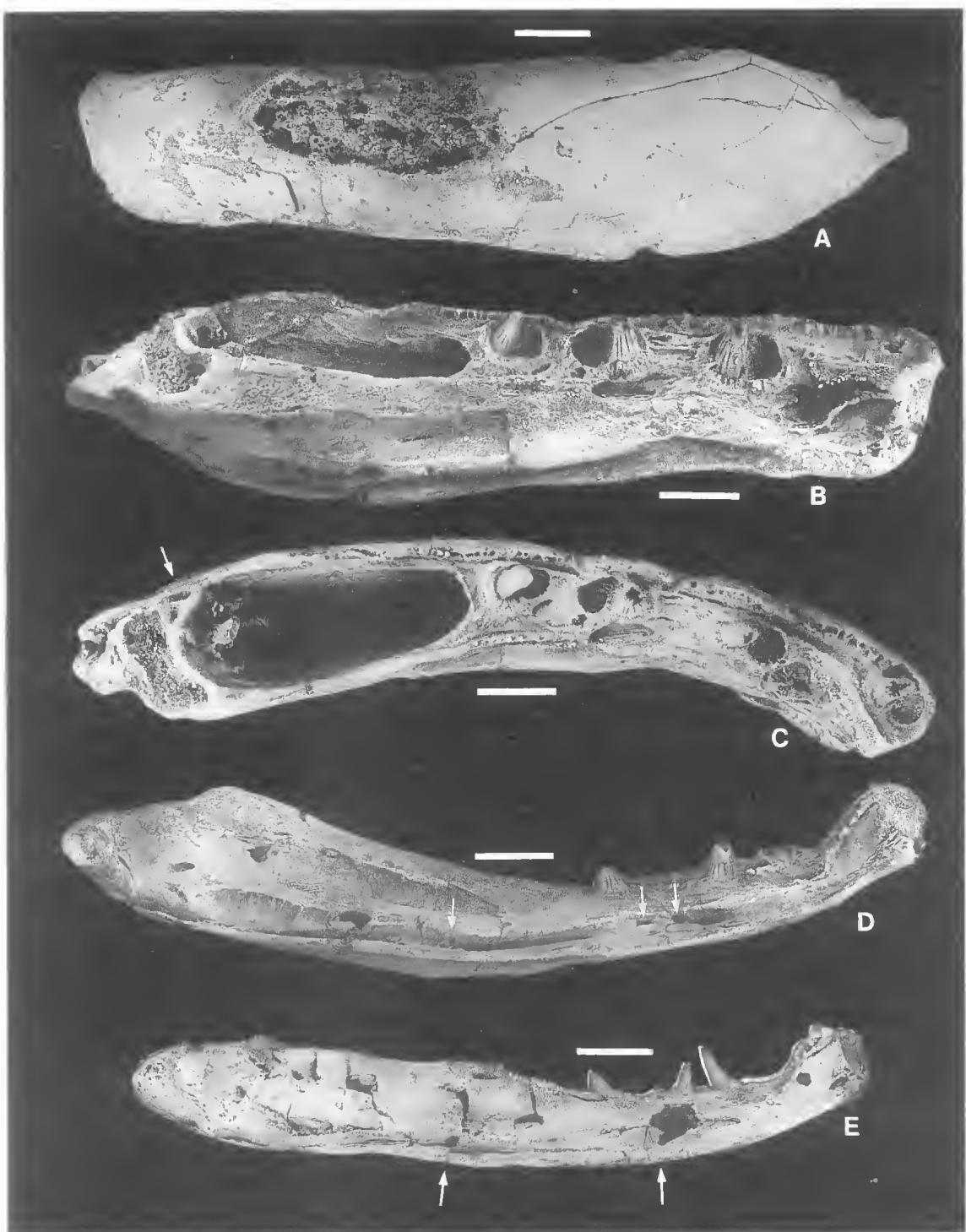


FIG. 46. *Cladarosymblema narrienense*. A-D, lateral, mesial, dorsal and ventral views of the best preserved left mandibular ramus, QMF21088. E, ventral view of left ramus, QMF21087. C. arrow indicates foramen for ramus mandibularis externus VII. D, E, arrows indicate major foramina in the submandibular furrow. Scale: 10mm.

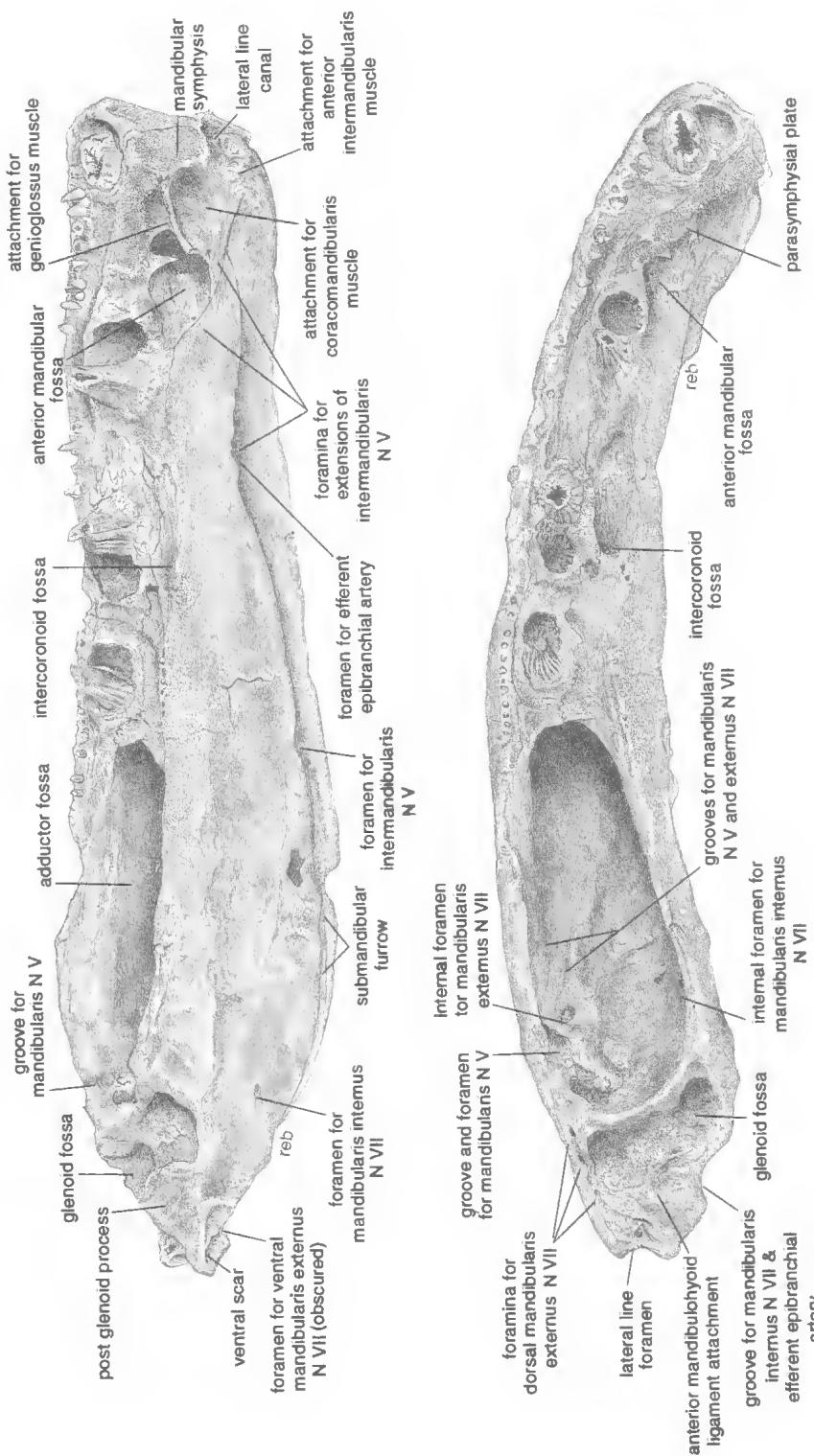


FIG. 47. A, B, labelled drawings of the specimen shown in Fig. 46B, C.

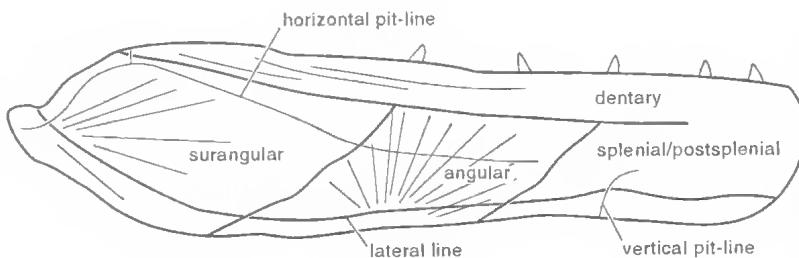


FIG. 48. *Cladarosymblema narrienense*. Outline drawing of external surface of a mandible showing bone boundaries, centres of ossification, pit-lines and lateral line canal. The radiation centres of the surangular and angular are derived from X-radiographs.

This arrangement is unlike that of *Gogonasus*, which is representative of the Osteolepididae in having a large number of denticles along the entire length of the coronoid crest, forming a continuous band with the denticles on the parasymphysial plate (cf. Figs 46C; 49C,F, with Figs. 52B,C).

In almost all instances the tusks and pits are paired, suggesting that as one is shed the adjacent pit gives rise to a new tusk. One distinctive specimen, QMF21087 (Fig. 50E), does not conform with this pattern. It has a tusk with two pits mesial to it on the dentary in front of the parasymphysial plate, two tusks with an intervening pit on coronoid 1, and a tusk on each of coronoids 2 and 3 separated by three pits, the middle one of which lacks radial ridges in its floor. Other variants usually involve paired tusks separated by a crowded pit on a single coronoid or on the front of the dentary. Around the bases of the tusks and the adjacent pits there is a raised ridge of bone, which in places shows a crenellated crest on the lingual side of the first and second coronoids (Fig. 46B,C).

Lying at the anterior end of the coronoid series is a transverse median plate with its lateral ends turned back above the pit for the vomerine tooth (Figs 46B,C; 47B; 50D,E; 57A-E). We refer to this as the parasymphysial dental plate, following Jarvik (1980). In some specimens the median edges of the left and right plates are seen to be finished, showing that they were not fused. This is an important point because the fact that the two rami always fell apart prior to burial, suggests that the symphysis was weak. That being so, the rami may have moved independently during mastication, a point supported by the strong double glenoid fossae (see Functional Interpretations below). The shape of the parasymphysial plate varies from specimen to specimen, but is always wide. In all except one small individual, its den-

ticulated surface bends posterolaterally and meets the coronoid 1 above the anterior mandibular fossa. The ventral edge of the plate lies on Meckelian bone, and its anterior side abuts the dentary. In most specimens the plate also extends ventrally to the oblique flange mentioned below, and in QMF21088, takes part in the formation of the dor-

sal part of that flange. The mass of vesicular bone that forms the main part of the symphysis (Figs 46B,D; 47A; 50D,E; 51A,B) and provides support for the central part of the plate, is composed of Meckelian bone that was probably completed by cartilage. In this *Cladarosymblema* is unlike the illustration and discussion of *Megalichthys hibberti* given by Watson (1926) and Borgen (MS), in which the prearticular is said to take part in the symphysis. The buccal surface of the parasymphysial plate is covered with small denticles; in some specimens it is bounded along the posterior edge by a row of significantly larger denticles.

Ventral to the parasymphysial plate, a sharp flange-like ridge curves obliquely downwards from the symphysis to the ventral edge of the anterior mandibular fossa (Figs 46B; 47A; 50D,E; 51; 58). Dorsally this ridge is formed of parasymphysial plate, but ventrally it is clearly Meckelian bone. On some specimens, this ridge has along its crest a number of flattened projections that are directed inwards and slightly downwards. A similar but much less prominent ridge occurs in *Gogonasus* (Fig. 52B,D,E). Ventral to the ridge is a relatively smooth surface of Meckelian bone that is overlapped to a variable extent by the infradentary ventral to it. This surface would have been a natural site for the attachment of large coracomandibularis muscles. Dorsolateral to the ridge the surface was possibly for the attachment of the genioglossus muscles (Jarvik, 1980: vol.2, fig. 117).

Immediately ventral to the surface for the coracomandibularis muscle attachment, the inner surface of the splenial is broad and roughened as though for the attachment of other muscles. This surface, which is well shown on Fig. 46B, extends posteriorly beyond the posterior edge of the anterior fossa. It was most probably for the attach-

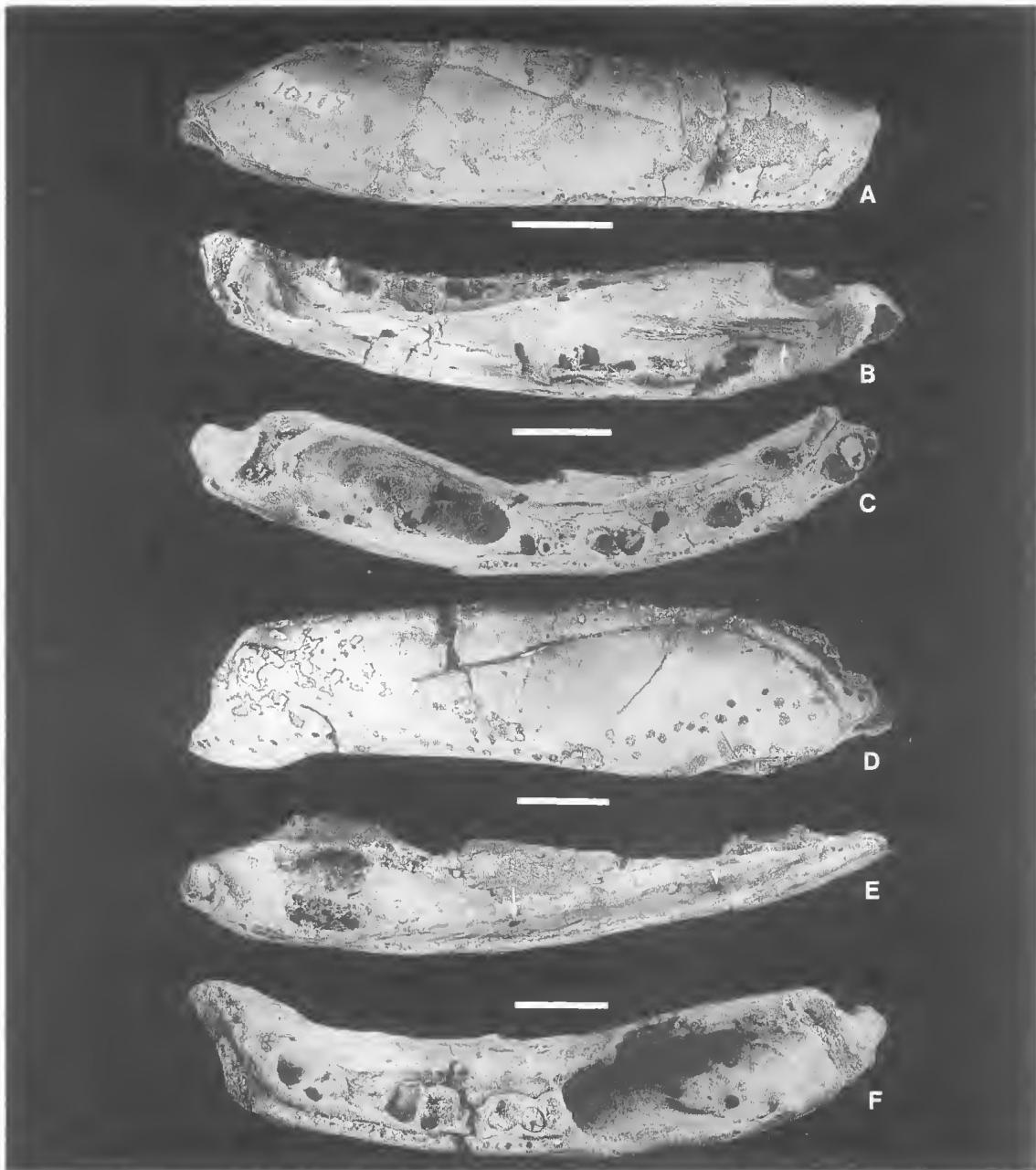


FIG. 49. *Cladarosymblema narrienense*. A-C, lateral, mesial and dorsal views of right mandible, QMF21101. A, showing row of pores for the mandibular lateral line canal and cosmine resorption towards the anterior. B, showing the anterior end of the prearticular, upturned edges of the external dermal bones immediately ventral to it, and the deep furrow anterior to the postglenoid process leading into a sharply defined furrow for the ramus mandibularis internus VII (arrow). C, showing the large postglenoid process, the pair of foramina in the lateral wall of the adductor fossa, and the regular tusk and replacement pit pairs. D-F, lateral, ventral and dorsal views of a left mandible, QMF21090, with its anterior end eroded away. D, showing unusually strong pit-lines and lateral line pores, and some unusual cosmine blisters anteriorly. E, showing the submandibular furrow; arrows indicate foramina in submandibular furrow. F, showing two foramina in the lateral wall of the adductor fossa, and an anomalous arrangement of tusks and replacement pits. Scale: 10mm.

ment of the anterior intermandibularis muscles. A similar, but much larger surface, is present in *Gogonasmus* (Fig. 52B).

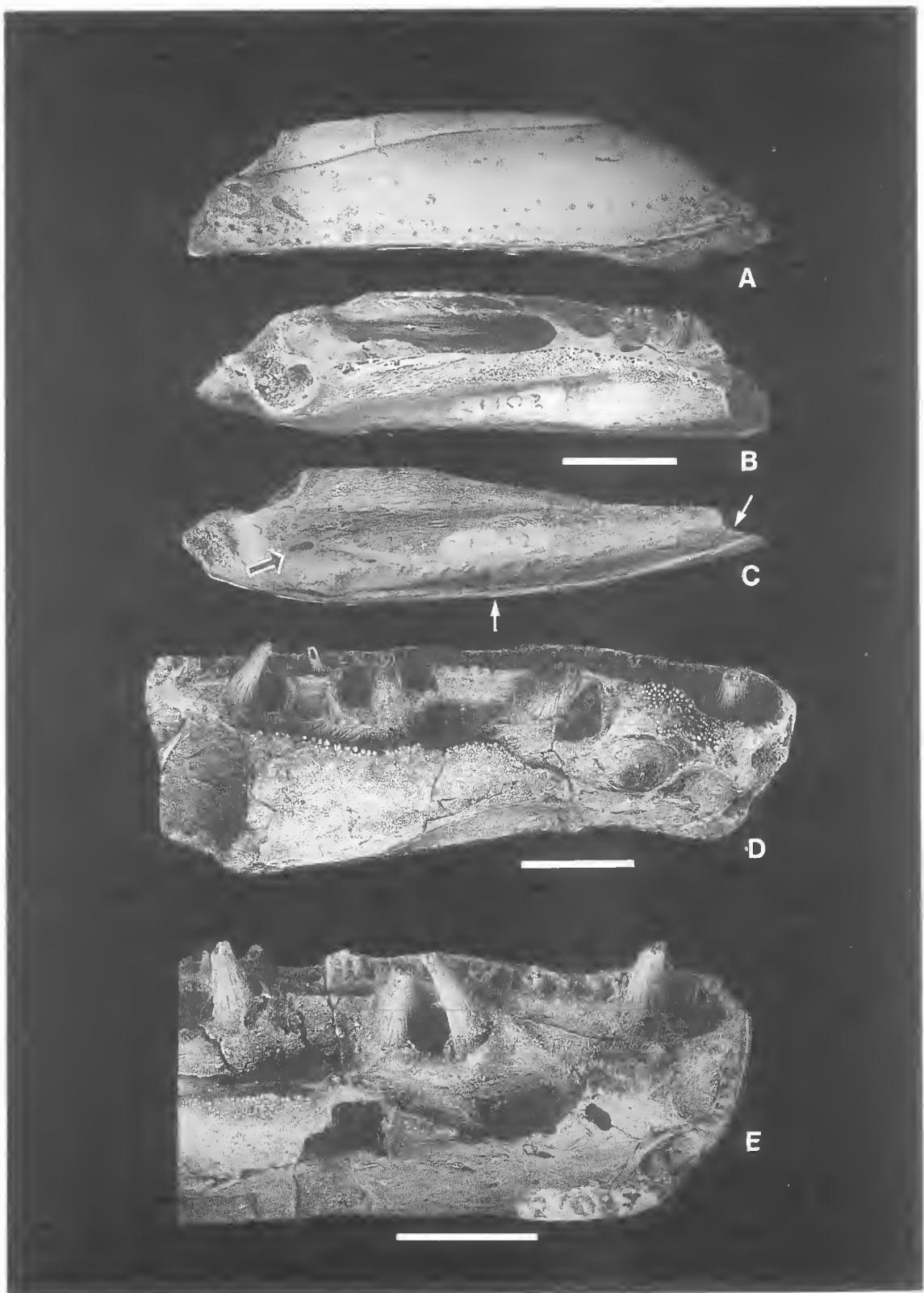
Grooves and Foramina. We are aware of no osteolepiform mandibles showing this degree of detail having been described. Gross (1941) described details of the grooves and foramina in some incomplete *Panderichthys* and several porolepiforms, but he was cautious about their interpretation. Jarvik's interpretation of the foramina in the mandible of *Eusthenopteron* is partly based on his views of the evolution of the tetrapod ear (Jarvik, 1980: Vol.2, figs 97-100), some aspects of which we do not find convincing. Hence we have had to fall back on data from extant sarcopterygians, such as *Neoceratodus* and *Latimeria*, and the basic knowledge of the nerves and vessels that occur in the mandibles of all primitive osteichthyans, for our interpretations. These are: the mandibularis V₃ and its branches such as the intermandibularis, which are motor nerves to the various muscles of the throat and the sensory structures of the symphysial region; the mandibularis externus and internus VII, which are sensory nerves to the internal and external surfaces of the mandible; the lateral line nerve to the mandibular lateral line; the efferent epibranchial artery; the hyoid artery; and the mandibular vein. The positions of these structures are comparable throughout all the groups of primitive fishes, and this gives us some confidence in the identification of grooves and foramina. However, we acknowledge the possibility of contrary evidence. In the following description, we deal first with those features that are uniform in their distribution in available specimens and can be confidently interpreted, and then move to more variable and obscure features.

On all specimens, the lateral line canal enters the mandible just behind the articulation and between the postglenoid process and the posterior tip of the surangular. The foramen is obvious, and the canal from it runs anteroventrally as is shown by the lateral line pores and the X-radiographs (Fig. 54A,B).

A groove of variable depth occurs between the articular and the dorsal edge of the surangular, and on most specimens runs into a small foramen (or a group of small foramina) between these two bones a few millimetres further forwards (Figs 46C; 47). This opens into a tube that issues through a distinct foramen between the articular and the surangular in the posterolateral wall of the adductor chamber. As is shown on QMF31861, this tube is quite expansive and has one or two small offshoots which seem to end blindly (Figs 55D; 56B), but are more probably connected to very small foramina on the posterior surface of the mandible between the articular and the surangular. The identity of the nerve occupying this canal and groove can be determined from its position and orientation. Although it enters the mandible anterior to the glenoid fossa, and is therefore in a position appropriate for mandibularis V₃, it is clear that the nerve impinged on the mandible from a posterodorsal direction, and therefore it is likely to be a branch of the facialis nerve VII. In that position, the only such branch would be from mandibularis externus VII. Gross (1941) observed a tube in this position in sections of *Glyptolepis baltica* and *Panderichthys rhombolepis*, and labelled it as the canalis articularis, although he did not assign a function to it. He also believed that this tube opened in a posteroventral position, as does the one dealt with in the next paragraph. Consequently his canalis articularis may have been connected to both dorsal and ventral foramina.

Another groove of variable depth extends along the ventral contact between the articular and the surangular into the submandibular groove. A short distance from the posterior end of the articular a branch enters a foramen that connects with a tube that lies between the surangular and the articular, and connects with a large foramen in the posterolateral wall of the adductor chamber. This canal, which is well displayed in Figs 55D, 56B & 57G, has several anteroventrally directed branches that open through foramina low on the posterior wall of the adductor chamber, in addition

FIG. 50. *Cladarosymblema narrienense*. A-C, lateral, mesial and ventral views of small left mandible, QMF21102. A, showing unusual sharp flexure in row of lateral line pores. B, showing face of prearticular and distribution of denticles on its surface, some of which have been removed during preservation, leaving pits. C, showing posterior foramen and incomplete edge of the anterior foramen in the submandibular furrow (external arrows), the furrow anterior to the postglenoid process, and the foramen for the mandibularis internus VII (internal arrow). D, mesial view of the anterior half of a left mandible, QMF31864, showing shape of anterior end of the prearticular, distribution of denticles on its surface, shape and denticulation of the parasympophysial plate, and anterior and inter-coronoid fossae for reception of tusks from the upper jaw. E, mesial view of QMF21087. Note the same features as in D, and the two tusks with an intervening replacement pit on the anterior coronoid. Scale: 10mm.



