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Crossopterygian Fishes from the Devonian of Antarctica: Systematics, Relationships and Biogeographic Significance

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ABSTRACT. Four new genera of osteolepiforms and a new rhizodontiform genus are described from the Middle-Late Devonian Aztec Siltstone (Beacon Supergroup) of Antarctica. Other indeterminate osteolepid, eusthenopterid and rhizodontid remains, and a single indeterminate porolepiform scale, are described from the same formation. *Koharalepis jarviki* n.gen., n.sp. is a large cosmine-covered osteolepiform with a broad flat head, two pairs of dermosphenotics, large extratemporals, a large postorbital in the cheek which does not reach the orbit, an elongate jugal, lachrymal separating the maxilla from the premaxilla at the jaw margin, and large anteriorly pointed median and triangular lateral extrascapulars. It is placed with *Canowindra* Thomson and *Beelarongia* Long in the new family Canowindridae. *Platyethmoidia antarctica* n.gen., n.sp. is a poorly known form with a very broad, flat fronto-ethmoidal shield with dorsomesially oriented slit-like nares, and a lower jaw with a deep articular region. It may be closely related to *Gyroptychius?* *australis* Young & Gorter. *Mahalalepis resima* n.gen., n.sp. is interpreted on the morphology of the fronto-ethmoidal shield as an early megalichthyid, and a new definition of this family is presented. *Vorobjevaia dolonodon* n.gen., n.sp. is a poorly known osteolepid with a distinctive jaw morphology. The rhizodontiform *Notorhizodon mackelveyi* n.gen., n.sp. was the largest fish in the Aztec fauna, attaining a length of over 3 m. It is characterised by elongate frontals and small dermosphenotics in the skull, *Rhizodus*-type tusks, and strong tooth flanges on the coronoid and dermopalatine series bones in the jaws. The braincase in a rhizodontiform is described for the first time, and in general morphology closely resembles that of Osteolepiformes. *Notorhizodon* resembles *Screbinodus* Andrews in dermal ornament and *Barameda* Long in skull pattern. All previously described crossopterygian material from the Aztec Siltstone is revised, and *Gyroptychius antarcticus* (Smith Woodward) is regarded as a *nomen nudum*. The stratigraphic distribution of rhipidistians in the Aztec Siltstone is summarised, and the biogeography and phylogenetic relationships of the

new taxa discussed. The canowindrids were an endemic group of East Gondwana. The megalichthyids and rhizodontiforms may have originated in the East Gondwana Province during the Middle Devonian, but did not reach Euramerica until the uppermost Late Devonian. They flourished in the Carboniferous Period following the decline of the eusthenopterids and the initial radiation of tetrapods.

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Crossopterygian fishes from Antarctica were first recognised by Woodward (1921) in his original description of the Devonian fish material discovered during the British Antarctic 'Terra Nova' expedition of 1910-1913. The original collection was made by T. Griffith Taylor's party which explored the coast of Victoria Land during the summer of 1910-1911, and discovered fossil remains in glacial moraine at Mount Suess, near the mouth of the Mackay Glacier about 18 km in from the coast of southern Victoria Land at Granite Harbour (Fig.2). Fossil fishes had been reported a few years earlier by

Woodward (1908) in a Tertiary vertebrate assemblage from Seymour Island, just off the Antarctic Peninsula, but the Mount Suess discovery was the first of Devonian fossils, and of fossil vertebrates, on the Antarctic continent itself. The provenance of the fossiliferous moraine at Mount Suess was at that time unknown, but Debenham (1921) concluded that it probably came from the thick sequence of sedimentary rocks called the 'Beacon Sandstone', well known from exposures in the region of the lower Ferrar and Taylor Glaciers.

The description of this fish fauna by Woodward

(1921) was significant in being the first record of Devonian vertebrates of European aspect from the southern hemisphere. Amongst the eight taxa of Devonian fishes he identified were two groups of osteichthyans, one of which he referred to the genus *Holoptychius*, a crossopterygian fish well known from the Old Red Sandstone of Europe.

Nearly sixty years after the original discovery, some *in situ* remains of Devonian fishes were collected by B.M. Gunn and G. Warren during the Trans-Antarctic Expedition of 1955-1958 (Gunn & Warren, 1962) from three localities in the Skelton Névé region between the Taylor and Mulock Glaciers of southern Victoria land (Fig.2). This material was described by White (1968) as coming from 'siltstones in the Beacon Sandstone'. This red and green siltstone interval had already been named by Webb (1963) as the Aztec Siltstone.

Many new fossil localities were discovered in the Aztec Siltstone during the 1968-1969 summer field season of the New Zealand Antarctic Research Program (NZARP) by a Victoria University of Wellington Antarctic Expedition (VUWAE 13). A preliminary report on these discoveries was presented by McKelvey *et al.* (1972). Two of the present authors (AR, GCY) joined the following Victoria University expedition to southern Victoria Land (VUWAE 15) in the 1970-1971 field season, when substantial collections of Devonian vertebrate material were made from a number of localities in the Aztec Siltstone, many of which lie to the west of longitude 160°E, and therefore within the eastern sector of Australian Antarctic Territory (Fig.1).