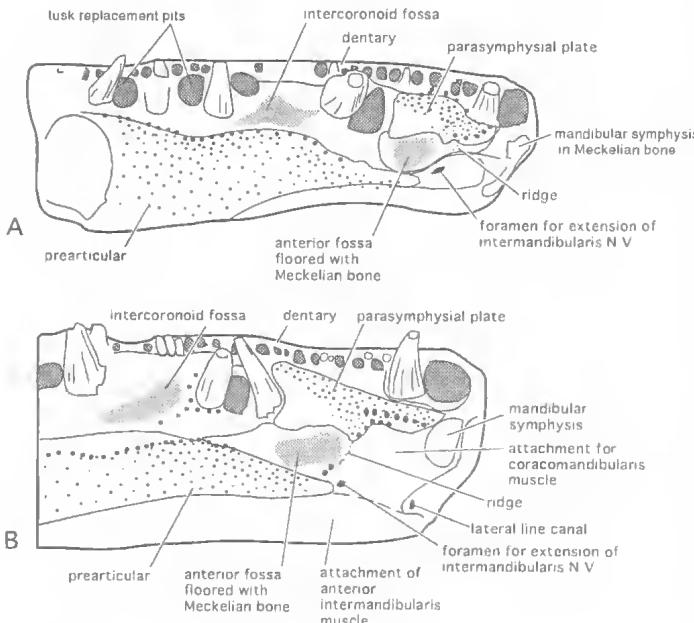


FIG. 51. A, B, labelled key to Fig. 50D,E.

tion to the main branch, which opens higher on the internal face of the surangular. The subsidiary branches vary in number between specimens. The fact that this system lies lateral to the ossified Meckel's cartilage shows that it cannot have carried a vessel, and so it must have been a nerve. This nerve must have passed behind the jaw articulation from a posterodorsal direction, and the only nerve to enter the mandible from that direction is the *facialis* nerve VII. It is therefore most probably the ventral branch of the ramus *mandibularis externus* VII.

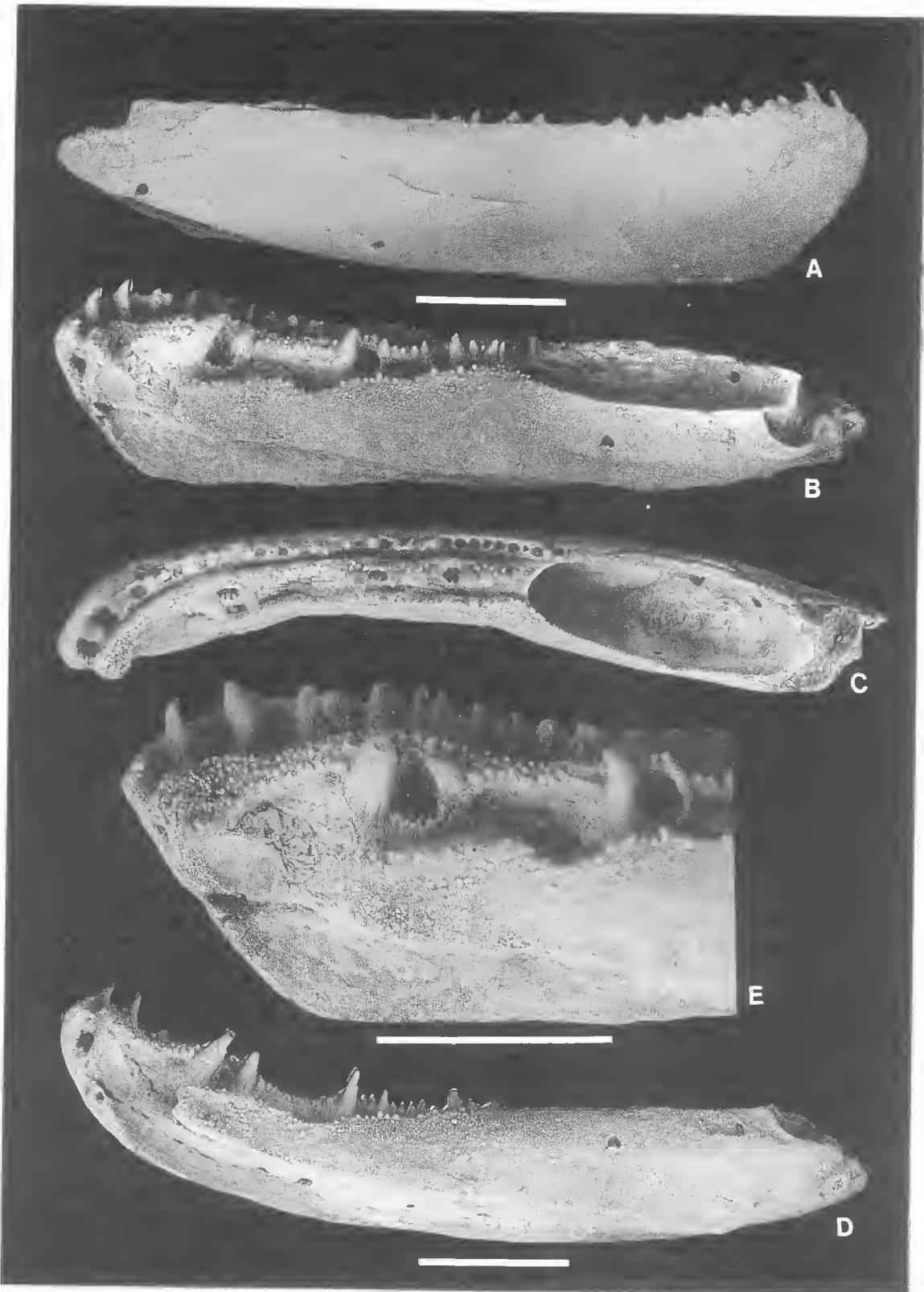
A constricting groove passes around the posteromesial surface of the postglenoid process of the articular on to its ventral surface. Although the connection is not completely clear on most specimens, one small individual, QMF21102, shows definitely that at least part of whatever occupied this groove passed anteriorly into a smaller groove that enters a foramen within the articular (Figs 49B; 50C; arrows). From this fo-

ramen, a tube runs anteriorly within the bone and opens into the posteromesial wall of the adductor chamber. Thence a groove runs forward along the inner wall of the prearticular; although its course is difficult to illustrate, it can be traced at breaks in the bone and on the internal surface of dissected specimens. Occasionally a branch of this groove opens through a foramen between the prearticular and the coronoid. These foramina and grooves are appropriately placed to transmit fibres of the *mandibularis internus* VII (*chorda tympani*). In *Amia* (Jarvik, 1980: 71) that nerve serves the mucous membranes on the buccal surface of the mandible. In addition, numerous small foramina on the inner surface of the jaw high on the prearticular and along the junction with the coronoids, probably carried fibres of the *mandibularis internus* VII.

Jarvik (1980: vol. 2, fig. 97) showed a foramen on the external surface of *Eusthenopteron* in the same position as the one we are considering. However, he believed that it connected via a tube in the articular with a foramen on the lateral side of the adductor fossa, and that it transmitted a branch of the *auriculotemporalis* V nerve from the anterior to the posterior. No such tube exists in *Cladaro-symblema*; nor can we find a foramen in the position he indicated for the *chorda tympani* (*mandibularis internus*). Gross (1941) noted a foramen entering a tube at the same position as in *Cladaro-symblema* in *Glyptolepis baltica*, and referred to it as the *canalis praearcicularis*. He claimed that it carried a blood vessel, a view with which we have to disagree.

The main constriction around the posterior end of the postglenoid process, referred to in the last paragraph, is much too large to have carried the ramus *mandibularis internus* VII only, and it is

FIG. 52. *Gogonasus andrewsae* Long. All figures of right mandible, ANU49259. A, lateral view. Note increase in height towards anterior and large isolated pores and intervening smaller pores for lateral line canal. B, mesial view. C, dorsal view. Note strong furrow along outer edges of coronoids, and weaker one along their inner edges; and the two foramina in the outer wall of the adductor fossa. D, ventromesial view showing abrupt anterior termination of the prearticular and broad submandibular groove with multiple foramina. E, enlargement of symphysial region in mesial view. Note continuous band of denticles on the parasymphysial and coronoid plates, the very broad band of external dermal bone exposed on the inner ventral surface for attachment of anterior intermandibularis muscles, and shape of symphysial junction. Scale: 10mm.



likely to have been occupied by a major vessel. In such a position this would have been the hyoid or the efferent epibranchial arteries or both. They would have been distributed in the soft tissues along the inner face of the mandible, including the various sub-branchial muscles.

In the submandibular furrow between the infradentaries and the Meckelian bone, there is one large foramen and, in some specimens, one or two smaller foramina lying in the deep embayment below the postsplenial or the angular. The large one passes up through the bone (Figs 46D,E; 47A; 55B) and joins a groove that runs from a posterodorsal direction past the foramen and thence along the floor of the Meckelian cavity (referred to by Gross, 1941, as the canalis primordialis) inside the submandibular furrow. As indicated below, we consider that this foramen transmitted the ramus intermandibularis V from the Meckelian cavity to the submandibular furrow. However, it probably also transmitted a branch of the efferent epibranchial artery from the exterior to the Meckelian cavity. This artery passed around the posterior end of the mandible in the groove as described above.

On the external surface, a groove continues in the submandibular furrow towards the anterior end of the mandible (Figs 46D,E; 49E; arrows), where it divides. The ventral branch runs to the symphysis and the dorsal one runs up into a foramen situated either in the splenial or in the plate of Meckelian bone (Figs 46B; 47A; 50E; 51 A,B). This foramen and its connections are described in detail in the next paragraph. The implication is that a nerve or a vessel, or both, supplied the soft tissues in the anterior part of the Meckelian cavity and the muscles attached in the region of the symphysis.

QMF31860 shows that within the symphyseal region the foramen joins with a perichondrally-

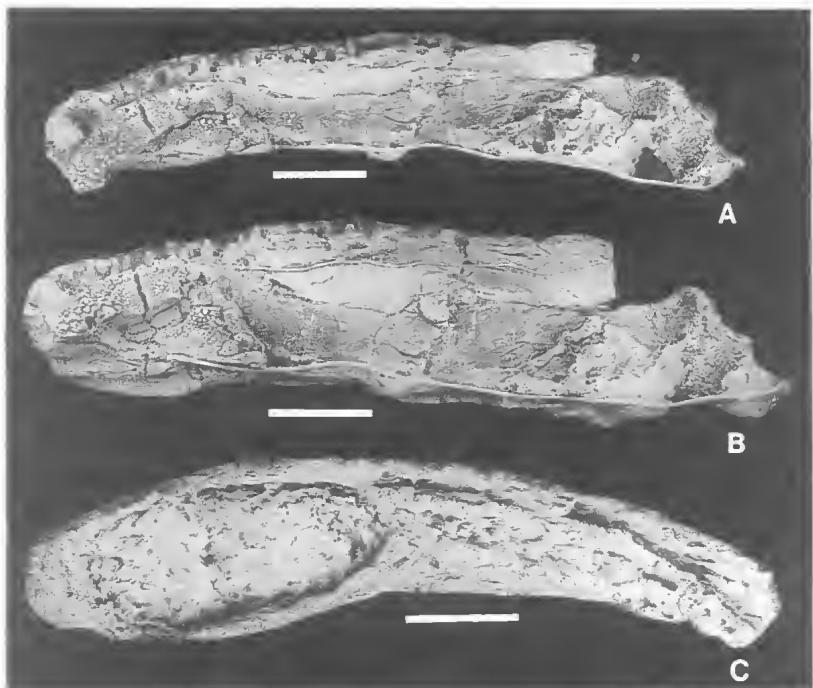


FIG. 53. *Ectosteorhachis nitidus* Cope. A, B, dorsal and mesial views of right ramus, MCZ8827. Note strongly denticulated parasymphysial plate and denticulated anterior end on the prearticular. The weakly represented radiation centre on the inner surface of B suggests that the surangular is large and its centre of ossification is posteriorly situated as in *Cladarosymblema*. (The threads along the dorsal and ventral inner surface have been cemented in place to strengthen the specimen.) C, dorsal view of MCZ8826. Most of the teeth and tusks on the coronoids were removed during the original preparation, but the strong groove between the dentary and the coronoids remains. (These specimens were among those used by Thomson, 1964a: fig. 4.) Scale: 10mm.

lined groove that is impressed on the inner face of the infradentaries, and runs in an anterodorsal direction towards the symphysis (Figs 57C; 58). This is just one of several similar grooves in the Meckelian lining of the external dermal bone. The others enter the symphyseal region from the Meckelian cavity. The main tubes branch and interconnect, and at first sight they seem to represent passages for nerves rather than vessels. For this reason, we conclude that the anterior as well as the posterior part of the submandibular furrow carried nerves as well as arteries. Such nerves would be extensions of intermandibularis V. Those in the Meckelian cavity would have been mandibularis VII. However, an alternative has to be entertained because we can find no external openings connecting with these grooves, and they do not connect with the lateral line canal. We can only conclude that whatever they carried ramified into the bone spaces, suggesting that they carried nutrients rather than nerves. Until sufficient ma-

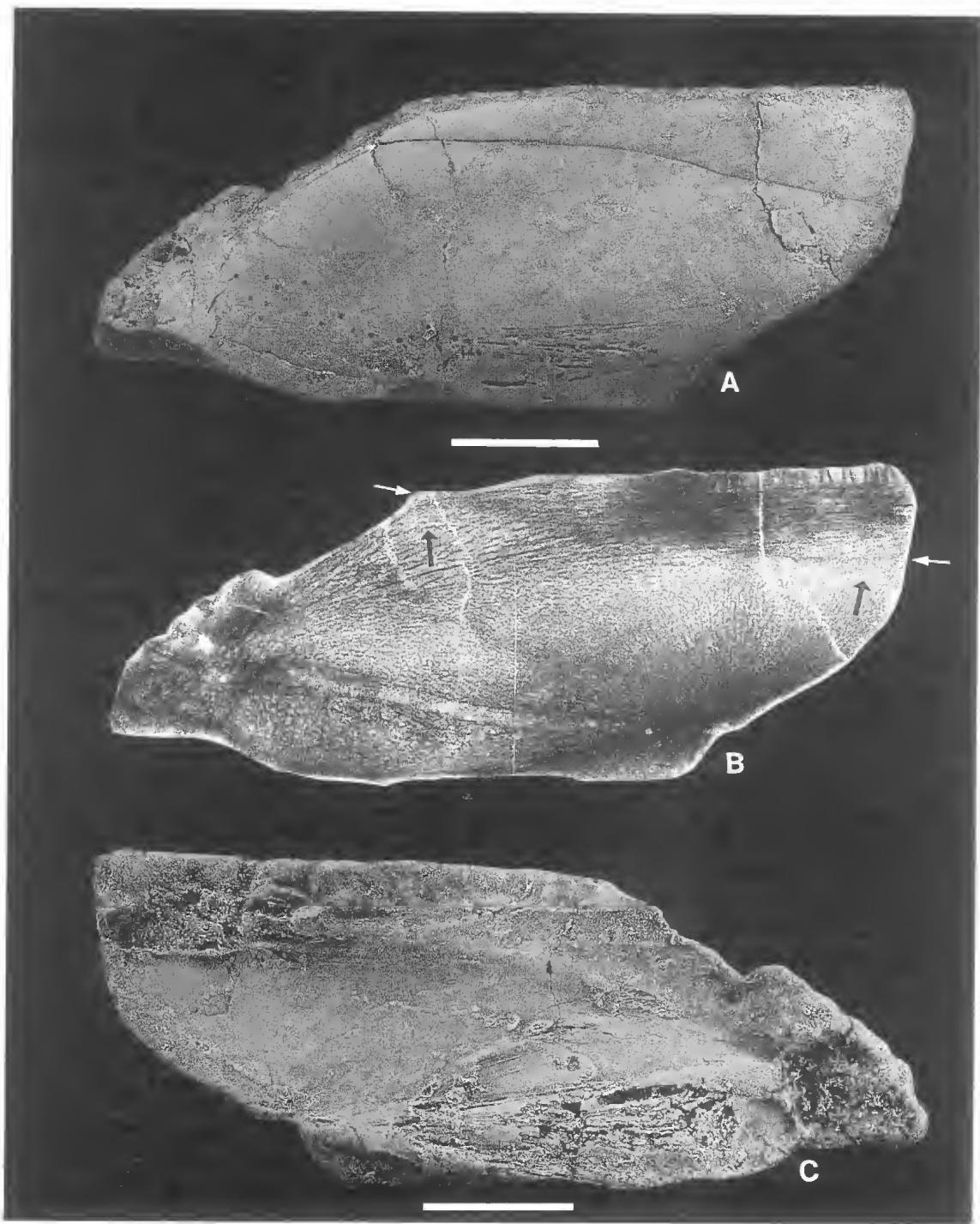


FIG. 54. *Cladarosymblema narrienense*. A,C, exterior and interior views of posterior part of external dermal bones of an incomplete mandible, QMF21100. B, X-radiograph of same. Note position of lateral line canal, ossification centres of angular and surangular, and horizontal pit-line. In particular, note the anterior and posterior divergence between the boundary between the dentary and infradentaries (horizontal arrows) and the horizontal pit-line (vertical arrows). Scale: 10mm.

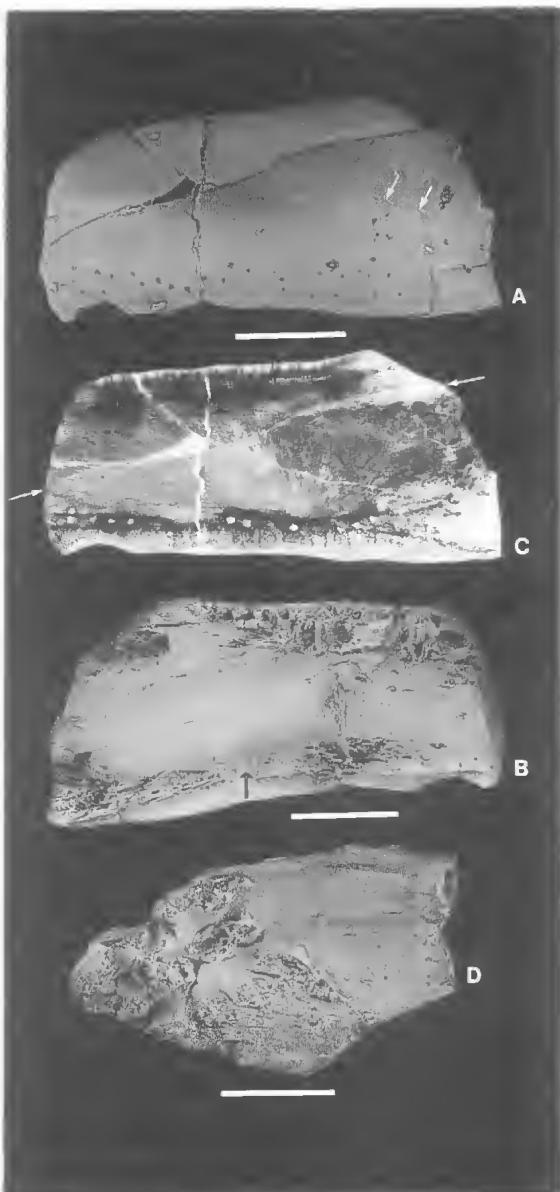


FIG. 55. *Cladarosymblema narrienense*. A, exterior view, external bones of part of mandible, QMF31867, showing lateral line pores, horizontal pit-line, and *en echelon* furrows (white arrows) marking approximate position of suture between angular and surangular. B, Interior view of same with the radiation centre of angular and superimposed foramen in submandibular furrow. Arrow marks position of foramen for intermandibularis V and possibly efferent epibranchial artery. C, X-radiograph of same in orientation of A; interpreted in Fig. 56A. Arrows indicate horizontal pit-line. D, internal view, posterior part of external dermal bones, QMF31861, showing various canals discussed in the text, and interpreted in Fig. 56B. Scale: 10mm.

terial becomes available to permit sectioning, their function will remain unknown. Gross (1941) also observed foramina and tubes entering the anterior part of the submandibular furrow in several of the genera he discussed, and referred to them as 'Känele im Medialrand des Mentomandibulare'.

Within the adductor chamber of QMF21101 and 21090, immediately dorsal to the previously mentioned main foramina for the mandibularis externus VII (Fig. 49C,F) are one or two foramina that are vertically directed. In other specimens no such foramina exist, but a shallow groove runs steeply down in front of the mandibularis externus foramen; this is continued anteroventrally as a pronounced groove along the junction between the articular and the infradentaries, and then directly anteriorly. In the floor of the forward extension there are four or five foramina, some of which may penetrate the bone to exit in the submandibular furrow, as has been discussed above. Some of them do not penetrate the bone and presumably serve the sensory structures in the bone. This system was probably for the mandibularis V, which entered the mandible through the posterior part of the adductor fossa. The foramina in the submandibular furrow are appropriately placed to have carried nerves to a sheet of muscle such as would be expected if they innervated the intermandibularis muscles. The main branch of this groove opens at a foramen in the submandibular furrow just below the ossification centre of the angular, and we consider that it carried the main branch of the ramus intermandibularis V. This interpretation would be consistent with the inferred position of the intermandibularis muscles served by this nerve. An entirely similar arrangement is present in *Gogonasus*, in which two other small foramina can be seen passing through the bone to enter the internal groove a short distance behind the main one.

The mandibular vein has not been discussed. We surmise that it joined the lateral venous sinus via the adductor fossa, and thence joined the orbital venous sinus, leaving no trace on the bone.

The adductor fossa is long and wide, its proportions changing slightly with age. The width/length ratio is 0.38 in the smallest specimen, and 0.46 in the largest.

Comparison with the Mandible of Ectosteorhachis. We have examined MCZ8826-8827 which, with MCZ8641, formed the basis of the description by Thomson (1964a: fig. 4). The specimens are figured herein as Fig. 53A-C.

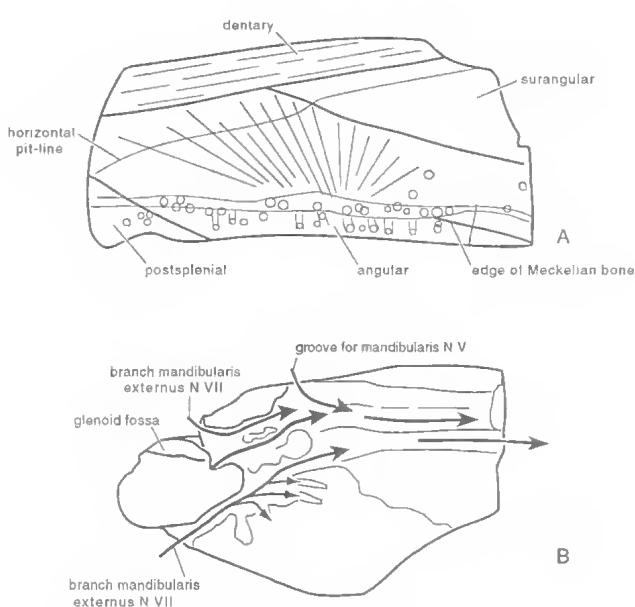


FIG. 56. *Cladarosymblema narrienense*. A, key to Fig 55C. B, key to Fig. 55D.

Firstly, we note that MCZ8827 is extensively crushed, and MCZ8826 is otherwise damaged, making it difficult to recognise the sutures shown on Thomson's diagrams, particularly those between the infradentaries. In our view there is no evidence that the splenial terminates behind the symphysis, as shown by Thomson (1964a: fig. 4A); in that region the arrangement of the dermal bones is no different from that of other osteolepiforms. The suture along the ventral edge of the dentary is strong and shows finished edges to a wide groove along parts of its length; it cannot be traced as far forwards as Thomson shows, but posterodorsally it leaves a broad band, as in his fig. 4A. This band is proportionately much larger than in any specimen of *C. narrienense*.

The posterodorsal edge of the mandible is naturally truncated, and exposes a large segment of articular bone in lateral view. This implies that the subopercular 1 overlapped the mandible to a greater extent than in *C. narrienense*, and that the submandibulars did not reach as far posteriorly as in that species.

We see no evidence to support the existence of three pairs of coronoid tusks in *Ectosteorhachis*. There is a strong gutter between the coronoids and the dentary, and more than one row of large

denticles along the outer rim of the coronoids (Fig. 53C). Large denticles are also present on the preserved anterior part of the prearticular in MCZ8827, although MCZ8826, which has the prearticular preserved, has had the large denticles stripped from all but a few patches during the original preparation.

The structure labelled 'crista dentalis' by Thomson (1964a), and said to be (p. 291) '... an enlargement of the anterior rim of the anterior dentary fossa', and (p. 302) 'a denticulate ledge' of the dentary, is really the parasymphysial plate (Fig. 53A,B); it is clearly a separate bone, the suture with the Meckelian bone behind and with the dentary in front, both being evident. The denticles on its surface are comparable in size with those on the prearticular, being much larger than those in equivalent positions in *C. narrienense*.

The glenoid fossa is transverse and double, unlike the representation given in Thomson's figures 4B&C. Although the preparation is not good enough to be certain of the point, it seems that the fossa is of the standard osteolepiform type. On MCZ8826 there is a definite postglenoid process that has been partly destroyed during the original preparation. Its lateral periosteal surface is clearly cut through, and the vesicular bone structure is still clearly visible on the other surfaces. On MCZ8827, part of the dorsal surface of the process is still present. Although examination of Thomson's illustrations may suggest that the reduction of this process may be useful in differentiating *Ectosteorhachis* from *Megalichthys*, examination of the specimens shows that this is not possible.

The adductor fossa is wide in comparison with that of *C. narrienense*; its proportions on MCZ8826 are original, and not the result of distortion.

Although its preparation does not permit the accurate identification of most foramina, MCZ8826 does show one feature very clearly. Lateral to and just in front of the glenoid fossa is a group of ten tubules filled with iron oxides. These tubules run ventrally from openings in the blade of the surangular, converging as they go. At first they join into twos or threes, and presumably in a more ventral position they coalesce com-

pletely, although that position is not exposed. In *Gogonasus* and *Cladarosymblema*, only one to three foramina instead of ten occur in this position. As indicated above, we have concluded that the foramina transmitted the mandibularis externus VII nerve.

Apart from the denticulated ridge on the lateral margins of the coronoids, and the possibility of the presence of only two coronoids, we see no evidence from the mandible to permit the separation of *Ectosteorhachis* from *Megalichthys*, although we note that many details of the former genus remain obscure. We note also that the new genus described from Norway by Borgen (MS), is comparable with *Ectosteorhachis* in its denticulated marginal coronoid ridges, and possibly in having only two tusk-bearing coronoids. Separation of *Ectosteorhachis* from *Cladarosymblema* can be made on the basis of the wide adductor fossa, the gutter between the dentary and the denticulated coronoid ridge, the size of the parasymphysial plate, and the size and abundance of the denticles on that plate and the prearticular. We note, however, that all these distinctions rest on an inadequate sample of *Ectosteorhachis*.

PECTORAL GIRDLE

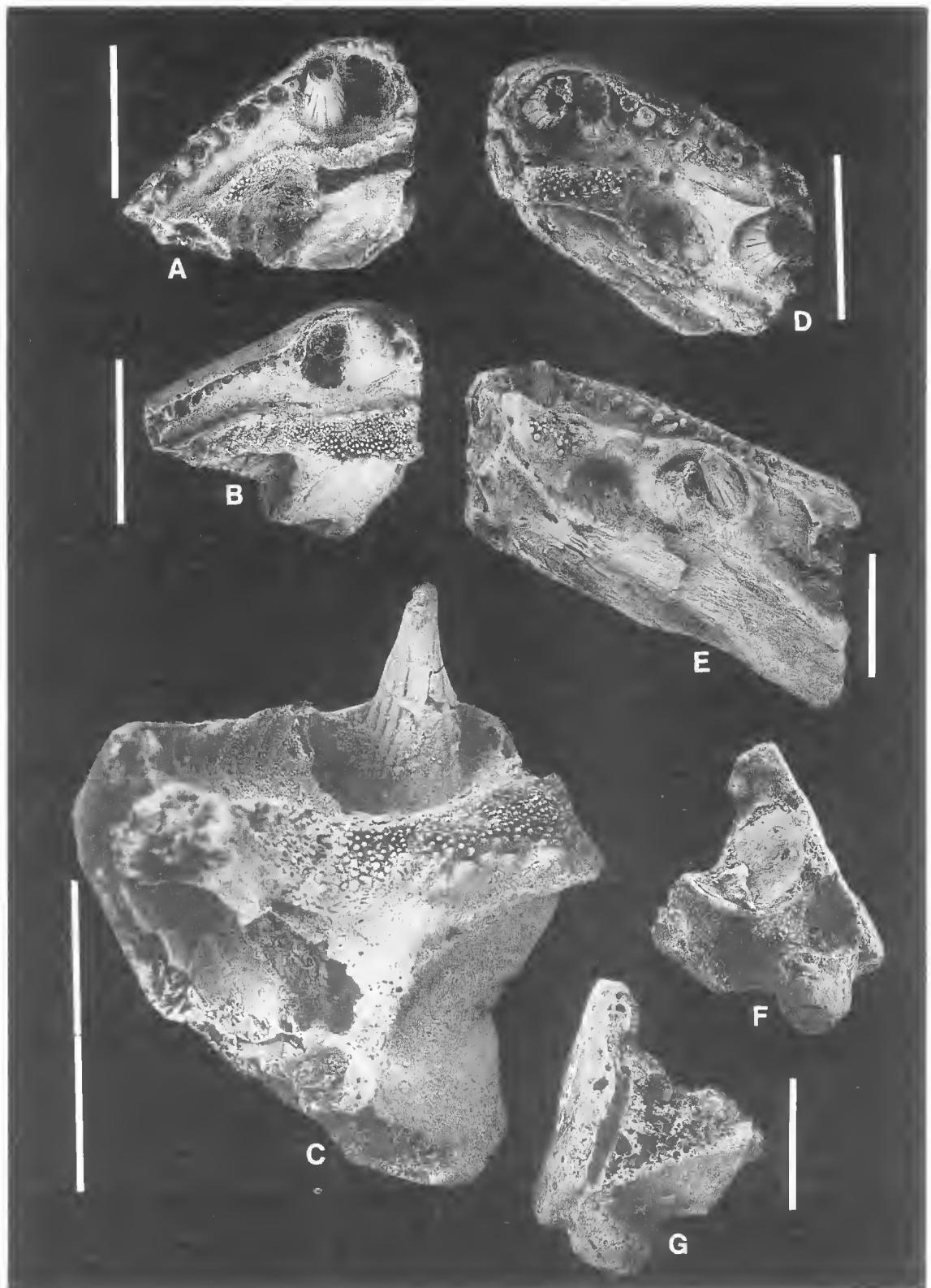
The pectoral girdle is known from one complete supracleithrum (Fig. 59A,B), two broken anocleithra (Fig. 59C,D), three broken cleithra (Fig. 60A,B,E), one isolated almost complete clavicle (Fig. 60F), an almost complete cleithrum and clavicle from one individual (Fig. 61A-C), the incomplete clavicles of the holotype, and two partly crushed scapulocoracoids still attached to the isolated cleithra (Figs. 60B; 61A). Because other genera are represented in the etchings, it is necessary to establish that these specimens belong to *Cladarosymblema*. We have concluded that they are properly assigned for the following reasons. The exposed part of the clavicles of the holotype, though poorly preserved, are largely covered with a network of raised ridges rather than cosmine. The same is true of what we regard as fragments of the cleithra of the holotype. In addition, one of the isolated fragmentary cleithra

has cosmine on its posteroventral corner, and another has patches of cosmine near the broken dorsal extremity of the bone. These isolated bones have a pattern of ridges on the external surface. The external surface of the anocleithrum and supracleithrum also have the distinctive pattern of ridges, and patches of cosmine in similar relationships. As Jarvik (1948) has pointed out, the cosmine-bearing *Osteolepis* itself has variably ridged surfaces on parts of the pectoral girdle along with cosmine. Its ornament differs from *Cladarosymblema* in the relative extent of the two types of surface.

Supracleithrum. This is represented by a single complete bone (QMF31859) from the right side (Fig. 59A,B). Its exposed surface has a tracery of fine ridges, similar to those on the posterodorsal part of the anocleithrum, and a small patch of cosmine at the posterior extremity. Two types of overlapped surface are recognizable; a large well-defined surface through which the lateral line passes, and which is traversed by branching radial grooves and some pits; and a much narrower strip along the anteroventral edge differentiated from the exposed surface by a distinct change in slope. The former was overlapped by the posttemporal and the latter by the opercular.

Anocleithrum. This bone is represented by two fragments (QMF26555, 31862), one from each side of the animal (Fig. 59C,D). The right one was partly destroyed during photography, but the left one was incomplete when found; both are robust. The exposed part has a tracery of ridges over the posterodorsal surface, decreasing in size posterodorsally, and a patch of cosmine posteriorly. The ridges carry a row of small pustules. The overlapped surfaces are extensive, and the anterior process is twice the size of that of *Osteolepis* (Jarvik, 1948: fig. 25). The process of the left bone (QMF31862) is complete; its anterior end is rugose and carries a vascular groove on its ventral edge. On its outer face is a sharp crest that marks the edge of the cleithral overlap, and so the tip probably represents the attachment of a ligament. The area overlapped by the cleithrum indicates

FIG. 57. *Cladarosymblema narrienensis*. A,B, symphysial parts of the left rami of two mandibles, QMF31869 and 31860, showing the tusks and replacement pits, the parasymphysial plates, and the variable arrangement of the marginal teeth in relation to the edge of the jaw anterior to the tusks. C, enlargement of B viewed from a posterolateral direction; for interpretation, see Fig. 58. D-E, symphysial parts of right rami of two mandibles, QMF31865, 31868, showing similar features to A-C, but with two anterior tusks in D, and two tusks in the anterior coronoid as well as the abbreviated area of denticles on the parasymphysial plate of E. F,G, posterior end of a right ramus, QMF31887, in dorsal and ventral views. F, showing double glenoid fossa and the rounded postglenoid process. G, has been eroded to expose the tube for the ramus mandibularis externus N VII. Scale: 10mm.



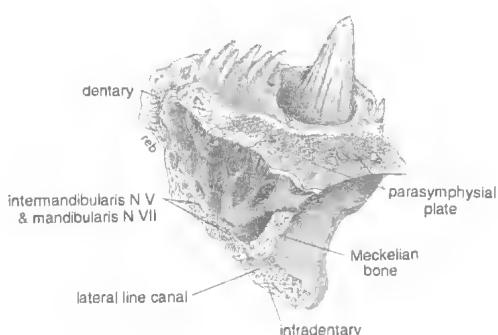


FIG. 58. *Cladarosymblema narrienense*. Reconstruction of the specimen shown in Fig. 57C to show the tubes servicing the symphyseal region.

that the dorsal edge of that bone is truncated, but with its ends rounded off.

Schultze (1987: 69), commenting on the work of Rosen et al. (1981), indicated that 'the character "anocleithrum without surface ornamentation" cannot be evaluated because the condition of the anocleithrum is not known in plesiomorphic dipnoans, or rhipidistians'. This is difficult to understand because the anocleithrum was buried and unornamented in the several Devonian dipnoans in which the bone is known; and Jarvik (1980) has figured a highly ornamented anocleithrum in *Eusthenopteron*. Jarvik (1985) and Long (1985b) have listed an ornamented anocleithrum as a distinctive feature of osteolepiforms. The presence of ridged ornament and cosmine on the anocleithrum of *Cladarosymblema* puts the matter beyond doubt.

Cleithrum. This bone (QMF26548, 26554, 26563, 26564, 26572 and 31875; Figs 60A-E; 61A-C) is robust and survived the preservation processes well. It is thin around the dorsal and posterior edges, but thickens considerably towards the anterior and ventral edges. In posterior profile, the upper part of the bone is almost planar, but the lower planar part is inflected at an angle of c.130°, and twisted slightly with the posterior edge deflected inwards (Fig. 61B). Although no dorsal margin is preserved, its outline can be established from the area of overlap on the anocleithrum, where it appears to have been truncated to gently concave. Although no complete specimen is available, it is clear that the posterior edge is deeply embayed just dorsal to the region of the bend between the two parts of the bone. In lateral view, the ventral part tapers to an acute termination. The branchial lamina is small, hav-

ing maximum dimensions at the bend in the bone and tapering away dorsally. Ventrally it tapers abruptly, providing the articulation for the long dorsal process on the clavicle (Fig. 61B). Between this abrupt taper and the ventral tip of the bone, there is a narrow flange with a groove on its inner face into which the anterodorsal edge of the clavicle was loosely articulated.

According to Thomson & Rackoff (1974), the cleithrum of *Ectosteorhachis nitidus* consists of two separate bones. We can find no evidence of such a construction in *C. narrienense*, either from external or X-ray examination. In this respect *C. narrienense* resembles *Megalichthys hibberti*.

Over most of the external surface the sculpture consists of raised ridges making a strong tracery pattern. Distinct dorsal and ventral parts are obvious (Figs 60A; 61C). The dorsal part has one or two long straight ridges parallel with the anterior edge, posterior to which the ridges retain their height but become shorter and less regular, and carry tubercles along their crests (Fig. 60C,D); near the posterior edge, they become weaker and form a finer reticulate pattern. On the ventral part of the bone a similar arrangement occurs, except that the ridges become reticulate closer to the anterior edge. On the posterior angle of the bone and on the posterodorsal extremity, the ridges give place to small but distinct areas of cosmine (Figs 60A,E; 61C).

Clavicle. This bone (QMF26548, 26572) is only about half the size of the cleithrum. In its orientation it is twisted so that its main plane lies at about 40° to the plane of the upper part of the cleithrum (Figs 61B; 62C). It is thickest dorsally and thins out gradually towards the antero- and posteroventral edges. Its ventral edge is broadly rounded. A thick dorsal process extends up the inner edge of the branchial lamina of the cleithrum, from which it separates slightly towards its dorsal extremity. Ventrally, the branchial lamina tapers away about half way down the bone. On its inner posterior surface is a pronounced furrow into which the edge of the ventral extension of the cleithrum fits.

The external surface of the clavicle is covered with ridges of similar type to those of the cleithrum, but the pattern is different (Figs 60F; 61C). Long ridges border the anterodorsal edge but immediately behind, they are replaced by a reticulum. Anteroventrally the ridges are even lower and the reticulum finer, but posteroventrally a strip of unornamented bone is replaced by a patch of cosmine.

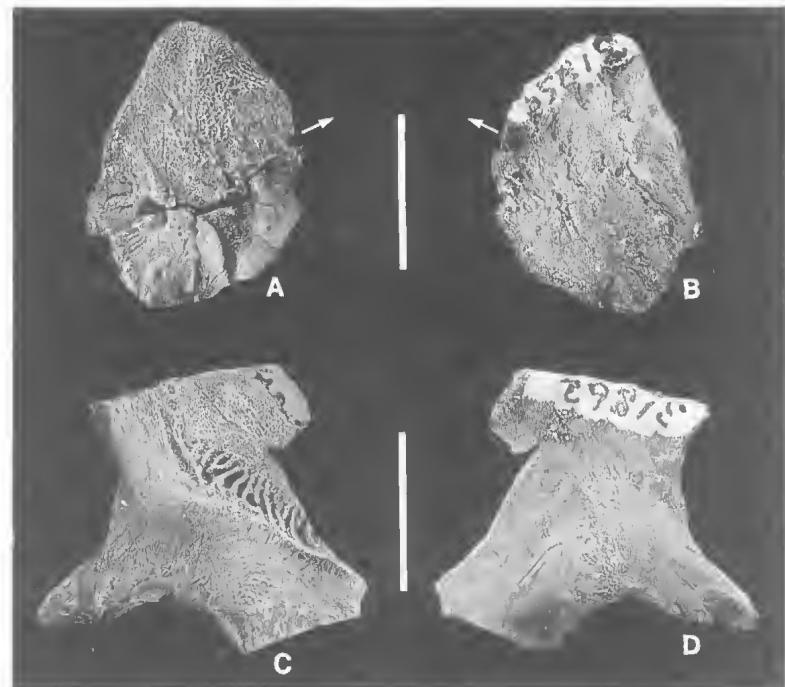


FIG. 59. *Cladarosynblema narrienense*. A,B, complete right supracleithrum, QMF31859, lateral and mesial views. Surface for the supratemporal overlap to the bottom left of the photograph in A. Arrows mark the entrance and exit points of the lateral line canal. C,D, incomplete anocleithrum, QMF31862, in lateral and mesial views. Both dorsal and ventral edges broken. Surface for overlap by cleithrum to the bottom left in C. Scale: 10mm.

The internal surface of the clavicle at its ventral edge has a large area showing that it overlapped another bone (Fig. 61A), which can only have been the interclavicle. We have not recognised any such bone in the etchings, probably because it would be rather nondescript and almost certainly broken. An interclavicle is recorded in *Eusthenopteron* and *Osteolepis*, but in each the overlap of the clavicle is small compared with that of *C. narrienense*.

Scapulocoracoid. This bone is known only from its areas of attachment to the cleithrum on QMF26548, and a crushed incomplete bone attached to QMF26554 (Figs 59A; 60B). It was a large and lightly ossified structure with three areas of attachment that are normal for osteolepiforms and Palaeozoic diploans (Andrews & Westoll, 1970a,b; Janvier, 1980). The attachments in *Cladarosynblema* are unusual, however, in their size and disposition. Anteriorly the scapulocoracoid is flattened on its mesial face and it apparently increases in depth rapidly as it approaches the fin attachment, which is not preserved. According to Jarvik (1980: 269) in

Glyptolepis groenlandica, which is a porolepiform, the scapulocoracoid is a small unperforated plate. Should this prove to be normal for that group, it would provide an excellent character for distinguishing it from the osteolepiforms.

The most posterior attachment ($ar^1Sc. cor.$ of Andrews & Westoll, 1970a: text-fig. 4), which lies in the posterior angle of the bone, is the smallest of the three, and is almost equidimensional (Figs 62; 63). Anteroventral to it is a much larger and more elongate attachment ($ar^3Sc. cor.$ of Andrews & Westoll), which tapers to an acute dorsal terminus. This attachment is for the infraglenoid buttress. The two are separated by a broad smooth surface which contained the subscapular fossa. The anteriormost attachment, which is for the supraglenoid buttress, is by far the largest. It extends dorsally along the anterior edge of the cleithrum in-

side the process on the inside of the clavicle and upwards on the inside of the branchial lamina; there it turns abruptly posteriorly towards the posteriormost scar ($ar^2Sc. cor.$ of Andrews & Westoll) to which it is joined by a low bridge of bone. This latter forms the floor of the supraglenoid foramen. The buttresses are so placed that the subscapular fossa is directed more anteroventrally and the scapulocoracoid foramen is directed more posteroventrally than the corresponding features in *Eusthenopteron* and in the unidentified specimen described by Janvier (1980).

The size of the scapulocoracoid and its attachment areas is greater than those of most other osteolepiforms. In this respect the species is similar to *M. hibberti* (see Andrews & Westoll, 1970b: text-fig. 2) and *E. nitidus* (see Thomson & Rackoff, 1974: pl. 2, fig. 1). As in these species also, the anteromesial face of the scapulocoracoid lies at a low angle to the blade of the cleithrum. The overall size of the bone correlates with the large basal part of the fin, which indicates the presence of unusually powerful musculature; the different orientations of the various fossae de-

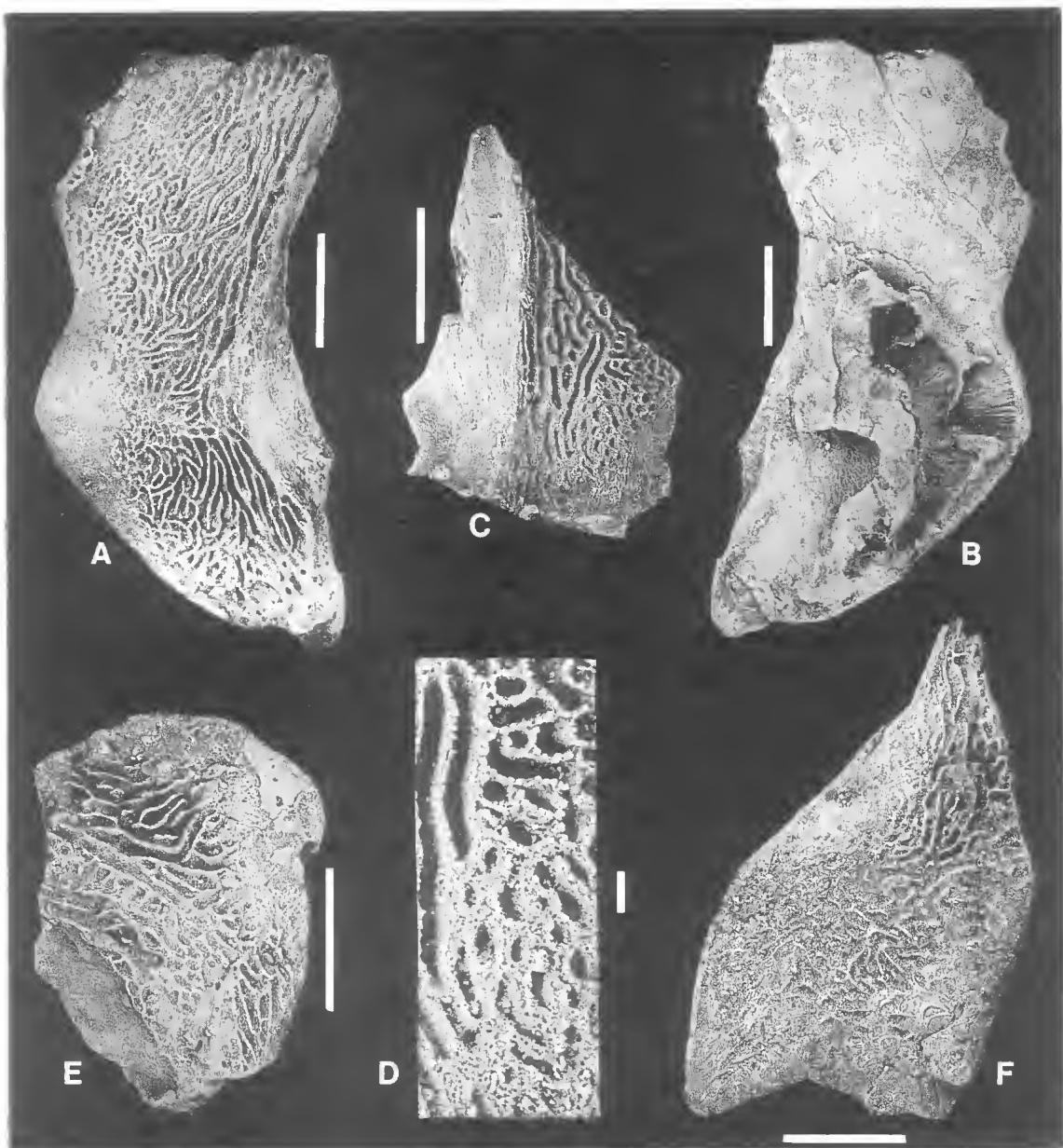


FIG. 60. *Cladarosymblesma narriense*. A,B, lateral and mesial views of an incomplete right cleithrum, QMF26554. B, showing large scapulocoracoid (see Fig. 63 for interpretation). C,D, part of incomplete cleithrum, QMF26563, showing the details of the ornamented surface. E, fragment of a left cleithrum, QMF31875, showing details of the surface ornament. F, almost complete left clavicle, QMF26572. Dorsal edge to top of photograph. Scales: A-C, E-F, 10mm; D, 1mm.

scribed above, indicate that the fin muscles were differently oriented.

PECTORAL FINS

The pectoral fins are known only from the holotype in which the fin on each side has been

prepared to expose as much as possible of its surface. In comparison with most (but not all) other osteolepiforms they are large, the distance from the base to the tip being c.10cm in a fish whose head exclusive of the operculars is about the same length. The proximal 6.25cm is covered

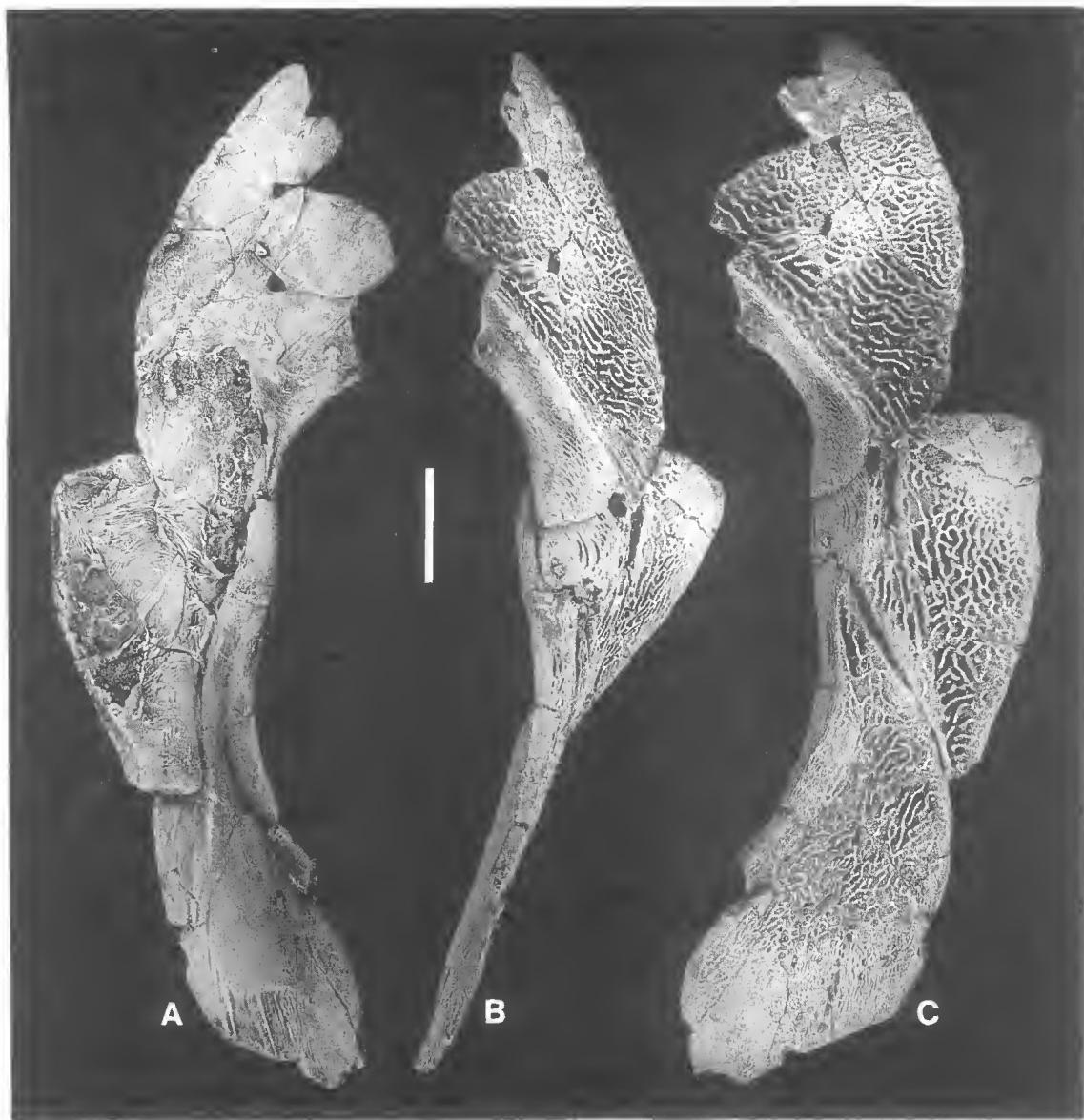


FIG. 61. *Cladarosymblema narrienense*. A-C, left pectoral girdle, QMF26548, A, mesial, B, anterior, and C, lateral views. (See Fig. 62 for interpretation.) Scale: 10mm.

with rhombic scales similar to those on the body (Fig. 64). They show a gradual decrease in size and become more elliptical in outline distally, the most distal scales being about one half as long as the proximal ones. The scales also change in shape towards the anterior edge of the fin, becoming similar to those at the distal tip about half way along the basal lobe (Andrews, 1973), whereas on the posterior side in equivalent positions, they are of the same size as the scales in the middle of the lobe. As noted above, one of the features of the

Osteolepiformes is said to be the presence of enlarged scutes on the edges of the basal lobes (Andrews, 1973), but we have not been able to recognise such on our specimen. This is probably an artefact of preservation. The ventral surface of the left fin has 60+ large scales.