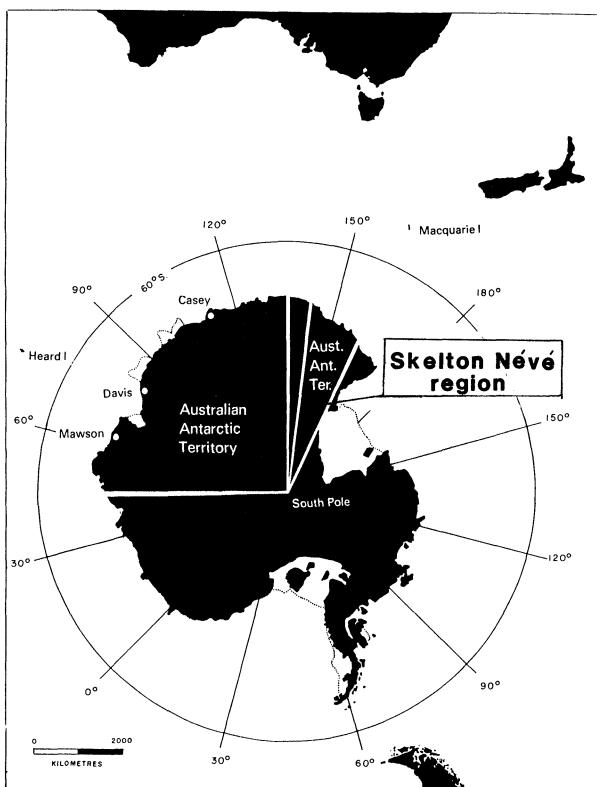


Fig.1. Location of the Skelton-Mackay Glacier region of southern Victoria Land, Antarctica.

Most of the large collection of 1970-1971 is housed in the Australian Museum, Sydney, and the Bureau of Mineral Resources, Canberra. More recent collections made in 1976-1977 by M.A. Bradshaw of the Canterbury Museum, Christchurch (NZARP, event 33), and in the 1988-1989 field season from near Mount Hughes in the Cook Mountains (Woolfe *et al.*, 1990) have not been dealt with fully in the present account.

The Aztec fish fauna as now known includes most of the major groups of Devonian vertebrates (thelodont agnathans, placoderms, chondrichthyans, acanthodians, palaeoniscoid actinopterygians, rhipidistian crossopterygians, and diploans). Some of the placoderms have been described by Ritchie (1975) and Young (1988), chondrichthyans by Young (1982), acanthodians by Young (1989a), and thelodonts by Turner & Young (1992). A recent summary of the fauna is given in Young (1989b). Placoderms are the most abundant and diverse element in the fauna, but second in abundance are the remains of crossopterygian fishes, the group commonly regarded as being most closely related to the higher tetrapod vertebrates. The present account describes the crossopterygian remains currently studied from the Aztec Siltstone, with a revision of previously described material.

The crossopterygians from the Aztec fauna belong to the group traditionally known as the 'Rhipidistia', a term used here informally because the monophyly of this group has been questioned. Rhipidistians are a well-studied group of Palaeozoic fishes, and are known anatomically in intricate detail largely through the works of Erik Jarvik (e.g., 1937, 1942, 1944a,b, 1948, 1950, 1952, 1959, 1980a,b, 1985). This special interest in their morphology has stemmed from their assumed close relationship to the earliest tetrapods, a group first known as fossils from the Late Devonian. Most studies on Devonian rhipidistians have been concerned with taxa from Europe and North America, and those from other areas have remained poorly known. However, over the last 30 years the diversity of the group has increased with descriptions from poorly investigated areas in Russia (e.g., Vorobjeva, 1962, 1975, 1977), China (e.g., Chang, 1982; Chang & Yu, 1981, 1984), Australia (Thomson, 1973; Long, 1985a,b,c, 1987a, 1988; Young & Gorter, 1981), the Middle East, and north Africa (e.g., Janvier, 1980, 1983; Janvier *et al.*, 1984; Lelievre & Janvier 1986). The detailed descriptions presented here are a further contribution to recent work which is establishing a global data base for phylogenetic and biogeographic studies of the group.