Distally the scale size and shape abruptly change as the basal lobe passes into the ray scales. These ray scales are square or rectangular in outline (Fig. 64C). At mid-fin, the proximal ray scales are square and average 0.75mm in length.

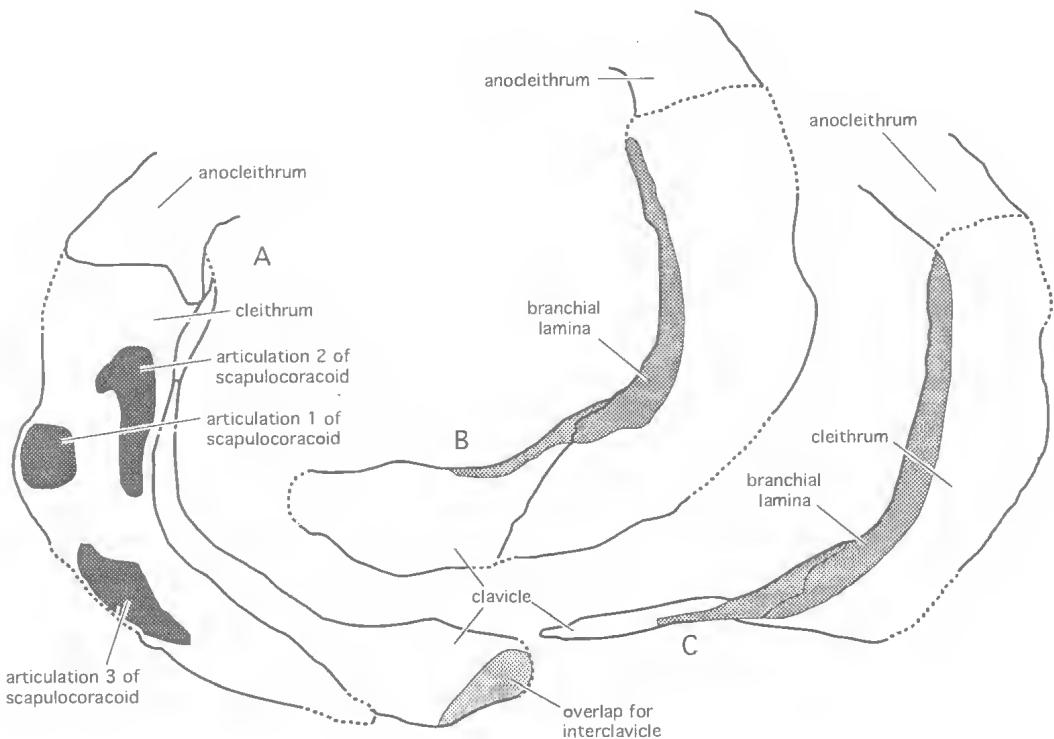


FIG. 62. *Cladarosymblema narrienense*. Outline restoration of the shoulder girdle based on the specimens shown in Figs 59-61. A, mesial, B, lateral and C, anterior views.

They increase slightly in size to a point about 0.6-0.7cm from the end of the basal lobe, where they abruptly divide into two rays. Further division takes place distally. Still further distally the scales become narrower and more elongate, ranging in length from 0.5-0.75mm and in width from 0.4-0.8mm. On the anterior of the left fin, the proximal fin ray scales are more elongate, measuring as much as 2.5 x 1.0mm. At mid-length of the dermal rays, the left fin has 120+ rays on its ventral surface.

An important feature of the ray scales is that they are all laterally contiguous; there is no evidence that they were able to separate to form an expanding surface with intervening membranes occupying a significant part of the fin surface. Another line of evidence suggests that expansion of the rays was not possible. The fins of *Latimeria* and such fossil sarcopterygians as *Eusthenopteron* have a limited number of long rays extending from only a small part of the basal lobe. In *Eusthenopteron*, about 80-100 long rays extend mainly from the distal part of the fin lobe, where

they could separate unimpeded by the shorter rays originating from the anterior and posterior edges of the lobe. Hence, if each ray was separated by only 1° from its neighbour, the fin fan could be expanded by up to 80-100°. In *Cladarosymblema* the rays are distributed much more evenly around the fin lobe, and there is no abrupt break in their length on either the anterior or the posterior edge. As a result, there is little space for an expansion of even 1° to take place between adjacent rays.

The basal lobe is clearly defined along its posterior edge where quite large scales give way abruptly to the fine dermal ray scales (Fig. 64C), but on the anterior edge the junction between the two types of scales is much less abrupt, some evidence of interdigitation being observed on the left fin. Unfortunately the anterior edge of neither fin is completely preserved.

An attempt has been made to excavate the axial skeleton of the left fin, but without success. The preservation of the whole structure is such that it

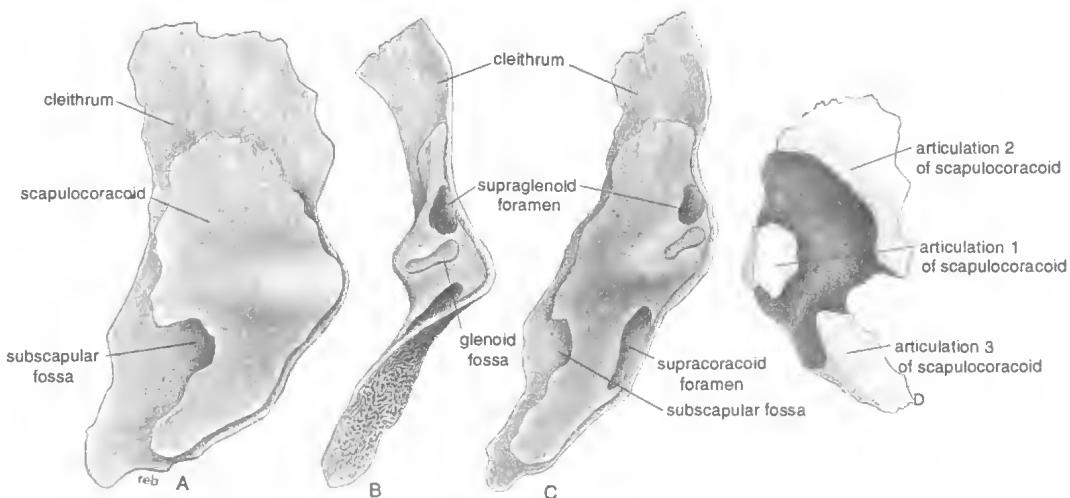


FIG. 63. *Cladarosymblema narrienense*. Restoration of the scapulocoracoid based on the specimens in Figs 60B and 61A. The restoration lacks control on the shape and size of the posterior part of the scapulocoracoid, and the size and shape of the glenoid fossa which may be too small judging from the reconstruction of *M. hibberti* by Andrews & Westoll, 1970b. All views, except D, with scapulocoracoid still attached to the coracoid. A, mesial, B, posterior, C, posteromesial and D, internal view of the scapulocoracoid after removal from the

would have been found if it were present. We can only conclude that it was poorly ossified.

nitidus presented by Thomson & Vaughn (1968: figs 1 & 2).

The outer surface of the ring is largely, or perhaps completely covered with periosteal bone, within which an anterior and a posterior groove can be distinguished laterally. The deeper groove is on what is considered to be the posterior side, based on the shape of the facet for the articulation of the neural arch. These grooves presumably mark the position of the myoseptum and the intersegmental artery. No semblance of a distinction between intercentrum and pleurocentrum is present.

We also have recovered one or two poorly preserved neural arches that possibly belong to this taxon but are not worth figuring or describing.

SCALES.

Gross Morphology. Numerous isolated scales are available for study in addition to those on the holotype. Although their outlines vary greatly according to their position on the body, the exposed cosmine-covered part is almost always rhombic in outline, with the long axis of the rhombs oriented approximately along the length of the fish (Figs 5; 6). As would be expected, the rhombs tend to be symmetrical in scales from the mid-line and the mid-flanks (Fig. 65B), but asym-

AXIAL SKELETON

Ring centra appear infrequently in the etchings, no doubt because of their fragility. The best preserved one is from the trunk and is 4.2mm long, 16.0mm in diameter, and 11.5mm in notochordal diameter (Fig. 64D,E). These proportions are approximately the same as those of a much larger specimen of *Megalichthys hibberti* figured by Andrews & Westoll (1970b: pl. 3, fig. H), although the bone tissue in our material is somewhat thinner. The preservation is adequate, but removing all the sediment from the surface has proved impossible. Ventrally there is a slight flattening marking the position of the dorsal aorta. Its anterior and posterior faces are approximately parallel up to the points where the neural arch was articulated; at those points it is obliquely truncated and the ring is not complete. As indicated by Andrews & Westoll (1970b: 421), although many centra of *M. hibberti* are complete annuli, some trunk centra have a gap dorsally, like the present specimen. Comparison should be made also with the figures of *Ectosteorhachis*

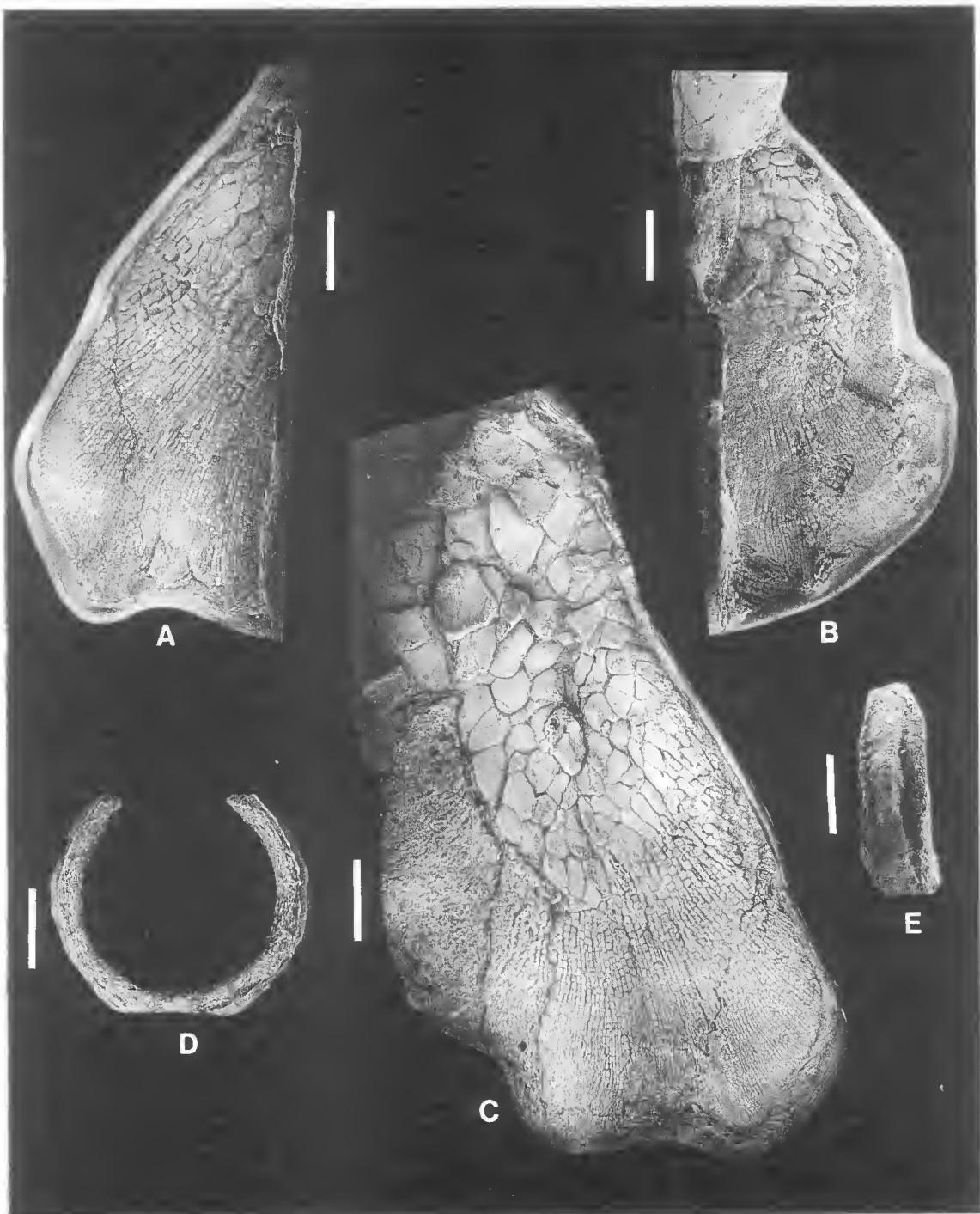


FIG. 64. *Cladarosymblema narrienense*. A, B, left and right pectoral fins of holotype (QMF21082) in dorsal view. Inner margins of fins are obscured by the overlying body of the animal. C, ventral view of left pectoral fin. (Note that edges of both fins are bordered by reinforcing wires used during preparation). (See Figs 5 and 6 for a more general perspective.) D,E, anterior and left lateral views of an isolated ring centrum, QMF31881. Scale: 10mm.

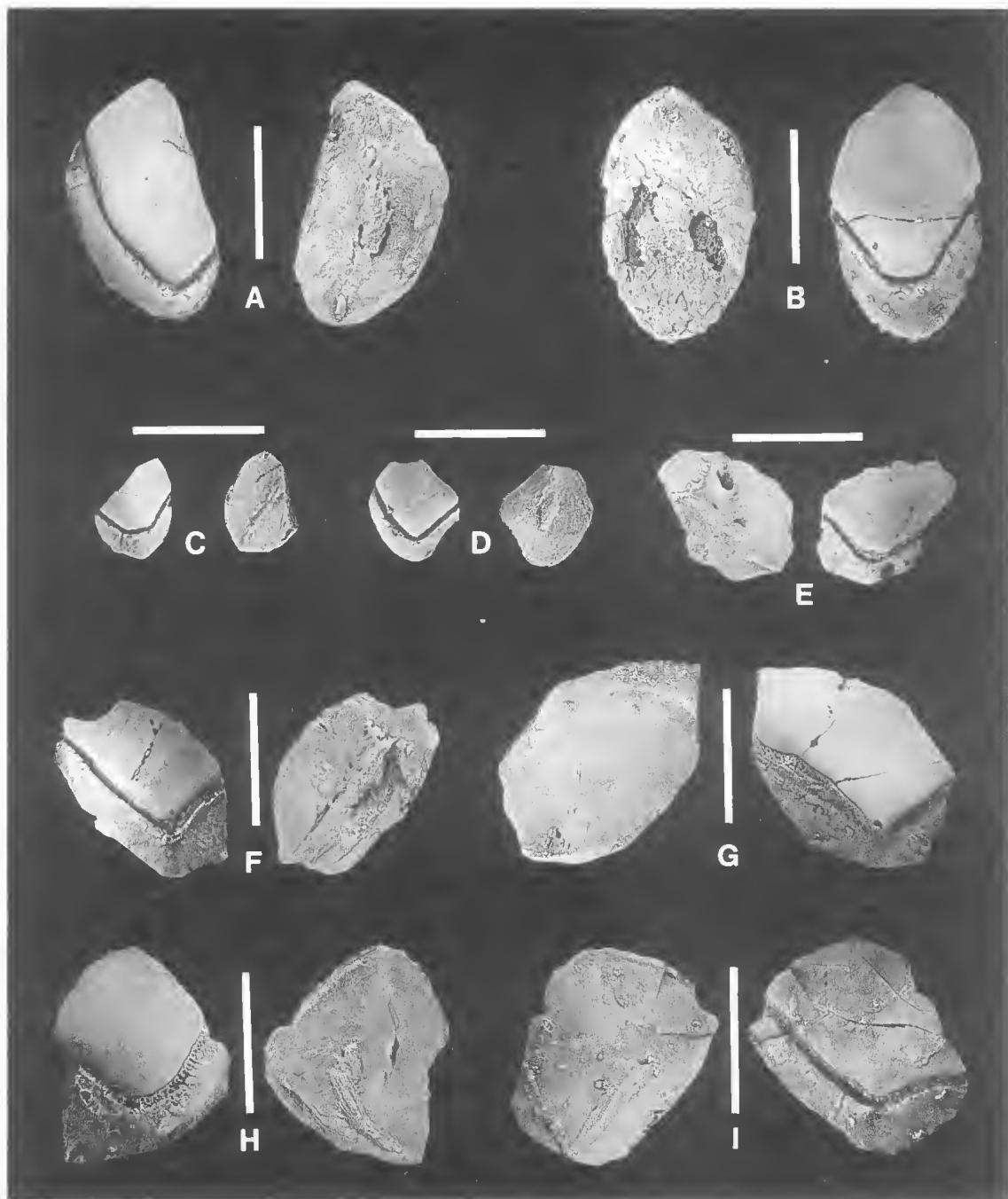


FIG. 65. *Cladrosymblema narrienense*. Scales from different parts of the body in external and internal views. Scales are almost complete. A, from left lower flank, QMF31889. B, from mid-flank, QMF31881. C,D, small scales from mid-line, QMF31891-2. E, lateral line scale from flank, with openings for canal shown, QMF31893. F, from right dorsolateral flank; posterior edge broken, QMF31894. G, overlap on left side of photograph turned down sharply, implying a position adjacent to a sharp change in body conformation, QMF31895. H,I, flat scales from anterodorsal or anteroventral body, QMF31896-7. Note variation in the nature of the ridges and irregularities on the inner surfaces. Exposed vascular bone in the gutter bordering the cosmine surface is well shown in A, G, H and I. Scale: 10mm.

metrical in those dorso- and ventrolaterally situated on the body. Symmetrically arched scales, assumed to be from posterior mid-dorsal positions, are included in our sample (Fig. 65C,D).

The rhombic part of a flank scale occupies about two-thirds of the surface area of the scale. It is separated from the overlapped bony surface by a strong groove or gutter which exposes coarse vesicular bone (Figs 65F-I; 66A). The remainder of the overlapped surface is usually covered with dense lamellar bone on both inner and outer surfaces. This overlapped part is usually in the plane of the remainder of the scale, but occasional individuals, which must have come from parts of the body where the curvature was high, show the overlap inturned at an angle (Fig. 65G).

The scales never have a peg and socket structure; they apparently depended entirely on overlap and soft tissue to maintain their position on the body. The inner surface of some scales has a strong ridge that could be interpreted as the remnant of an original peg and socket ridge. This ridge is very variable in form and orientation, ranging from narrow and sharp-keeled to broad and flattened. Normally, the ridge shows a series

of striations parallel with its length, these indicating the addition of successive layers of bone independently of the layers forming the remainder of the internal surface (Fig. 65F,H,I). In addition its margins are commonly undercut, suggesting either resorption or the failure of the collagen-rich isopedin to mineralise (see below) (Figs 65F; 68C). It should be noted that the ridge is absent, or only poorly developed, on many scales.

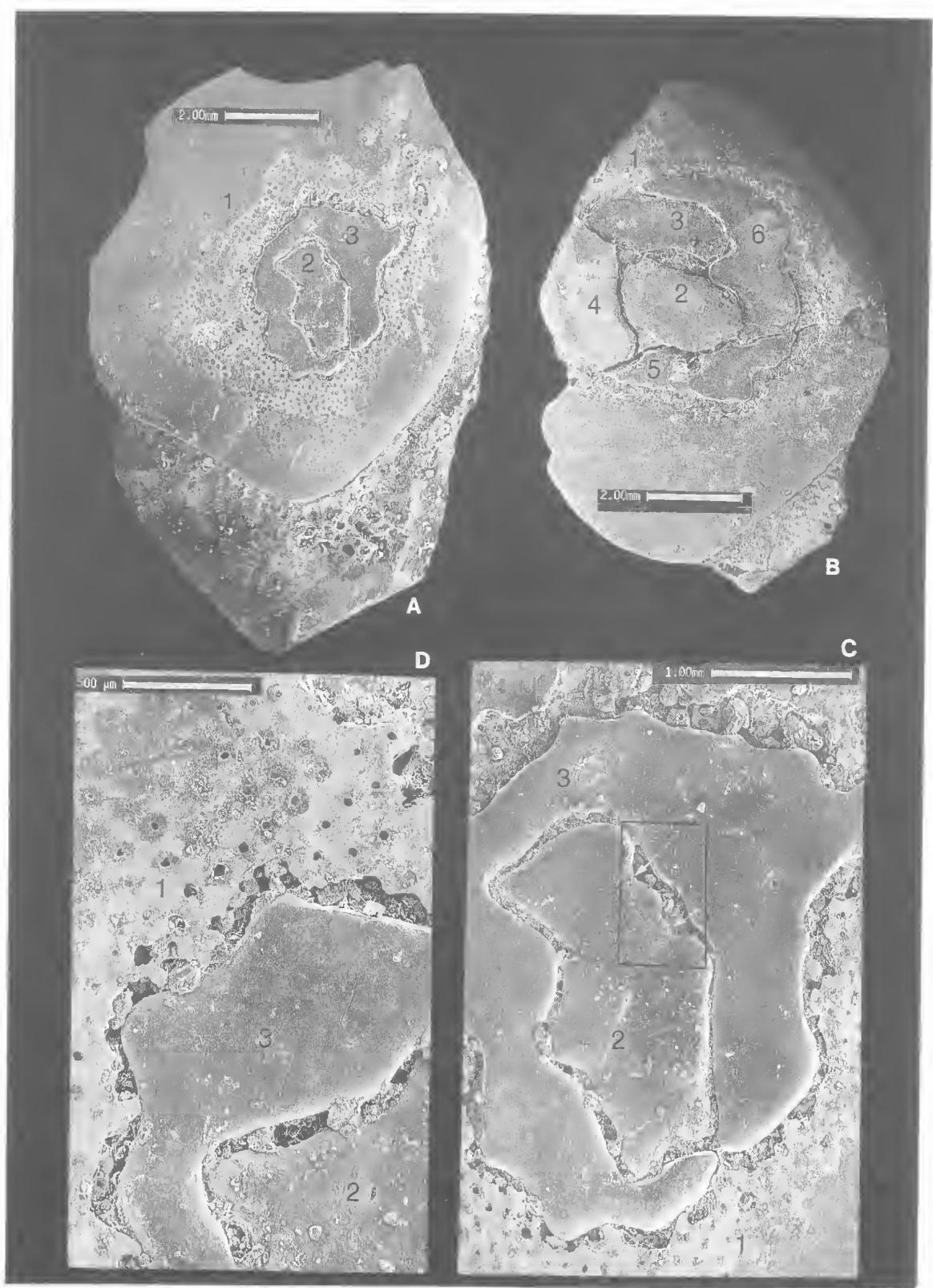
As well as the ridge, several other features of the internal surface are noteworthy. Many scales are not smooth but show a variety of apparent resorption features, from an extreme in which almost the entire lamellar layer is missing and the vesicular layer is exposed, to a condition in which a number of irregular mounds are scattered over the surface, to one in which only a few small depressions separate broader flat surfaces (Fig. 65B). In addition, it is not uncommon to find a scale in which one or more of the lamellar layers is only loosely attached to other inner layers. As indicated above, we take this to mean that mineralisation of the collagen-rich isopedin layers was incomplete when the animal died, allow-

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FIG. 66. *Cladarosymblema narrienense*. A,B, SEMs of two incomplete scales showing resorption and new cosmine growth. A, shows removal of the enamel layer in a broad band around the resorption ring, exposing the tops of the enlarged flasks, QMF31902. Near the bottom of the scale (arrow) only part of the enamel has been removed. B, a similar scale, QMF31903, with a central patch of replacement cosmine (2), and an incomplete annulus of replacement cosmine which is composed of four incomplete segments, (3-6). Note that at the time of death, parts of the margins of 3 and 4 were in process of resorption, and all the margins of 5 and 6 were in process of growth, indicating they may have been part of the same growth phase. C, enlargement of central part of A. In the centre of the resorption patch is regrown cosmine in process of resorption again. Note that in places its margins are entire, but at the points marked (arrows) they are irregular. An enlargement of the area (rectangle) is shown in Fig. 70A. These two scales demonstrate that cosmine replacement is a multiphase phenomenon. D, shows an enlargement of the bottom left of C in a rotated orientation. Note the resorption edge in the old cosmine is highly irregular and in places seems to have been progressing without the coalescence of enlarged pores. Note also dark rings around the pores in both the old and the new cosmine. The specimen was gold-coated, and hence these rings represent slight depressions in the surface. We consider that the depressions are the result of slight *post mortem* shrinkage around the flasks after the decay of soft tissues in the flasks. Those in the old cosmine may be emphasised because the underlying dentine around the walls of the flasks has been resorbed. In all figures, 1 denotes the oldest, and subsequent numbers, successively younger phases of cosmine growth.

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FIG. 67. A-D, *Cladarosymblema narrienense*. All SEMs. A-B, central part of a scale, QMF33055, at two magnifications. In A note the unchanged pores at the top of the photograph, the progressive increase in size downwards as the enamel becomes thinner, and finally the area of complete resorption around the newly formed cosmine towards the bottom of the photograph. B, enlargement of part of A to show the finished edge of the new cosmine and the details of the resorption edges above. C, part of the surface of a large scale, QMF31904, showing new cosmine occupying almost all available resorbed space. Old cosmine adjacent to the resorbed edge shows no evidence of enlarged flask chamber openings. New cosmine stands a little higher than the surrounding old surface, forming low blisters. Scale: 1 mm. D, surface of a scale on which resorption has just begun. Unlike the previous figure in which no enlargement of the pores has taken place, and Figs 66A,B and 67A,B in which the walls of the flasks have been resorbed in an irregular fashion, the more deeply resorbed pores in this figure show regular walls down as far as the mesh canals. Cosmine phases numbered as in Fig. 66.



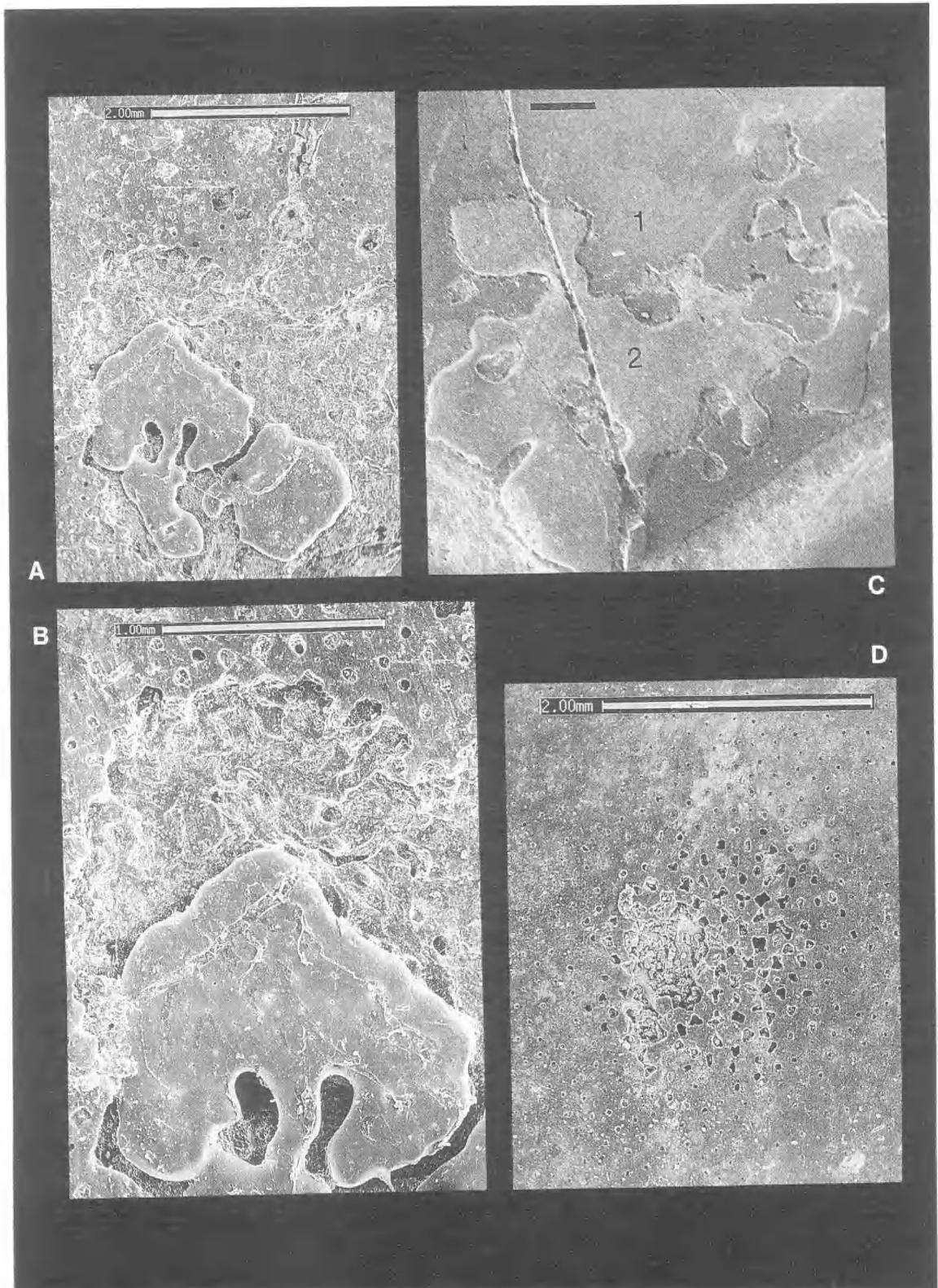


FIG. 67

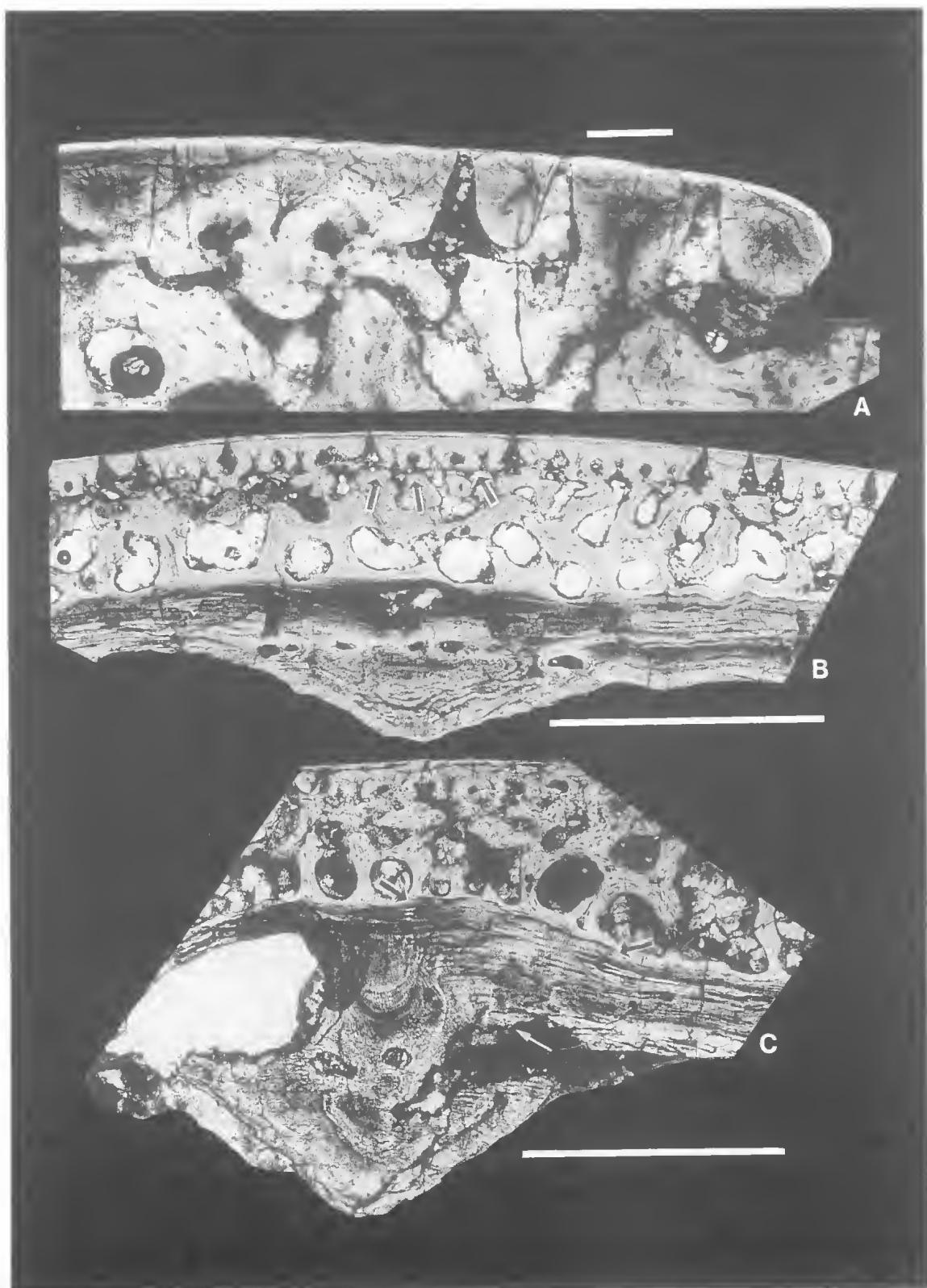
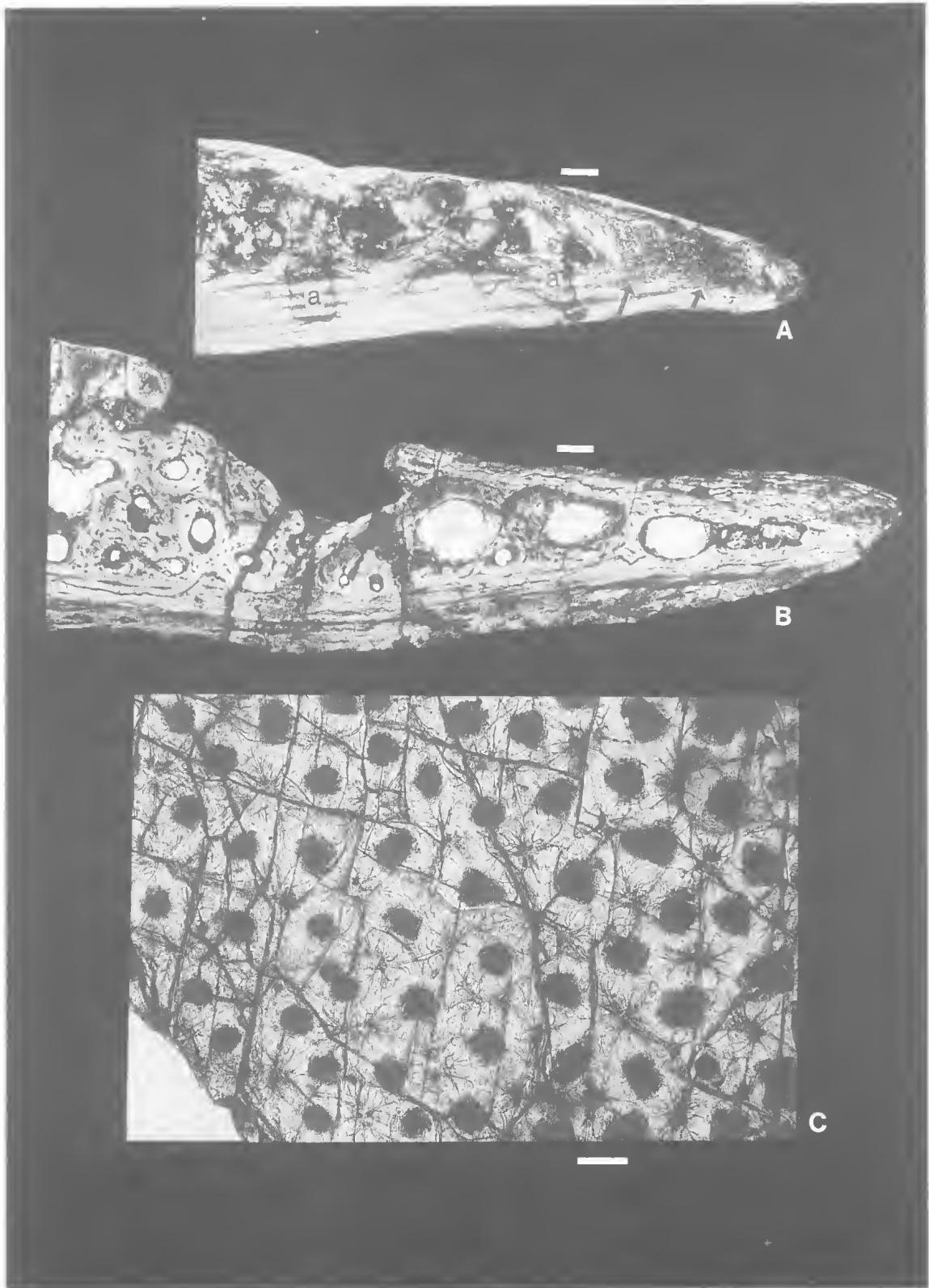


FIG. 68



ing separation of the ossified layers to take place after the collagen decomposed. As Kerr (1955) has shown for extant dipnoans, and Smith et al. (1972) have shown for *Latimeria*, the lamellar isopedin is composed mainly of collagen fibres, some of which become mineralised. In Devonian and Carboniferous dipnoans the mineralisation of these lamellae has proceeded almost to completion (Pridmore & Barwick, 1993). This then raises the question of whether the above-mentioned patchy appearance is the result of resorption or incomplete mineralisation. We have reached the conclusion that resorption is at least a partial cause. Thin sections show that the internal ridge is often bounded by gaps in the lamellae, but in some sections, the ridge lamellae terminate sharply against the truncated ends of other lamellae (Fig. 68C: black arrows). This has the appearance of resorption prior to the growth of the ridge.

The lateral line has been observed on isolated scales (Fig. 65E). It enters the scale anteriorly in front of the deep groove, and exits it posteriorly on the inner surface well anterior to the edge of the scale. Thus the line is completely covered from the exterior, and opens to the surface only through a number of large pores. A dorsoventrally oriented thin pit-line is visible on some scales.

The preservation of the holotype does not allow an exact count of scale rows, but we estimate that

there were c.15 vertical rows on each side of the trunk between the pectoral fin and the broken end of the specimen.

We have not recognised Westoll lines on any of the cosmine, but irregular resorption patches enclosing some regrowth have been observed. An occasional specimen shows resorption lines subparallel with the edge of the cosmine (Fig. 66A,B); however, most patches do not show any pattern with respect to either position on the scale or shape (Fig. 67C). As a result, our material supports previous studies (Westoll, 1936; Borgen, 1989, 1992), which have concluded that resorption is not normally, if ever, related to marginal growth of the cosmine. Those resorbed patches that are within the cosmine area are unevenly distributed, and the replacement cosmine was obviously expanding rapidly to fill the vacated spaces at the time of death. This new tissue was sometimes at the same level as the surrounding surface, and sometimes slightly raised to form a low blister.

A common phenomenon in the scales of *Cladarosymblema* is the resorption of the superficial layer of enamel in a wide band around a resorption zone that cuts through the whole cosmine layer (Fig. 66A). This is taken to represent the first stage of cosmine resorption. Subsequent to the removal of the enamel, but in advance of the deep resorption edge (Fig. 66A-D), the size of

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FIG. 68. *Cladarosymblema narrienense*. Thin sections of scales showing internal structures. A, section, QMF31900, showing the edge of the cosmine with the enamel layer wrapped around the end of the dentine. Three flask chambers open vertically into the bone vesicles, the osteocyte spaces being conspicuous. The dentine 'trees' are well developed. B, part of vertical section, QMF31899, through the whole thickness of a scale including the ridge on the inner surface. Note the clearly defined cosmine layer and the cross-canals in the centre of the photograph (arrows) showing greater regularity than normal. The inner lamellar layer is thickened at the median ridge which shows some lamellae folded back on themselves, indicating that the ridge was not formed simply by thickening of the lamellae. C, vertical section, QMF3898, of a scale to show the structure of a ridge in detail. Note resorption on the right (white arrow), some continuous lamellae between the ridge and the vesicular bone, the interrupted lamellae immediately under the vesicular bone (black arrows), and the irregular, almost chaotic arrangement of the tissue forming the bulk of the ridge. Scale: 1mm.

facing page

FIG. 69. *Cladarosymblema narrienense*. A,B, two vertical sections through the overlapped parts of two scales. A, QMF31899, basal lamellar layers are progressively truncated against the vesicular layer, and towards the right extremity, note the breakdown of the lamellae (arrows) immediately prior to resorption and replacement by vesicular bone. Irregular patches (a) are gas bubbles in the slide. B, QMF31900, section cuts across edge of the cosmine and its surrounding gutter, exposing the vesicular layer. Note basal lamellae truncated against the vesicular layer, but outermost ones continue around the scale margin on to the outer surface. C, QMF31901, horizontal section through the dentine layer of the cosmine of a scale, cut near the level of the top of the pulp canals, QMF31901. Large black openings are flask chambers and radial arrays of the dentine tubules are obvious. Note that the tubules are bent so that they are approximately radially arranged around the flasks as well as the pulp canals. Contrast this with the organisation in the unidentified osteolepidid scale figured by Gross (1956: pl. 10, fig. 3). Scale: 0.1mm.

the flask-chamber pores is enlarged in a systematic fashion, indicating that scleroclasts occurred within the flask chambers, as Borgen (1989, 1992) has argued. However, in our material the resorbing edge is not formed from coalescing enlarged flasks, but rather from the junction between an advancing front of resorption and the resorbing margins of the flasks. This evidence indicates that scleroclasts were present in the bone and that some of them migrated into the flasks in advance of the resorbing front. This view is confirmed by examination of Figs 66D & 70A, in which a zone of resorption is bordered on one side by an advancing edge, and on the other by a ragged edge of resorbed cosmine. The latter shows no sign of enlarged cosmine pores, indicating that resorption took place by an advancing front alone. In addition, Fig. 67C shows a scale in which there is no evidence of enlarged flask openings in advance of the resorbing front. We conclude from this that the function of the flask chambers could not have been *only* to house the cells involved in cosmine removal, although such cells did function from the flasks in at least some specimens during resorption phases. As Borgen has pointed out, the soft tissues on the surface of the scale could have been supplied with nutrients only via the flasks, and presumably this must have been a second function. The degree of organisation of the flasks and the cross canals, however, is far in excess of what would be necessary to serve these two functions.

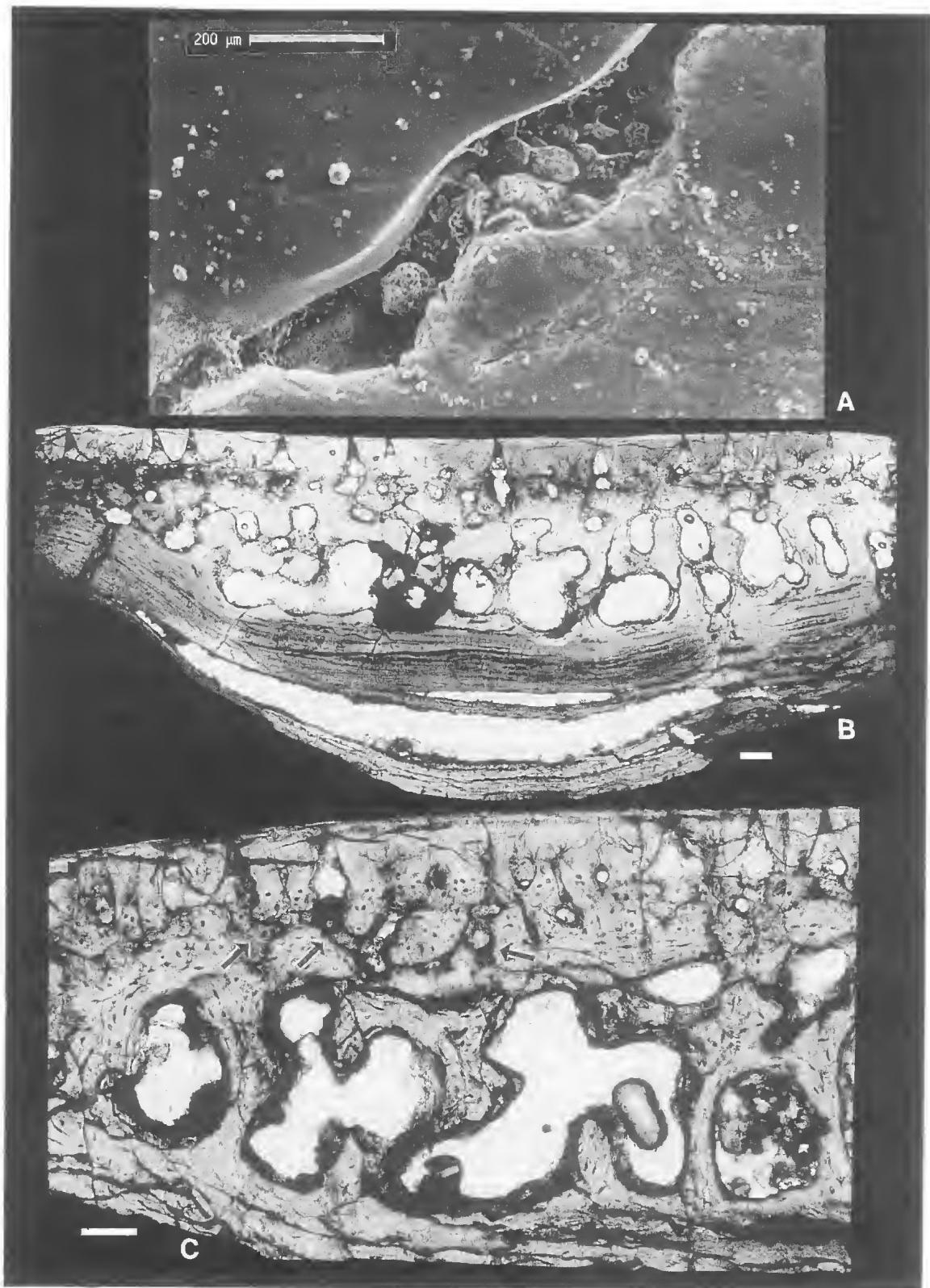
Scale Histology. Sections of the scales are shown in Figs. 68-74. The enamel layer (or enameloid according to Meinke & Thomson, 1983) is thin and overlies a thick dentine layer in which the cosmine flask chambers lie. The enamel layer folds over around the finished edges of the cosmine as shown in Fig. 68A, but as that section shows, no downturned enamel edges are seen buried within the cosmine. This means that at least the margins of the cosmine would have had to be resorbed to allow growth (Gross, 1956; Thomson, 1975). The matter is discussed below under Scale Growth.

The flasks are very fine, and their openings to the surface are only 7 - 10 microns in diameter.

They are closely spaced, the count being c.60 per square mm. In vertical thin sections the upper parts of the flasks are almost conical in shape or have concave walls, there being little outward curvature of the walls to produce pear shapes (Figs 68A,B; 70B,C). In horizontal section, the flasks show irregularities in the lower half of the chambers because of folding to produce the mesh canals (Figs 71A; 72A). These mesh canals are highly variable in shape (Figs 68A,B; 70B,C; 71A,B). Some have their greatest diameter where they join the flasks, but decrease dramatically to less than half that value where they interconnect with those from adjacent flasks. In this respect the mesh canals are very similar to those figured for *Megalichthys laticeps* by Gross (1956: fig. 51), but unlike those figured by Thomson (1975: figs. 26-28) for *Ectosteorhachis nitidus*. On the other hand, some scales have flasks and thin mesh canals closely comparable with the latter. Nor are the canals regular in number. Some chambers have three and others four mesh canals joining their bases, in some areas three dominating and in others, four. An occasional flask shows five mesh canals. The arrangement depends on the packing arrangement of the flask chambers. The mesh canals are always on one level rather than two, as Gross (1956: figs 34A,B) figured for certain osteolepiforms from Estonia. In those specimens he recorded 'Unter-Maschkanalen' as well as 'Maschkanalen'.

At their bases the flasks extend into vertical canals, some of which are so broad that they occupy almost the whole width of the base of the chamber (Figs 68A,B; 70B,C; 73B). These are joined laterally in an irregular fashion by branches to the vertical canals of adjacent flasks and to the pulp canals to form the cross-canals (Gross, 1956; Thomson, 1975). Although their arrangement is much less regular than in *M. laticeps*, these are very roughly sub-radially organised around the pulp canals, and only incidentally join the bases of the flasks. As can be seen from Gross (1956: figs 48A; 50C) the diameter and arrangement of these canals is very variable in *M. hibberti*, and some of them, instead of joining into the base of an adjacent flask chamber,

FIG. 70. *Cladarosymblema narrienense*. A, SEM of part of scale, QMF31902, in Fig. 66C, to show partial resorption of the second generation of cosmine (bottom right) and the advancing third generation (top left). B,C, two vertical sections through a scale. B shows well-preserved tissue layers and flask chambers, QMF31900. Basal lamellae show gaps that are the result either of separation during preservation, or failure to mineralize layers of collagen. C, section QMF31898, has the lamellar layer disrupted, but shows the flask chambers opening down into irregular cross-canals (arrows) and the relationship between bone containing osteocyte spaces, bases of flasks, and pulp canals. Scales B-C: 0.1mm.



turn down into the vesicular bone. Many of them do the same in *C. narriense*.

Each dentine column between adjacent flasks is almost invariably organised around a single pulp canal that terminates in very variably arranged tubules (Figs 68A,B; 69C; 70C; 71A,B). Occasionally two closely-spaced pulp canals are present between a group of flask chambers (see right end of Fig. 70B and the region to the right of centre in Fig. 69C). The tissue flanking the flask chambers above the level of the mesh canals is dentine, whereas the deeper tissue around the vertical and cross-canals contains osteocyte spaces (Figs 68A; 70C), some of which have arachnoid shapes like those figured by Thomson (1975) for *E. nitidus*. The space between the vertically standing cylinders was filled with dentine deposited from and between the variously oriented branched ends of the tubules. From the outer ends of the pulp canals, branches radiate in the usual way (Fig. 69C), and these give rise to dentine tubules that are easily visible, many being stained by iron compounds. In vertical section the vertical pulp canal itself is often apparently devoid of surrounding tubules, although the tubules can be distinguished at high magnifications with appropriate illumination. On the other hand, horizontal sections show that dentine canals ramify from the trunk in much the same way as at the top of the pulp canals (Figs 69C; 75C). The reason for this apparent discrepancy is the fact that it is unusual for a vertical section to intersect one or more of the main lateral trunks from the canal, and only the intersections with the more numerous fine tubules are seen.

The dentine shows distinctive patterns in thin section. The crystallites forming on the flanks of the flask chambers are disposed normally to the surfaces of the flasks. This is inevitable because the first-formed layers of mineralisation were deposited around the flasks, as they indeed have to be because the flasks, which open to the exterior, must have been present when the first dentine tissue formed. Subsequently, mineralisation retreated towards the pulp canals. However, although in thin section it is difficult to see growth lines of the kind illustrated by Thomson (1975: fig. 21) around the flask chambers of *E. nitidus*, they can be readily recognised in SEMs of etched surfaces (Fig. 71A,B). We have illustrated such growth lines in Fig. 75.

There is optical continuity in the crystallites surrounding each flask chamber, and under crossed polars the extinction cross moves as though it formed a unit with the optic c-axes of

the crystallites radially arranged. For obvious reasons, the crystallites must have a radial disposition around the pulp canals as well as the flask chambers. Because the dentine tubules are also disposed normal to the surface of the pulp canal at each stage of growth, the shape of the tubules reflects the orientation of the dentine crystallites. This means that the dentine tubules must be standing in a radial array over the top of each pulp canal, and hence the arrangement of the crystallites in that region is only partly radial around the point marked by the top of the pulp canal. As can be seen from Fig. 69C and from Gross (1956: pl. 10, fig. 3), the branching and the bending of the tubules allows their ends to be arrayed normal to the surface of the flask chambers, reflecting the radial arrangement of the crystallites with respect to the flask walls. The arrangement of the tubules at the different levels in the cosmine is illustrated diagrammatically in Fig. 75.

As has been indicated above, at a deeper level in the cosmine the concentric layering of the dentine around the pulp canals becomes obvious (Fig. 71A). This is because growth in the later stages of deposition was restricted to the narrow cylinders around the canals. Before these cylinders were formed, the spaces between the successive positions of the cylinders had been occupied by dentine deposited from much larger pulp canals, whose form can be inferred from the variously oriented branched ends of the dentine tubules. Because the earliest dentine was deposited around the flasks, and it had to be deposited from a pulp canal, the walls of each flask were contributed to by three or four different pulp canals (Fig. 75B,C). This inevitably results in zones of interference between neighbouring pulp canals. These zones are stippled in Fig. 75B,C. Thomson (1975) referred to this tissue formed in the interference zones between the cylinders as 'interstitial dentine', a name that he also applied to the dentine formed over the top of the pulp canals. We see no need for a separate term for this dentine, which is really only the result of the changing shape of the pulp canals during growth (Figs 72A,B; 75).

The dentine overlies a coarsely vesicular bony layer (the spongiosa of Gross, 1956, and Thomson, 1975) that usually extends across the whole width and length of the scale, although it is missing in the overlapped zones of some specimens. The vesicular layer consists of one to three irregular layers of vesicles. If the vesicles are of more than one size, the largest ones tend to occur at the base of the layer (Figs 68B,C; 70B,C); in addition

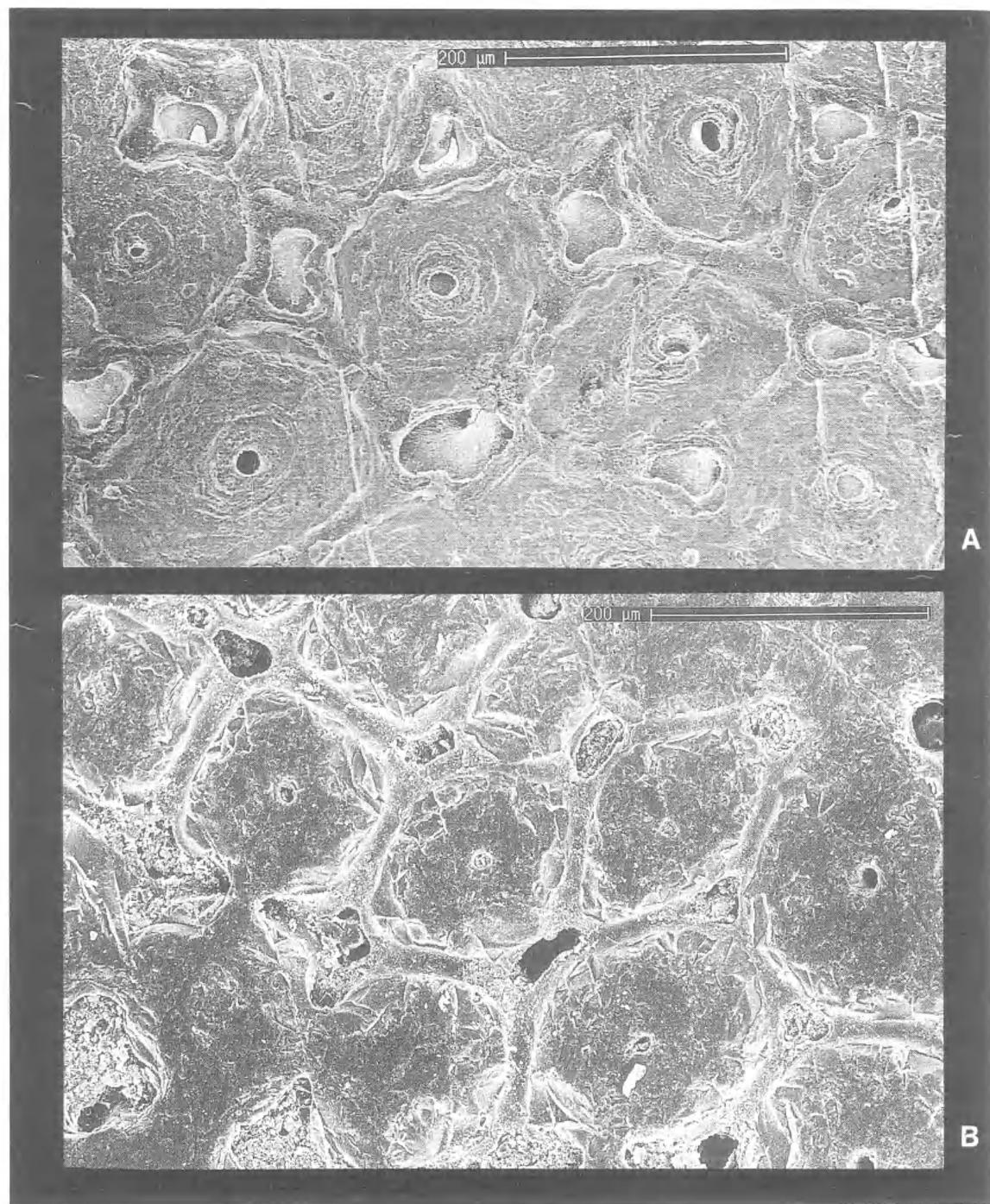


FIG. 71. *Cladarosymblema narrienense*. A,B, two SEMs of a polished horizontal section of a scale, QMF33052, cut near bases of flask chambers. In each, small holes are the pulp canals which are surrounded by concentric layers of dentine. In A, which is cut a little deeper into the scale than B, highly irregular bases of the flasks are well seen, in places also showing the mesh canals. In B, mesh canals are almost complete. The bottom left of the photo is slightly above the mesh canals and the top right is below them. Both sections are from polished surfaces etched for about 90 seconds in 1% HCl.

there is a tendency for the size to decrease marginally. Within the overlap area, the vesicles have no preferred size.

The basal layer is made of dense lamellar bone that is added both marginally and at the base of the scale. Sections through the overlapped part of the scale show that the lamellae fold around from the internal to the external surface (Figs 69A,B; 73A), indicating that they were laid down from the tissue of the enveloping scale pocket. At the scale margins, where the lamellae can be followed around from the basal to the external surface, only the outer layers are complete, the inner layers being truncated against the vesicular layer where it is present, as is shown in the above-mentioned figures. The vesicular layer in this marginal zone tends to lose its coherence, and towards the outer limit the vesicle size becomes small. This implies that the vesicular layer expanded marginally by resorbing the lamellar layer, which it then replaced, the vesicles gradually growing in size as growth removed them from the marginal area.

The lamellar layers were added as sheets to the inner surface of the scale. Their internal structure is distinctive as is well shown under crossed polars and in SEMs. Under crossed polars, alternate layers go into extinction almost as a unit, indicating that these layers are composed of crystals set normal to the surface. In plane polarised light, each layer is seen to be crossed by fine lines that may define the crystal boundaries, but the lines are marked by films of iron oxides, suggesting that they may be infillings of very fine pores. Scanning electron micrographs show no sign of such pores, but can be interpreted as supporting the vertical crystal hypothesis (Fig. 73C). The alternate lamellae show no such pattern under crossed polars, being partly extinguished in all positions. Presumably, therefore, the mineralising tissue has the capacity to change its mode of action in a regular way during growth. This must be in some way related to the orientation of the fibres in the collagen, the mineralisation of which has been referred to above. Gross (1956: figs 33A; 35A) illustrated this phenomenon in other osteolepiforms. He referred to the vertical crystal layers as 'quergetroffenes Fasserbündel', and the

alternate layers as 'längsgetroffenes Fasserbündel'.

The contact between the vesicular and lamellar layers over the width of the scale does not follow the boundary of a single lamellar layer. Instead, several basal lamellae are truncated obliquely against the vesicular layer (Fig. 69A,B). At several points the wall of a vesicle can be seen to have increased its thickness at the expense of the adjacent lamellar layer (Figs 68C; 70B). Some resorption of the latter must have taken place to allow the vesicle walls to grow.

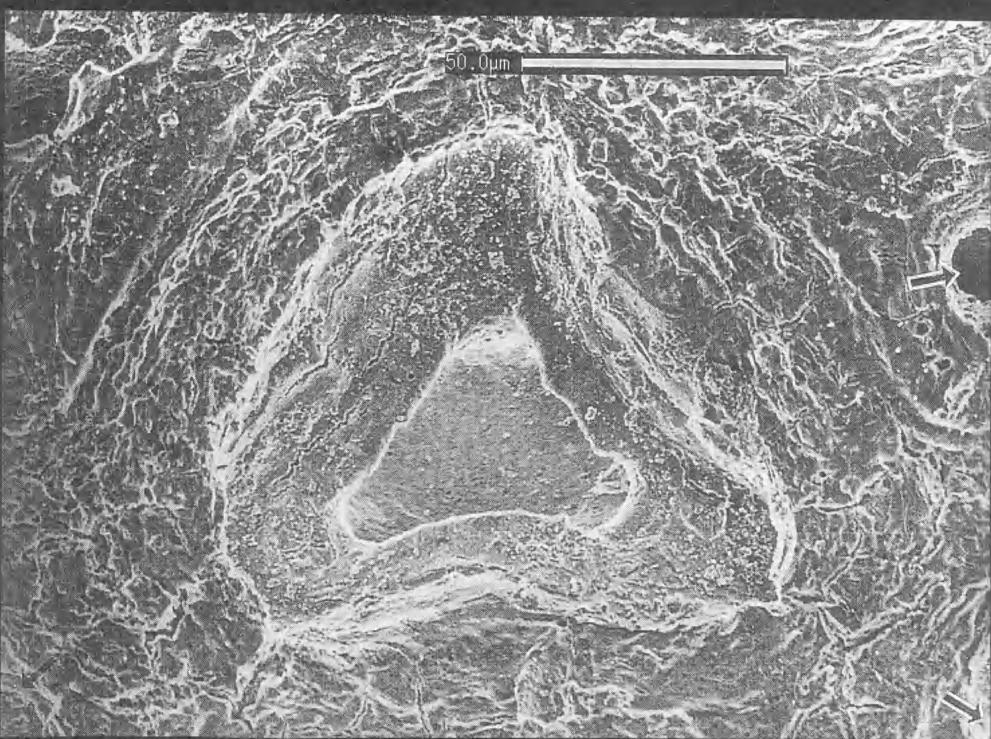
As indicated in the section on gross morphology of the scales, some of the layers fall free during acid preparation, and we have attributed this to the absence of mineralisation in some of the lamellae. Thin sections tend to confirm that interpretation. As shown in Fig. 70B, gaps are completely conformable with under- and overlying lamellae, which in turn show no corrosion. This pattern would be difficult to produce by selective resorption. On the same thin section, patches of resorption are present and are easily distinguishable. Hence, we prefer the non-mineralisation hypothesis.

Sections of the ridge on the inner surface of some scales show that it was not formed by thickening of one or more lamellar layers. Instead, it is a highly discrete structure that is composed of thin layers showing complex folding and radial features of unknown origin (Figs 68B,C; 73B).

Scale Growth. Several of the above features provide clear indications of the mode of growth of these scales. The absence of Westoll lines in the cosmine, the presence of infolded edges of enamel around the cosmine margins, and the absence of older enamel rims incorporated in the cosmine, indicate that the enamel margins were completely resorbed during growth phases. On the other hand, thin sections show no sign of discontinuity within the cosmine itself. As we can find no evidence of the resorption of the cosmine layer from a whole scale at any one time, the only conclusion seems to be that the downfolded enamel margins were resorbed in advance of growth.

Resorption patterns on the scales vary tremendously. Examples are shown in Figs 66-67. A

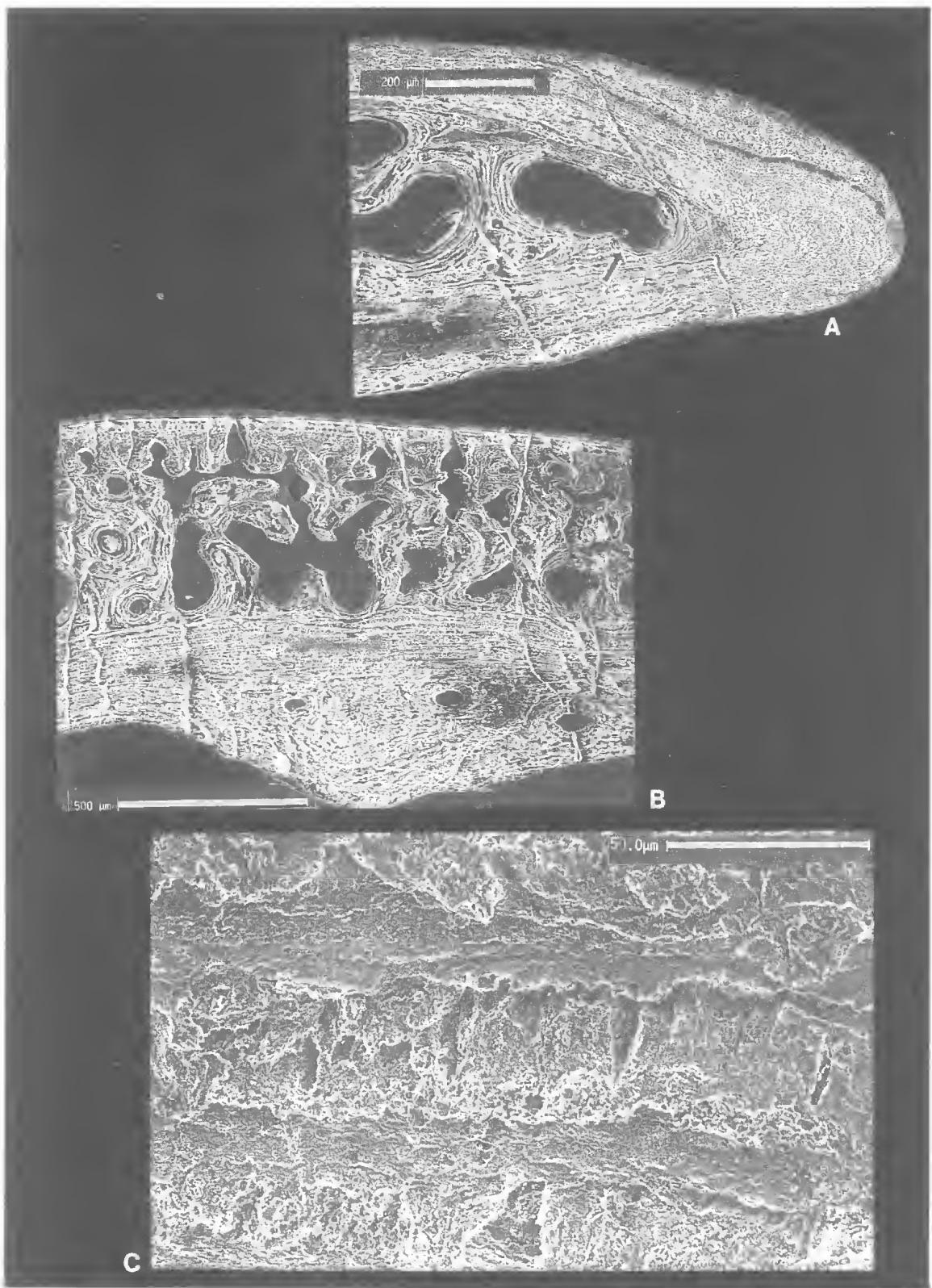
FIG. 72. *Cladarosymblera narrienense*. A,B, SEMs of the dentine layer of the cosmine in a scale, QMF33051, prepared from a polished section cut down to just below the base of the flask chambers. A, the base of a flask chamber with adjacent pulp canals (arrows). B, pulp canal with adjacent flasks (arrows). The flask at the bottom left of the figure is the one shown in A. The concentric layering of the dentine around the pulp canal, and the so-called interstitial dentine of Thomson (1975) are apparent. In the interstitial dentine note the well-defined sub-circular pores, 0.5 - 2.5 microns in diameter, towards the bottom right of the figure where the dentine tubules have been cut across obliquely.



A



B



pattern of resorption has been clearly established. First the enamel layer was removed from a patch on the surface (Figs 66A; 67A,B,D). Presumably this could be accomplished only by the action of the overlying dermal layer. Then removal of the dentine layer began progressively from the inner edge of the area from which the enamel had been removed. This progression was marked by an increase in the size of the flask chambers (Figs 66A,B; 67A,D). Such increase in size could be produced by two different processes. The first involves the removal of layers of dentine from the surface by continued action of the dermis, thus exposing progressively deeper sections through the flasks; this seems to have been the case in Fig. 67D, which gives the impression that the dentine surface was progressively lowered until the mesh canals were exposed. Alternatively, it could result from resorption of the inner walls of the flasks by osteoclasts housed within the flasks; where this occurred the inner walls of the flasks show progressively more irregular shapes as they increase in size (Fig. 66D), and eventually a point was reached where all the dentine was removed along a sharply defined vertical edge, indicating that resorption was taking place from beneath the dentine. This alternative view is espoused by Borgen (1989, 1992). The shape of the resorbing front indicates that osteoclasts were located not only in the flasks, but also in the underlying bone spaces. Indeed Borgen reached a similar conclusion, but tentatively identified the deep source as the pulp canals. We see no evidence in our material of the involvement of the pulp canals. Thus it seems that resorbing cells were located in the epidermis, in the tissue lining the flask chambers, and in the bone spaces.

The specimen in Fig. 66A,C,D shows three phases of cosmine growth. The oldest phase is the most extensive, but the thinnest; it covers most of the cosmine surface and is labelled 1. The second oldest is in the central patch, labelled 2. Some of its edge is still entire but other parts show evidence of resorption (Figs 66A,C; 70A). The youngest, labelled 3, forms the almost complete annulus around the centre; it was growing both

centripetally and centrifugally, and its margins are entire everywhere. In Fig. 66B the annulus seems to have formed from more than one centre. Details of this figure are given in the caption to the figure itself. Several other scales show quite different patterns (see Fig. 67A), and some of them have only tiny areas of resorption or none at all. Space forbids the illustration of the full range of variation in cosmine growth that we have observed.

As mentioned in the description of the gross morphology, there is a gutter between the cosmine and the overlapped part covered by lamellar bone. Vesicular bone is normally, but not invariably, exposed in this gutter. For the area of cosmine to expand in the direction of the overlapped part, resorption of the free edge of the lamellar layer against the gutter would have to take place in advance of the growing front, thus exposing the vesicles. That some of this resorption went deeper than the surface is demonstrated by the occurrence in the gutter of vesicles with their tops removed (Fig. 69B). In other scales, the continuity of the lamellar layer of the overlapped surface to the edge of the cosmine, shows that resorption was lagging in at least some individuals. This variation could indicate different stages of growth rather than individual differences.

TEETH AND TUSKS

In addition to the teeth in the jaws, the matrix has yielded several isolated teeth and tusks. We have been able to section and study some of these in isolation. The infolding of the dentine and enamel is simple and, as in other osteolepiforms, it is polyplacodont (Schultze, 1969; Warren & Davey, 1992: 118). The folding reaches less than half way up the tusk from the base. The surface layer of the tusks is covered with very fine anastomosing longitudinal striations (Fig. 76B,C). As is normal for osteolepiforms, these are best developed towards the base of the tooth on the outfolds of the enamel and dentine, but can still be traced almost to the tip. At the base they are spaced c.60 per mm transversely, which is about four or five

FIG. 73. *Cladarosymblema narrienense*. A, SEM of the overlapped part of a scale, QMF33053. Note continuity of the lamellar layers around the margin, breakdown of the lamellae in advance of the growth of the vesicular layer, and how newly-formed rings around the most lateral vesicle cut the lamellae of the lamellar layer (arrow). B, deeply etched vertical section through the ridge on the inner surface of the same scale. Note laminac in the enamel, irregular orientation of the cross canals, continuity of the lamellae of the inner layer between the vesicular layer and the ridge, and internal irregularity of lamellae in core of the ridge. C, SEM of part of the lamellar layer of a scale, QMF33053, to show the different orientation of the crystallites in alternate layers. The surface was polished and etched in 1% HCl for about 90 seconds.

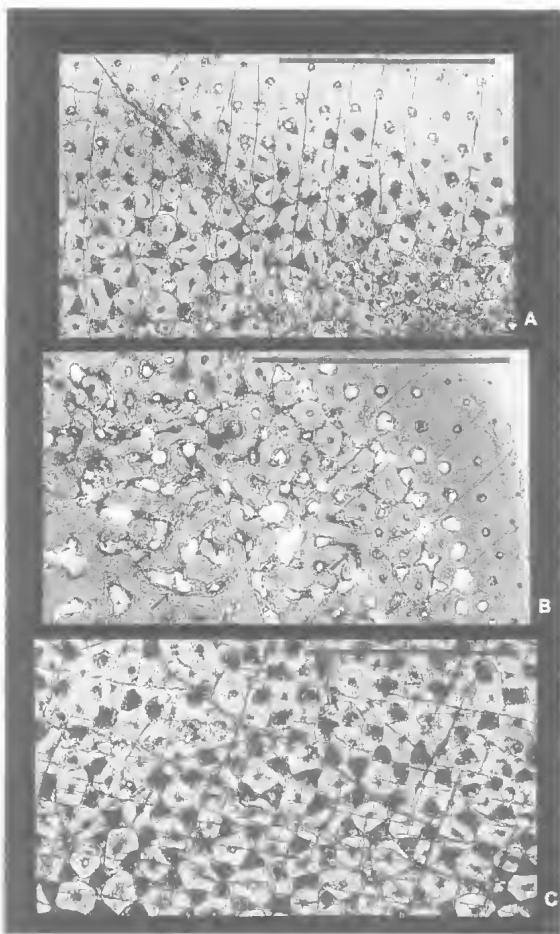


FIG. 74. *Cladarosymblema narrienense*. Thin sections of scales showing shape variation in elements of the cosmic layer and immediately underlying bone. A,B, sections slightly oblique to scale surface; outer edge of scales to the upper right. Narrow openings into flask chambers become progressively greater in diameter away from the edge; mesh canals then become obvious. A, many flask bases are filled with a ferruginous compound. Annuli of dentine around pulp canals are obvious. Dark spots in the annuli of A indicate that the level of true bone has been reached; cf. Fig. 70C. B, more obliquely cut, bases of dentine annuli open out into crude and irregular cross-canals (arrows). C, QMF31901, section is cut mostly through level of the mesh canals, which are filled with an iron compound. Note also fine radial dentine tubules in dentine columns. Scale: 1mm.

times the number found in *M. hibberti* (personal observation).

A tusk broken from the holotype, and two other isolated tusks, have been transversely serially sectioned. Sections from the former series are figured as Figs 77A,B and 78A,B. At the base of

the tusk, the pulp cavity is very wide and is surrounded by a thin layer of folded dentine. In places the folds themselves are slightly folded (Fig. 77B). Progressively higher on the tusk, the dentine thickens rapidly and the folds are more clearly defined. Towards the base of the tooth, the gaps between the folds are crossed by tissue isolating as many as four spaces (Fig. 77B). This crossing tissue is honey-coloured like the dentine, but it contains no dentine tubules. Presumably it is bone of attachment, a view that is supported by the fact that further up in the tusk this 'crossing tissue' disappears and the folds are open to the external surface.

The surface of the tusk is covered by enamel in most specimens. Where it is clear (Fig. 78C,E), the enamel is usually thin in comparison with that on the tusks of *Megalichthys* sp. figured by Smith (1989). In others it has broken down diagenetically, as shown in Figs 77A; 78A,B). The enamel shows little lamination in transverse and longitudinal section (Figs 78C; 79A), and we have not been able to produce details of crystal bundles similar to those produced by Smith (1989: figs 13-14) for *Megalichthys*. This could be the result of preservation or of faulty technique, rather than absence of the tissue in question.

Immediately beneath the enamel is a thin but distinct layer of so-called globular dentine within which the tips of the dentine tubules ramify (Fig. 78C,E). This is very similar to the layer in *Rhizodus* and *Megalichthys* figured by Smith (1989: figs 8A,B; 14C). Its presence throughout the length of the tooth cannot be established with certainty, but we consider that such a distribution is most probable.

Towards the distal part of the tusk, near the limits of and beyond the region of folding, transverse sections show the dentine tubules closely packed and dividing repeatedly towards the outer surface. In thin sections they seem to maintain their diameter throughout (Figs 77; 78), but as the SEMs reproduced in Figs 79C & 80 show, this is not always so. In Fig. 80C, for example, the tubules decrease in diameter considerably lateral to the division points and remain that way to the tooth margin.

The dentine tubules in the proximal sections of the tusk are straight or slightly curved to accommodate to the differences in shape between the inner and outer surfaces (Figs 77A,B; 78A,B). In vertical sections the tubules are straight to slightly curved, and in the basal part of the tooth are oriented at approximately 70° to the external surface; as is required by simple geometry, the

tubules are progressively more acute to the external surface towards the tip of the tooth. In optical thin sections the tubules seem to be similar to those of *?Megalichthys* figured by Schultze (1969: pl. III) and those of *Megalichthys* sp. figured by Smith (1989: figs 12A-C) in their close spacing, their orientation and their diameter. On the other hand, they are unlike those figured by Gross (1956: fig. 119, pl. 14, fig. 4) for *Latvius grewingki* in their spacing, in the obvious combs of fine tubules between the main ones, and in tubule diameter. However, SEMs show a variety of tubule morphology in *C. narrienense*. Although some of this variety could be the result of our failing to recognise different taxa in the collection, it is considered more likely to be the result of different phases of growth under different environmental conditions in the one taxon.

One of the noteworthy features of the teeth is the extent to which they show variation in growth. Three distinct types of growth laminae are known:

(1) The first involves major breaks marked by layers of amorphous tissue that survives etching in HCl. In some specimens such breaks mark total reorganisation of the tubules as shown in Fig. 79B,C; in others the branching pattern and diameter of the tubules changes as in Fig. 80E; and in still others the tubules are comparable on both sides of the break but they are not aligned on opposite sides. In thin sections it is not possible to discriminate structure within the tissue defining the growth halts, and in SEMs the breaks stand up as structureless walls as is shown in the above-mentioned figures. The tubules cannot be traced across these boundaries. During preparation it is not uncommon for the tooth to break up along these surfaces (Fig. 76D). The specimen of *?Megalichthys* figured by Schultze (1969: figs 1a, 1b, 3a) shows breaks of this kind.

(2) The second type is seen in optical thin-sections as dark coloured bands through which at least the major canals can be observed to pass (Figs 77A; 78A). These breaks are not so strongly marked as those of type 1. SEMs of these boundaries indicate that at least some of them are distinguished by changes in the branching pattern of the pulp canals (Fig. 80C,D). This type of surface apparently indicates the initiation of a new growth phase.

(3) The third is minor in comparison with the other two, and is recognised by thin sheets of some unspecified tissue that survives etching in HCl; these are closely spaced, and usually mark surfaces across which bifurcation or trifurcation

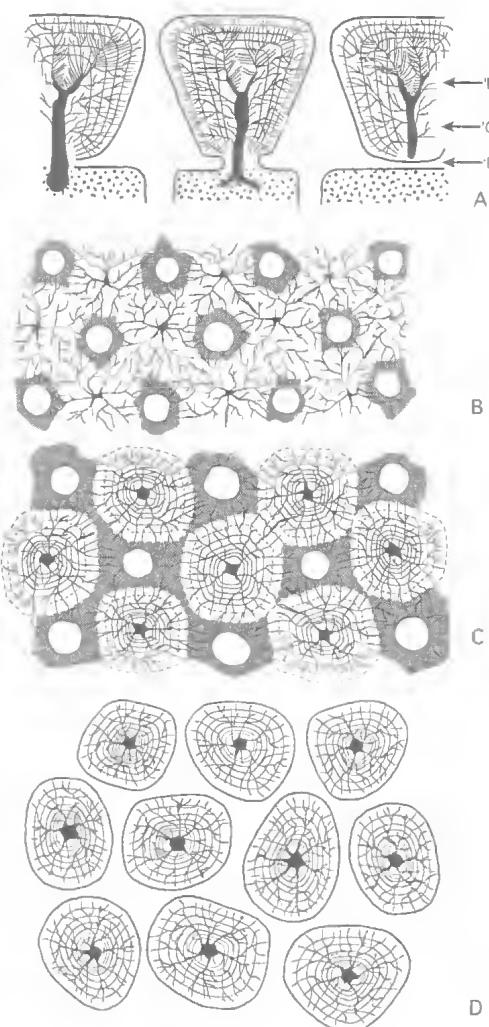


FIG. 75. *Ciuarosymblema narrienense*. Diagrammatic reconstruction of the cosmine of a scale. A, vertical section through two flasks and three pulp canals, showing the postulated growth lines in the dentine, the orientation of the tubules, and the osteocyte spaces at the base. Positions of sections B-D indicated. B, horizontal section cut at the top of the pulp canals. The stippled areas are Thomson's (1975) interstitial dentine; compare Fig. 69C. C, section cut half way down the pulp canal; compare Fig. 72B. D, section through the mesh canals; compare Fig. 71A-B.

of canals occurs (Fig. 80F). There is no interruption of canals at these boundaries, which are spaced at intervals of c.5 microns.

The different types of growth laminae are not mutually exclusive in teeth. For example, those

of the third type occur on the same tooth as the major breaks of type 1 above.

Our interpretation of the significance of these variations is inadequate, and needs much more work. It is in part hampered by the fact that our material is not from known positions in a jaw, and we are unable even to say if any one specimen is a small tusk or a large tooth. As a consequence, it is not possible to indicate if all the teeth and tusks in a single animal have a similar range of structures. At first sight, it is reasonable to conclude that there were major interruptions to the life history of many animals during which growth ceased, and following which reorganisation of the tubules took place. These could have been events such as droughts. Other animals need not have suffered such major changes, but nevertheless did experience lesser changes that produced the structures of type 2. Seasonal changes suggest themselves as an explanation. The minor breaks are possibly daily increments.

FUNCTIONAL INTERPRETATIONS

SWIMMING

Little attempt has been made to interpret the swimming mode of rhipidistian fishes since the work of Thomson (1969), although Ahlberg (1992) has commented on the porolepiforms, and Belles-Isles (1992) has examined both osteolepiforms and porolepiforms in this respect. Both these treatments dealt primarily with the caudal region of the animal, which our material lacks. Hence we have been forced to attack the problem independently, using such features as the scale structure and pattern, the body form, and the shape and structure of the pectoral fins.

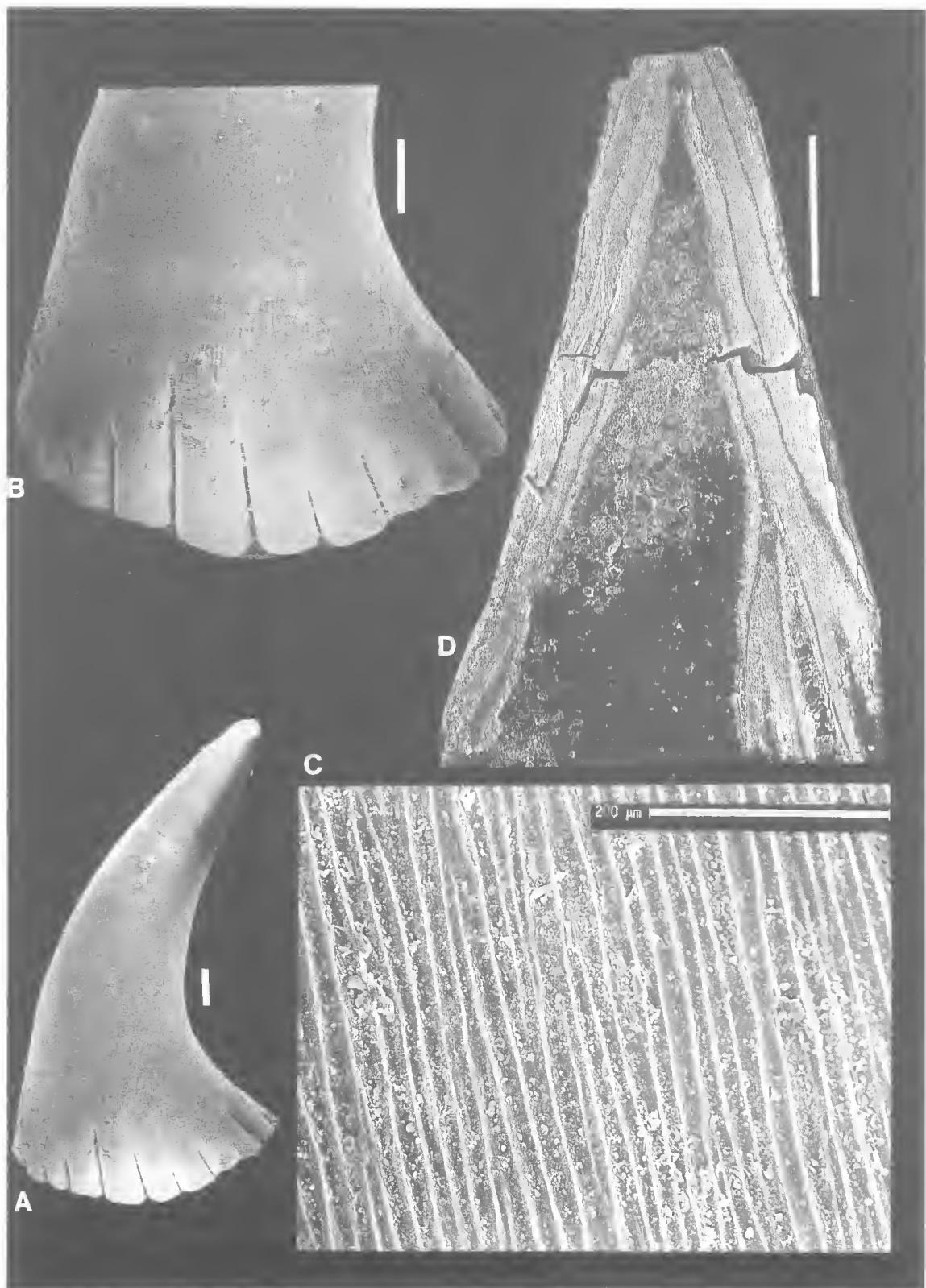
Scales and Body Form. The exposed area of each flank scale is large relative to the total scale size. The scales show no sign of a peg and socket articulation. The overlapped areas are convex rather than flat, and thus provide a neat surface over which the adjacent scales could slide during flexure. The presence of a gutter between the overlapped and exposed parts of the scales provided a groove into which the cosmine-covered edges of the adjacent scales could tuck when the body on that side was on the concave side of a flexure. These features suggest that the entire post-craniad body was flexible. The short ring

centra, which demonstrate a large number of bending units, also suggest body flexibility.

The holotype is the only articulated specimen we have, and it is depressed. However, the mode of flattening, the reconstruction of the cross-section of the head at its posterior end, and the number of body scale rows, indicate that *Cladarosymblema* was not a deep-bodied fish. In addition we have an uncrushed pectoral girdle with a flat-sided dorsal part and a relatively sharply inflected ventral part of the cleithrum, together with a flat clavicle. From this information we conclude that the body was somewhat flattened ventrally in the immediate post-craniad position, a view that is supported by the shape of the large gulars. The preserved part of the holotype, which is 28cm long, and 19cm long behind the otico-occipital unit, shows no sign of the anterior dorsal fin, which therefore must have been posteriorly situated on the animal. If allowance is made for the two dorsal fins and the caudal fin, we estimate that the total length of the fish would have been c.40cm. Estimates of the vertical and horizontal axes of the body behind the pectoral girdle are 6.5 and 7.0cm respectively. Hence the fish must have been long and slender. Having taken account of the previous argument that the body was generally ovate in section, although somewhat flattened ventrally towards the front, and that the body was flexible throughout, we consider that the total design would be consistent with subcarangiform movement. This, together with the posterior position of the median fins, suggests that the propulsion was predominantly caudal. Such an arrangement is consistent with a life style that requires slow movement over long periods and short bursts of high acceleration. However, no conclusion can be reached without a consideration of the pectoral fins.

Function of the Pectoral Fins. The pectoral fins are different from those of any other osteolepiforms with which we are familiar, except perhaps for *Megalichthys hibberti* itself. The fins of that species have not been well photographed. Andrews & Westoll (1970b: pl. 4, fig. A) have figured a relatively complete right fin that has many features shown by *Cladarosymblema*, although the boundary between the basal scales and the ray scales is not as sharp.

FIG. 76. *Cladarosymblema narrienense*. All SEMs. A, isolated tusk, QMF31906. B, enlargement of base of same. C, enlargement of the surface of QMF31907 just above the zone of folding. D, deeply etched vertical section of a small tusk, QMF31905. Note the section through the deep folds at the bottom right, and the strong growth breaks (compare Fig. 77B). Scales: A,B,D, 1mm.



The basal lobes of *Cladarosymblema* are unusually broad, and their extremities are broadly rounded rather than tapered to a point. The number of dermal fin rays is very large, and they are all contiguous, leaving no space for membranes between the rays. Unlike other osteolepiforms, long rays extend around the trailing edge of the fin almost as far as they extend around the anterior edge. This produces a large, flat, paddle-shaped structure. Such a fin shape would not be for propping the animal on the bottom, but was either for swimming in a steady fashion, or for orienting the animal during rapid movement. The problem of distinguishing between these options can be approached either by comparison with other lobe-finned fishes such as *Neoceratodus* or *Latimeria*, or by direct hydrodynamic considerations.

A second important feature bearing on this issue is the position of the fins, which are placed in a low position on the body at an angle formed by the sharply rounded flexure of the cleithrum. This means that the fins would apply a force low on the body, below the centre of gravity. Modern actinopterygians that use the pectoral fins for locomotion rather than orientation, are usually deep-bodied, with fins attached high on the side of the animal (Webb, 1982). This applies equally well to those that use their fins for 'rowing' and to those that use them for 'underwater flying'. Hence the body shape and pectoral fin position suggest that these fins in *Cladarosymblema* were not primarily locomotory.

A third point is that, being situated on a sharply rounded flexure in the body profile and having such a thick proximal lobe, it would be difficult to fold the fins back smoothly against the body. This suggests that they could not easily be rotated out of the water flow at continuously high speeds. Although this argues against long-continued fast swimming, it does not eliminate the possibility of short bursts of high acceleration. In such circumstances the large fins would be useful for directional change.

The basal lobes are covered with scales that decrease in size distally, show no evidence of significant overlap between scales, and have no peg and socket articulation. We have found no evidence that the lobes had an ossified axial skeleton; presumably the skeleton was cartilaginous, and therefore relatively flexible. Although the basal lobes were long and thick, they presumably retained some flexibility. So far as can be determined from the inadequately preserved specimen, the attachment of the fin to the body was

broad and thick, thus limiting the capacity of the fin to rotate about its articulation with the shoulder girdle. In all these respects it seems to be similar to *Latimeria*. However, that is where the similarities end. The fins in *Latimeria* are situated higher on the side of the fish than in *Cladarosymblema*, and the fin pattern is different in the two genera. In *Cladarosymblema* the fin is paddle-shaped and the rays are covered with a double layer of closely spaced cosmine-covered scales that are set in juxtaposition, whereas in *Latimeria* the fin is drawn out to a point, the rays are less numerous, more widely spaced, separated by membranes, and made of a vast number of very short lepidotrichs. Consequently the distal parts of the fins would have been more flexible in *Latimeria* than in *Cladarosymblema*. Fricke et al. (1987) have reported that *Latimeria* does not use its fins for walking on the bottom, but is able to use its paired and unpaired fins for generating thrust. The paired fins are also used to stabilise and correct drift motion in up- and down-welling currents. It is highly unlikely that such drift was a factor in the life of *Cladarosymblema* in semi-permanent shallow bodies of fresh water. *Latimeria* uses its paired fins in generating thrust by adopting an 'underwater flying' fin motion. Fins that are functionally adapted for such motion tend to have a high aspect ratio and are situated on the flanks of the animal, features not shared by the fins of *Cladarosymblema*. Consequently we are unlikely to be able to gain much information from an analysis of *Latimeria*, and again we are forced to make a judgment on the basis of hydrodynamic considerations.

Finally, it is as well to use the geological data to assist with interpretation of the animal's function. The inferred habitat of semi-permanent pools of fresh water suggests that persistent (steady) swimming was unlikely unless swimming against frequent floods was selected for; we note, however, that the sediment and the distribution of the strata indicate that the water was normally quiet and that flood events were infrequent. If they were frequent, it would be difficult to account for the concentration of the carbonate and the algal overgrowths that must have required long-continued stable conditions. In such an environment, the feeding type is more likely to be at a premium in controlling the design of fins. This fish was a carnivore, with tusks in the anterior part of its mouth for penetrating and holding active prey. The associated fauna shows that there was an abundance of actinopterygians of various sizes available as prey. This suggests an emphasis

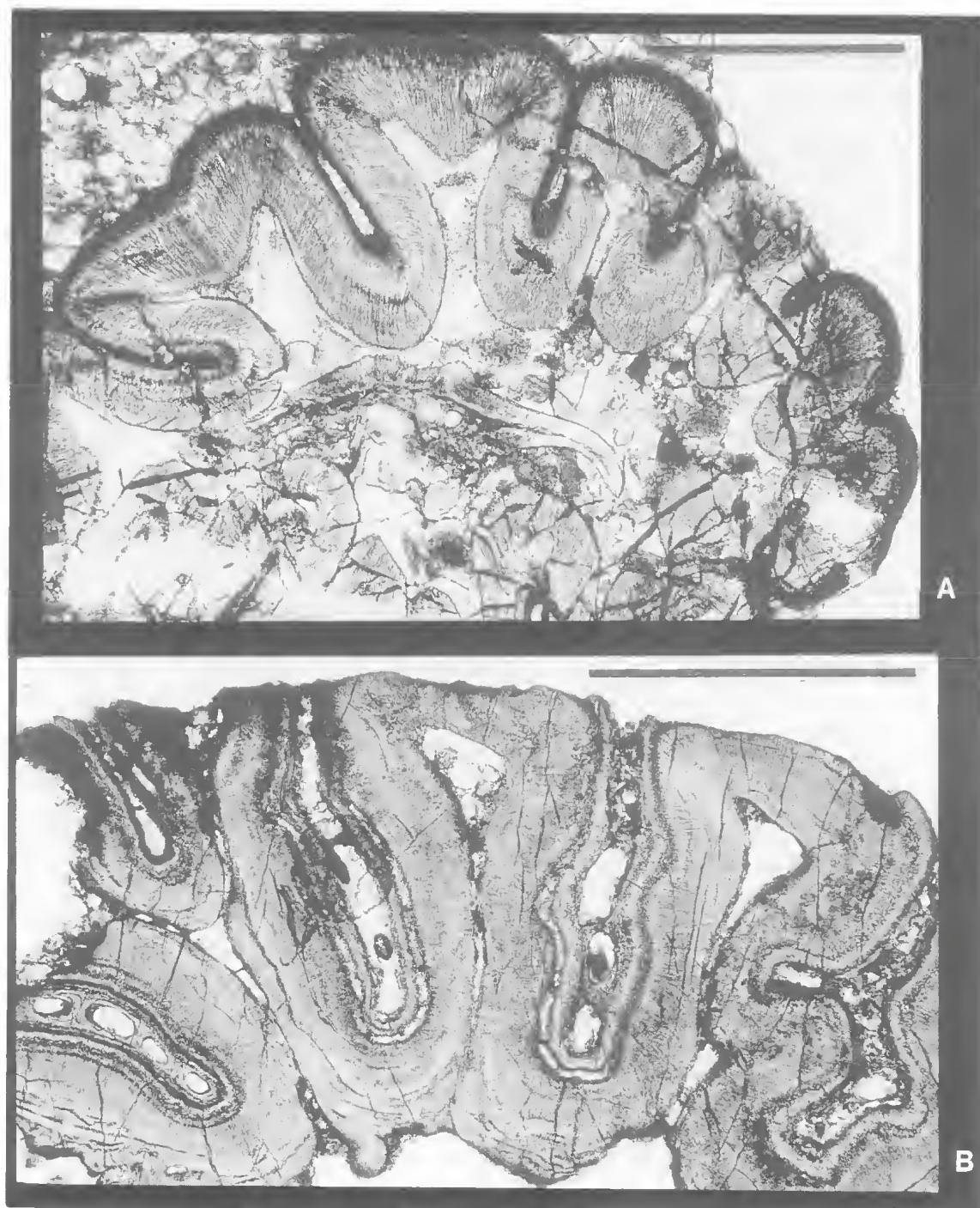
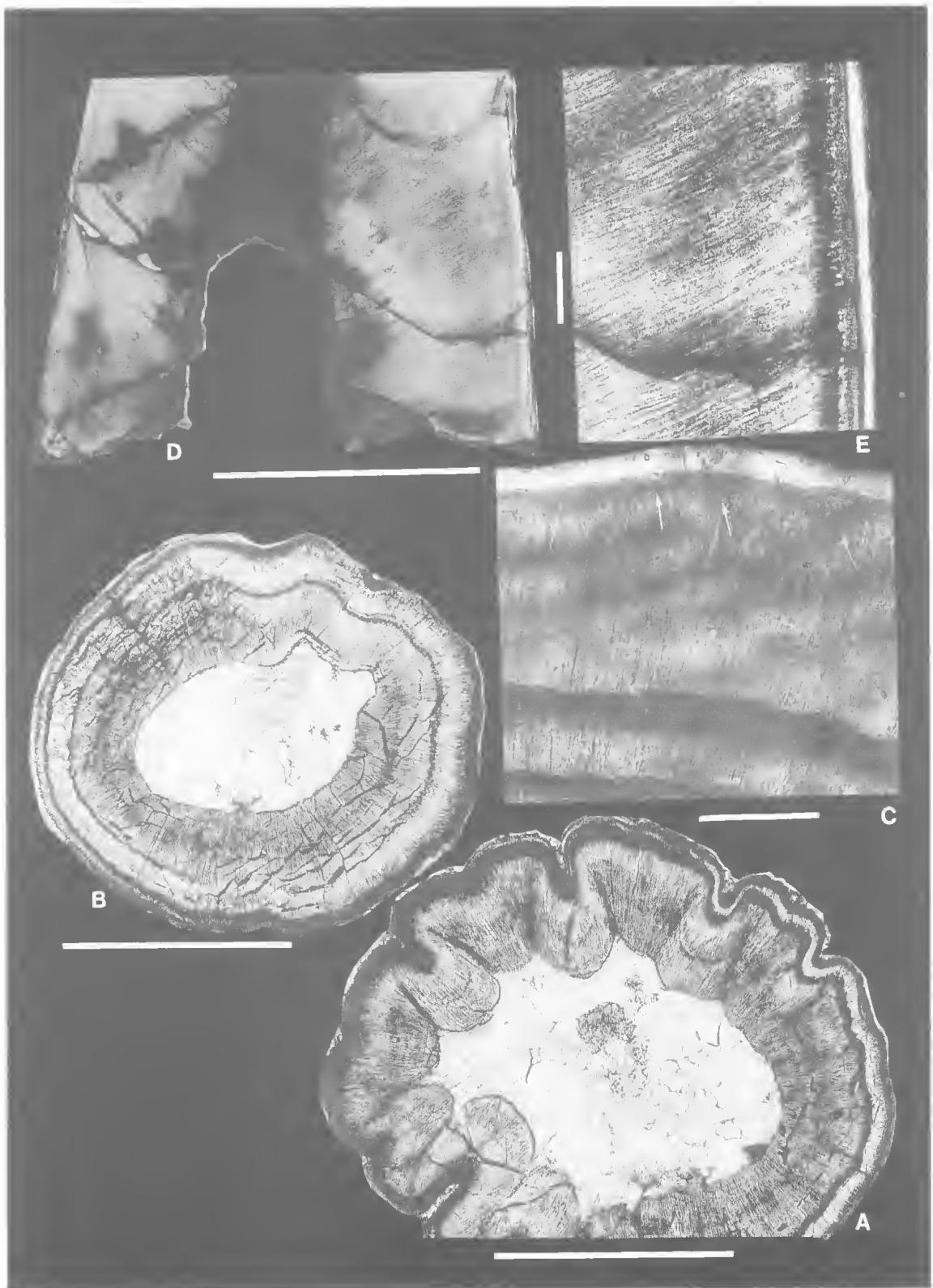


FIG. 77. *Cladarosymblema narrienense*. A,B, transverse sections of tusks, taken near the base. A is more distal than B. A was broken from the holotype, but the thin sections are numbered QMF31907. B, separate tusk, QMF33046; note the cross-bars of bone of attachment in some of the infolds (arrows), and the more complex folding on the right. B also shows two growth breaks towards the outer surface of the tusk. The dark layer around the outer surface in A, where the thin layer of enamel should be, is apparently the result of diagenetic destruction of the surface layers. Scale: 1mm.



on fast starts and abrupt turns. A similar view was espoused by Andrews & Westoll (1970b: 481) who commented that 'Some of the osteolepids seem to have been lurking predators ...', and that they lived in environments where they could avoid strong currents '... where sustained strong swimming would have been necessary'.

Thus, by a process of elimination, we are left with the view that *Cladarosymblema* was a fish that was propelled by subcarangiform movements, was generally a slow mover, but was capable of considerable acceleration in short bursts, during which time it had an excellent capacity to reorient itself in the water using its pectoral fins. This hypothesis is to some extent supported by the caudal fins of the new genus described from Norway by Ulf Borgen, and it could be tested by the discovery of the more posterior median fins of *Cladarosymblema*.

FEEDING

Discussion of biting and feeding in rhipidistians had been dominated by what authors concerned think of cranial kinesis. Thomson (1967) has given an extensive discussion of the pro-kinetic position, and Jarvik (1942, 1980) has advocated the non-kinetic position. We see no point in adumbrating these well-worn arguments, particularly as our material provides no additional information on the nature of possible movements of the intracranial joint. We will focus on the significance of features that have been relatively ignored by previous workers.

Musculature of the Mandible. The large adductor fossa in the mandible is indicative of large adductores mandibulae. This view, if it needs support, is corroborated by the large space under the otico-occipital roof to provide space for the contraction of adductor muscles. There is no doubt that the animal had a massive bite.

Judging from the size of its attachment area, the coracomandibularis muscle (see above) must have been powerful. But did it serve to depress the mandible? Lauder (1980b) has shown that in *Latimeria* the line of action of this muscle was above the jaw articulation when the jaw was closed, and therefore it cannot have been used to initiate jaw opening as it does in many

actinopterygians. He also noted that as the jaw opened, although the line of action dropped below the articulation and therefore is seemingly in a position to contribute to the later phases of depression of the mandible, this does not occur. With the downturn of the posterior end of the mandible in *Cladarosymblema*, it is difficult to be certain if the line of action would have passed above or below the articulation, but we consider it probable that the situation was similar to that in *Latimeria*. Lauder showed that electromyograms indicate that the prime function of the coracomandibularis is compression of the buccal cavity rather than opening the mouth. That leaves the sternohyoideus muscle as the main depressor mandibulae, but we are unable to comment on that muscle in the absence of the ceratohyal in our material.

The retroarticular process in *Cladarosymblema* is large; in *Latimeria* such a process serves for the attachment of the anterior and posterior mandibulohyoïd ligaments. The former is attached to the hyomandibular and the latter to the symplectic. The surface of the process in *Cladarosymblema* displays two areas that could well have been for the attachment of ligaments. As Lauder (1985) has shown, in primitive teleostomes the mandibulohyoïd ligaments mediate mandibular depression, and so this seems to be an appropriate function for these structures in *Cladarosymblema*. The large, anteriorly tapering muscle scar along the Meckelian bone ventral to the edge of the posterior face of the prearticular, has been interpreted as an attachment for strong posterior intermandibularis muscles. These would have extended as a sheet across the top of the posterior end of the gulars, and would have served two main functions; the constriction of the floor of the branchial cavity thus forcing water out across the gills, and helping to control the two mandibular rami during a biting strike at a large item of prey (see below). Smaller areas of attachment for the anterior intermandibularis muscles have been identified near the front of the mandible, and these would also have served to control the movement of the symphysial part of the mandibular rami during a strike.

FIG. 78. *Cladarosymblema narrienense*. A, B, transverse sections through the more distal parts of holotype tusk (QMF31907) illustrated in Fig. 77. B is more distal than A. C, transverse section of part of another tusk, QMF33046A, showing unusually thick enamel and branching tubules in the mantle dentine immediately beneath it. D, vertical section through base of a tusk (QMF33047) cut between folds. E, enlargement of right side of same, photographed under crossed polars, showing enamel layer and multi-layered nature of immediately underlying dentine. Scales: A,B,D, 1mm; C,E, 0.1mm.

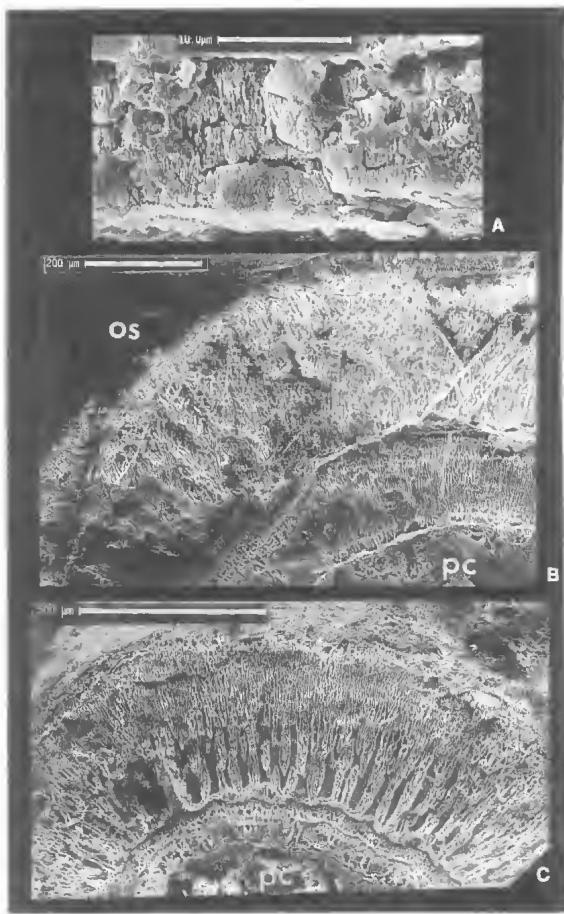


FIG. 79. *Cladarosymblema narrienense*. Specimens all lightly acid-etched; SEMs. A, enamel layer of a tusk, inner surface to bottom. Note the poor lamination and the lack of obvious bundling of crystallites. B, transverse section of tusk, QMF33049, distal to the zone of folding. Note the more or less regular tubules to the bottom right separated from the peculiarly arranged pattern of the outer layer by thick structureless wall of tissue. C, similar section through another tusk, QMF33048, showing disrupted growth around the pulp cavity, and ramifying tubules in the thick outer dentine layer. (pc = pulp cavity; OS = outer surface.)

Movement of Mandibular Rami during Biting. As indicated in the above description, the median symphysis was probably completed by a cartilage pad which would have allowed a degree of flexibility between the jaw rami. This conclusion is in agreement with two other aspects of the anatomy of the mandible. The first is the presence of the small, rhombic, loosely attached plate between the infradentaries, alluded to above. Secondly, the glenoid fossa is divided into two distinct surfaces of articulation, and if the median

symphysis is held vertically the inner half of the fossa is at a lower level than the outer. As a result, the load during biting could have been carried in one fossa or the other depending on stress distribution. The two glenoid surfaces are much more similar in size than those of Devonian dipnoans, in which the lateral surface is much the smaller of the pair. A paired arrangement of the articular surfaces is desirable under two quite different sets of circumstances. If, as in Devonian dipnoans, the mandibular symphysis was rigid and a large prey item was held on one side of the mouth, exertion of pressure would tend to dislocate the jaw articulation on the opposite side. Hence, a second glenoid articular surface would be desirable so that it would be able to carry the stress when the adductor muscles on both sides contracted. If a flexible symphysis were present, an entirely different mechanism would have operated. A large food item caught on one side of the mouth would cause the ramus on that side to rotate outwards and thus the articulation would jump from the outer to the inner glenoid fossa, the articulation on the opposite side of the animal remaining stable. Such a view is supported by the fact that the teeth on the mandible are turned slightly inwards so that they would be more effective when the ramus rotated outwards. The dipnoan design would be an advantage for an animal grinding its food on tooth plates because pressure could be exerted effectively on both sides of the mouth. The osteolepiform design would be an advantage for an animal holding and killing struggling prey by puncturing. It is probably significant that we have recovered from the fauna no invertebrates that could have provided a relatively passive food source, but there are large numbers of actinopterygians and acanthodians of many sizes that would have provided active, struggling prey.

A second factor related to both feeding and respiration has to be taken into account in any discussion of jaw movement. As Lauder has pointed out on many occasions (see especially Lauder, 1985), primitive aquatic vertebrates suck in their prey by rapidly expanding the buccal cavity. This is accomplished by three separate means - dropping the mandible, dropping the gular plates, and laterally expanding the quadrate/mandible articulation. This latter movement is possible only if the quadrate is mobile and if the mandibular symphysis is flexible. Hence, symphyseal flexibility is an important factor in both feeding and respiration. Lateral expansion of the jaw articulation is also a factor in explain-

ing the double glenoid surface. As pointed out above, the inner fossa is slightly anterior to, as well as lower than, the lateral one. Assuming that the articular process on the quadrate was also double, lateral movement of the whole would be facilitated if the articulation could jump from one surface to the other depending on the degree of lateral expansion. Obviously, feeding and respiration are intimately linked in fishes, and hence if the above hypothesis is of any significance, the positions of the articulations for biting and for respiration would have to be consistent. This means that because suction has to be at a peak at the time of a strike at prey, the articulation would be at maximum spread, and the inner glenoid would be engaged. This is the position of the articulation required when maximum pressure is exerted on prey. Such internal consistency is supportive of the above hypothesis.

SENSING THE ENVIRONMENT

Tubules in Snout. Tubules occur in the rostrum and in the symphysial region of the mandible. They are not nearly so numerous nor apparently so inter-connected as those in the Dipnoi, nor do they have the same longitudinal arrangement. Foramina in the antorbital wall connect with these tubules in the same way as do the profundus and ophthalmicus superficialis nerves in extant and fossil dipnoans. These nerves are sensory, and are generally considered to have served electroreception systems. To have this function they would have to open to the external surface. In Devonian dipnoans these openings are numerous, but they are smaller than those for the lateral line canals. In our material, it is not clear that the tubules open to the exterior via a set of small openings, although there may be connections via the lateral line pores.

In the mandible of *Cladarosymblema* the tubules are restricted to the immediate inner surfaces of the dermal bones, and although they divide and penetrate these surfaces, they never make the diverse patterns seen in the Devonian dipnoans. Also they do not seem to connect with external openings in the dermal bone to anything like the same extent as do the tubules in the mandibles of Devonian Dipnoi. As indicated in the descriptive section, it is impossible to reach a definite conclusion on their function.

Special Cutaneous Sensory Pit Groups. These groups, consisting of between five and fifty pits, occur on the snout mesial to the narial opening, on the posterior nasal, the parietal, the supratemporal, the squamosal, the postorbital, the an-

terodorsal corner of the opercular and suboperculars 1 and 2, and near the vertical pitline on the mandible. Bjerring (1972: fig. 6A) made serial sections of part of a roof of *M. laticeps* that show that the small group on the supratemporal (his intertemporal) is served by fine canals connected directly to the lateral line canal in that bone. We have not sectioned a specimen, but X-radiographs show an abundance of relatively coarse branches from the main canal in the supratemporal. Although some of these branches are present beneath the pit groups, others extend well beyond the area covered by pit groups. The same kinds of comments can be made about the groups of pits in the ethmoidal unit. Hence, we can produce no evidence that the multiple branches from the main canals are involved with the supply of nerve fibres to the pit groups. It is unlikely that the X-radiographs would pick up structures as fine as those Bjerring figured.

Another way of approaching the problem of the necessary interconnection of the lateral line canals and the pore groups, is to examine the proximity of groups to lateral line structures. Jarvik (1948: 137) commented: 'No doubt the fine canals leading to the pores transmitted fine nerve twigs, and the position of the pores close to the sensory canals and pit-lines indicates that these nerve twigs are of lateralis branches'. Whereas it is true that the groups on the roofing bones and the squamosal lie close to either canals or pit lines, those on the opercular and subopercular do not. It may be significant, however, that the group on the opercular is in the anterodorsal corner where it would lie close to the lateral line in the preopercular; but even if this is accepted as significant, no such proximity can be argued for the pore groups on the suboperculars. We conclude that no necessary connection between the lateral line system and the pore groups has been established.

The function of these pit groups is unknown, but Bjerring (1972: 85) has speculated that they may have been thermal receptors. Why an organism living in the environment postulated for *Cladarosymblema* would need thermal receptors is difficult to understand. In any case we know of no modern analogue for such organs having such a distribution. It is unlikely that these pits would be mechanoreceptors, because on the ethmoidal unit and the intertemporals they are surrounded by normal neuromast pores, and hence subsidiary receptors of the same kind would seem to be superfluous. On the other hand, modern paddlefishes, which live in a riverine environ-



ment, do have clusters of ampullae distributed on the elongate rostrum, the cheek and the gill cover (Grande & Bemis, 1991: figs 1A-D). These are known to house electrosensory organs similar to the ampullae of Lorenzini (Jorgensen et al., 1972). The innervation of these structures remains unknown, but in other fishes the ampullae of Lorenzini are innervated from electrosensory fibres associated with the lateralis system. The pit groups in paddle fishes are far more extensive than those of *C. narrienense* and the analogy may be inappropriate; but two points give confidence that it has some merit: in *C. narrienense* some of the pit groups are associated with the lateral lines, and in paddle fishes, as in *C. narrienense*, clusters of pores occur on the gill covers, which carry no lateral line.

Should this interpretation be accepted, one residual point remains. That is, the cosmine between the individual pits retains flask chambers, which elsewhere in this paper are interpreted as having an electrosensory function also. The close proximity of the two types of receptor requires explanation.

Flask Chambers in the Cosmine. These structures have been interpreted as housing electrosensory organs (Thomson, 1975), osteoclasts (Borgen, 1988, 1992), or dermal papillae supplied by cutaneous blood vessels (Bemis & Northcutt, 1992). Another possibility is that they were the sites of mucus-secreting cells. In the descriptive section above we have concluded that osteoclasts functioned from the flasks, and that conclusion implies a blood supply. However, it does not imply that their only functions were resorptive. That they had additional functions is indicated by two other observations. First is the fact that pulp canals are spaced evenly between the flasks; these must have been supplied with blood to provide the nutrients for the deposition of the dentine, although not for the dermis on the external surface of the cosmine, because no dentine tubules penetrate the enamel layer. Hence the nutrients for the dermis outside the scale pockets

must have come from the flasks, the only structures that connected with the surface layers which, as shown above, must have had a blood supply. The blood would have been carried via the irregular deep cross-canals that made connections between the bases of the pulp canals and the flasks. The second important observation is the regularity of the mesh-canals between the adjacent flasks. Because we have already determined that a blood supply was available to the flasks via the cross-canals, the mesh-canals would be superfluous as blood conduits. In addition their regularity is not characteristic of a blood distribution system. Nor is it comparable with any mucus gland system of which we are aware. On the other hand, their array is reminiscent of the design of elementary sensory receptors such as are found in the compound eyes of arthropods. We can only conclude at this stage that the flasks served at least three functions: a nutrient supply to the dermis, sites for osteoclasts involved with the periodic resorption of the cosmine, and sites to house sensory receptor cells. Such receptors would not have been mechanosensory because the lateral line system was well developed, nor chemosensory because such a distribution is not known in any living organism. On the other hand, electrosensory receptors are widely distributed on the body of many aquatic vertebrates (Northcutt, 1986). Consequently we consider that the interpretation of Thomson is the most adequate interpretation available at present.

Denticles in the Narial Opening. We have commented that the presence of these denticles, in this genus at least, seems to rule out the possibility that the embayment in the wall of the naris carried a gland. The function of the denticles is more difficult to determine. Presumably they were covered with epidermis containing sensory cells of some kind, but beyond that we are unable to speculate, apart from noting that they would be ideally placed to monitor currents entering the nasal capsules.

FIG. 80. *Cladarosymblema narrienense*. Specimens all lightly acid-etched; SEMs. A, vertical section of small tusk, QMF33050, showing growth layers and strongly folded base. Scale: 1 mm. B, enlargement showing tubules different from those observed in other tusks in the collection; and therefore may not belong to the same taxon. Note, however, the difference between the two growth breaks; some tubules pass through the upper break but not the lower one. C, part of a vertical section through a deeply etched tooth, QMF33059, top to the left. Some of the tubules have broken during washing after the section had been etched, and are lying across the tubules that remain in place. D, enlargement of part of same to show that at least some of the growth banding results from multiple division of the tubules in the outer layer. E, enlargement of part of a section across a growth band, also of QMF31905. Note that the break consists of a layer of structureless material separating layers with tubules of different diameter and pattern. F, part of the same specimen showing closely spaced partitions within a main growth band.

RESPIRATION

Two main factors control the flow of water over the gills - the production of negative pressure (suction) in the buccal cavity by depression of the mandible and the gulars and lateral movement of the quadrate/mandible articulation, followed by the build-up of positive pressures in the buccal cavity by mouth closure, inwards movement of the quadrate/mandible articulation by contraction of the intermandibularis muscles, and the raising of the floor of the buccal cavity by contraction of the interhyoideus and intermandibularis muscles. Accompanying the build-up of positive buccal pressure is the production of negative pressures in the opercular chamber by movement of the opercular. The effectiveness of the pumping mechanisms can therefore be approached by examining the size and position of the submandibular muscle attachment areas, and the limits on the capacity of the opercular to move as reflected in the overlaps and muscle attachments of the opercular bones.

Muscles of Submandibular Region. In the absence of a ceratohyal, we are unable to comment on the size of the interhyoides muscles, but the intermandibularis muscle attachments provide a good indication of the ability of those muscles to contract the buccal cavity. In *Latimeria chalumnae* both the anterior and posterior intermandibularis muscles are strongly developed (Millot & Anthony, 1958: vol. 2, fig. 28). Lauder (1980a) has shown that, primitively, the intermandibular musculature served to compress the buccal cavity rather than to take part in the depression of the mandible. In *Cladarosymblerma* the posterior intermandibularis attachment surfaces are large, and are situated on the posterior half of the mandible. This suggests that they exercised a significant control on the extent of the lateral movement of the jaw articulation, as well as raising the floor of the buccal cavity during feeding and buccal pumping. The posterior intermandibularis muscles of *Latimeria* are attached to the anterior three-fifths of the mandible (Millot & Anthony, 1958: vol. 2, fig. 28); according to Jarvik (1963, fig. 20A) those of *Eusthenopteron* extend much further posteriorly, but the evidence for this interpretation is not clear. *Gogoniasus* has an attachment of the intermandibularis extending posteriorly almost as far as the jaw articulation. This, taken in conjunction with the evidence from *Cladarosymblerma* and *Eusthenopteron*, suggests that in osteolepiforms this may have been a normal feature. Assuming that the above interpretations are correct, we incline to the view that the

intermandibularis muscles played a more important role in buccal constriction in osteolepiforms than in *Latimeria*. The role of the hyomandibular in controlling the lateral movement of the jaw articulation is impossible to determine because, as indicated above we have no ceratohyal, and the ventral end of the hyomandibular appears to have been cartilaginous.

Egress of Water from the Gill Chamber. The posterior position of the intermandibularis muscles in osteolepiforms has another important consequence, viz. that egress of water from the gill chamber would have been anteroventrally restricted. The filament-bearing gills would therefore have been limited to a posterior and posteroventral position. This is consistent with the reconstruction of the gills in *Eusthenopteron* by Jarvik (1980: figs 109-110). In that genus, the anterior part of the buccal cavity contains a long sublingual rod that occupies the space containing the anterior ends of the gill arches in *Latimeria* and other primitive osteichthyans.

Opercular overlaps. The opercular is strongly overlapped anterodorsally by the lateral extrascapular, suggesting a severe restriction on its lateral movement. This overlap is larger than that of other osteolepiforms. However, as indicated in the descriptive section, the dorsal part of the opercular is inflected at a high angle, and lateral movement would require only a slight lift of the lateral extrascapular. Nevertheless, extensive lateral movement would be precluded. The subopercular I has a large surface where it was overlapped by the opercular, thus restricting its lateral movement unless the two bones moved in concert. At the same time, we note that these overlaps would have provided a stable form for the lateral and ventrolateral walls of the opercular chamber, thus maintaining the negative pressures generated by the limited lateral movement of the opercular and subopercular bones. We conclude that in comparison with the buccal pressure mechanism, the opercular mechanism provided only limited support for the respiratory water flow. This is not surprising, as Lauder (1985) has shown that in primitive fishes the negative pressures in the buccal cavity are five times those of the opercular cavity.

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collected by de Bretzel, and subsequently gave us access to maps that she had prepared during a collecting trip to the region. She also identified the microvertebrate material etched from our samples, and has continued to give support during the whole exercise. We thank William Ellis, Arvid Buskas and Laura Barwick for their assistance in the field. Dr Clinton Foster of the Australian Geological Survey Organisation has examined specimens from our samples for spores. Our Research Associate, Dr Peter Pridmore has consistently discussed matters of interpretation with us. Dr George Miklos and Prof. David Ride have discussed problems related to sensory reception. Dr. Ulf Borgen, of the Swedish Museum of Natural History, who has been studying the genus *Megalichthys* for some time, has freely made the results of his work available to us. Without this cooperation we would have been at a serious disadvantage. We thank Charles Schaff of the Museum of Comparative Zoology, Harvard, and John Maisey of the American Museum of Natural History for the loan of specimens of *Ectosteorhachis* for comparative study.

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*NOTE ADDED IN PROOF

Dr Oleg Lebedev has drawn our attention to a couple of points in our interpretation where details of a new Russian osteolepiform, described in the proceedings of the Miguasha Symposium on early vertebrates, indicate that we may be in error.

Firstly the bone described and figured as a urohyal is not sufficiently compressed and does not have the anterior articulation surfaces of that bone. Instead it is more likely to be a basal radial from the second dorsal or anal fin (see Jarvik, 1980; fig. 99). This is an attractive interpretation.

Secondly the anterior edge of the parasphenoid may have been placed in a too posterior position on our Fig 20A. In the Russian specimen the anterior edge is approximately along the posteromesial edge of the vomers. Our best preserved specimen has a clear boundary in the position we have indicated, and the more anterior boundary near the edge of the vomers is not so well preserved. Hence, whereas we acknowledge the possibility that we are in error, our opinion on the issue remains ambiguous.

ADDENDUM

The specimens extracted from the limestone block collected by de Bretzel, and said to be from the Telemon Formation, have been catalogued as QMF26522. They have many features in common with *Cladarosymblema narrienense*, but in view of their unknown provenance, and the record by Turner (pers. comm.) of fish remains *in situ* in carbonates of the Telemon Formation within the Narrien Anticline, we have decided to keep the material separate. The following notes concentrate on differences from the type material of *C. narrienense*. Some of the specimens have been illustrated in Fig. 12.

The single fragment of the ethmoid shield has a large median postrostral, posterior nasals that indent the outline of the parietals, and a patch of sensory pores lies on the posterior nasal as in *C. narrienense*. The lateral margins of the parietals converge posteriorly unlike those of *C. narrienense*.

One lachrymal is available. It is one third as high as long, and in dorsal view is seen to be flexed inwards near its anterior end. Its posterior end is acute and it has a distinctive overlap arrangement with the jugal. This shape and overlap pattern does not match the anterior edge of the jugal of *C. narrienense*, which is much more upright. The ventral edge has cosmine to its margin, and a slight furrow of irregular depth internally, into which the maxilla fits. The notch for the articulation of the anterior process of the maxilla is not pronounced. The anterodorsal edge also has cosmine to its margins and a distinctive groove and peg for articulation with the lateral rostral. Anterior to this peg and immediately dorsal to the lateral line canal is a complementary articulatory socket. The edge forming the orbital margin is very short and is bevelled as is normal. According to Borgen (MS), in *M. hibberti* the suture between the lachrymal and the jugal does not reach the orbit, implying that the jugal forms the entire ventral margin of the orbit. This is clearly not the case in this species. The infraorbital lateral line canal runs close to and parallel with

the ventral margin, opening to the exterior via large pores some of which are almost on the bone margin. A number of offshoots run up from the main canal to open on the anterior part of the bone.

A relatively complete isolated lateral extrascapular is known. The bone is subtriangular in outline, but with all the edges slightly curved. The anterior margin bears a narrow overlapped surface, and its lateral edge is finished. The mesial edge is finished and rather thin, showing that it overlapped the median extrascapular. A 7 mm long, flexed, longitudinal pitline runs down the axis of the bone, and a second much longer line loops around this one, presumably having run onto the bone from the median extrascapular.

About half of a maxilla is well preserved. It has a ridge like that of *C. narrienense* supporting the tooth row on its internal surface, but it lacks protuberances on its dorsal edge and the overlapped edge is more extensive. As described above, the anterior process is large and has a folded dorsal tip which probably formed the posterior edge of the choana as in *Gogonasus andrewsae*.

Only a small fragment of a mandible is available; it does not provide an adequate basis for comparison.

A well-preserved opercular and a median gular match those of *C. narrienense* except that the median gular has well-developed pitlines. The opercular even has the small patch of sensory pores in its anterodorsal corner. The scales of the two are entirely comparable.

Two isolated specimens that may be subopercular 1 have been recovered, but they are very long and have overlap patterns that cannot be reconciled satisfactorily with that identification.

Consequently, we have concluded that this species is closely related to *C. narrienense*, but in view of the small differences in the shapes of the parietal and the mandible, and the failure of the lachrymal to fit the jugal of *C. narrienense*, it is not possible to say that they are conspecific.