It is evident from studies of other groups from the Aztec Siltstone of southern Victoria Land (e.g., bothriolepid antiarchs; Young, 1988) that the widely occurring 'Aztec fish fauna' in fact represents a number of discrete assemblages, which biostratigraphically encompass several associations not previously encountered in Devonian fish faunas (Young, 1989b). It is also the case that while some of the 25 known localities in the Aztec Siltstone which have yielded significant specimens of rhipidistians (e.g., Mount Crean; locality 8, Fig.2) have been well sampled, others (e.g.,

lower horizons in the Boomerang Range; locality 19, Fig.2) until recently, had not been visited by a vertebrate palaeontologist and properly collected. Taking into account the initial expense of Antarctic fieldwork, and the practical and logistic difficulties of recollecting from known sites, our approach in this study has been to consider material currently available from each locality and horizon as potentially discrete taxonomically from other material, unless there is good contrary evidence. We predict that future collecting from the Aztec Siltstone will vindicate this approach by proving a much greater taxonomic diversity in the rhipidistian component of the fauna than is evident from material

currently available. In addition, our treatment of indeterminate material from different localities and/or horizons has been more detailed than might be appropriate for fossil localities on other continents, which are readily recollected. This should provide the most useful basis for future palaeontological fieldwork in Antarctica, and any subsequent more comprehensive taxonomic treatment of the rhipidistians in the fauna that might be expected to result from the study of new material. The biostratigraphic and biogeographic significance of the Aztec fauna has been discussed in more detail elsewhere (Young, 1989b), and rhipidistian evidence bearing on these aspects is considered further below.

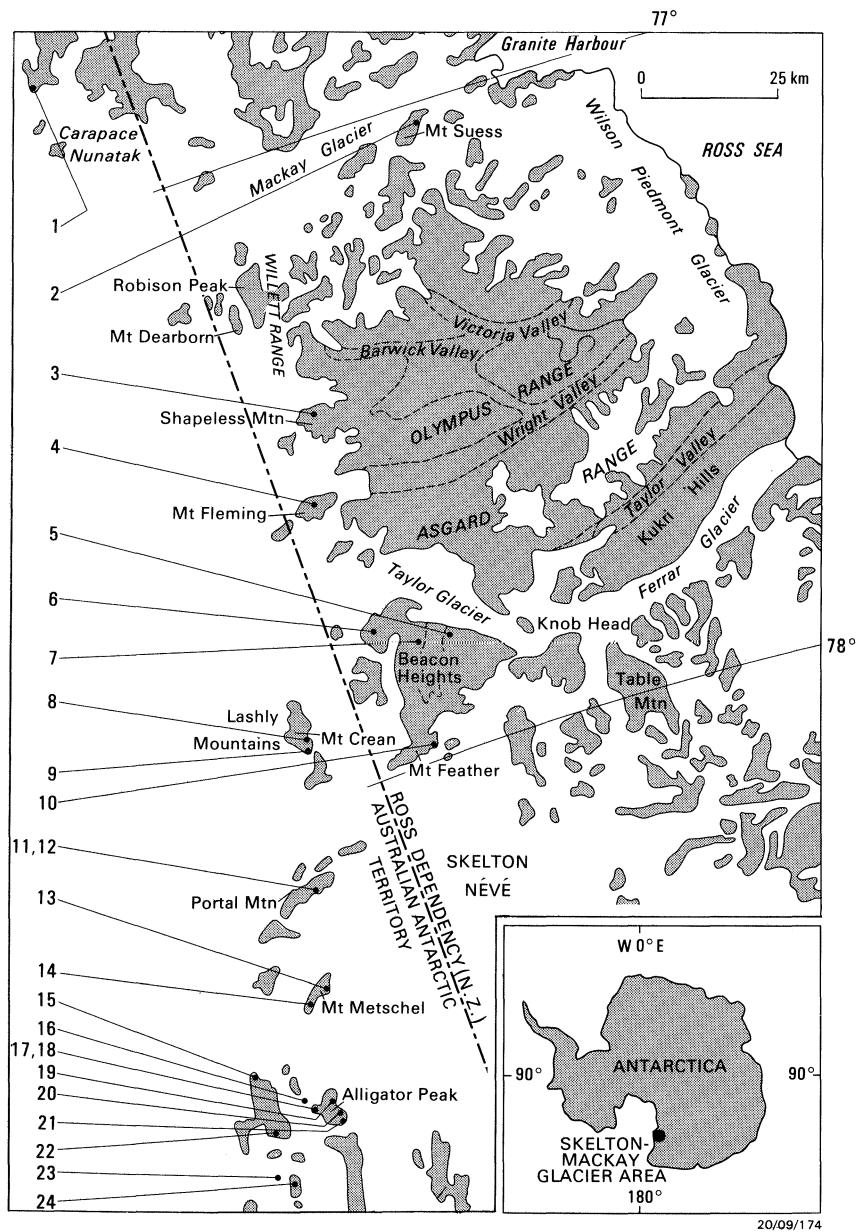


Fig.2. Twenty four localities for Devonian fish remains from the Aztec Siltstone of southern Victoria Land modified after Young (1988). New material was collected by J.A. Long in the 1991-1992 field season from some of these, and also new localities (Fault Bluff, Mount Gudmundson) near Mount Hughes in the Cook Mountains (see Woolfe *et al.*, 1990), some 100 km south of the map area. These include diverse assemblages from several horizons.

There is no consensus on the higher classification of rhipidistians, but some agreement that the group is not monophyletic (e.g., Andrews, 1973; Rosen *et al.*, 1981; Maisey, 1986; Forey, 1987; Schultze, 1987). Debate continues about rhipidistian inter-relationships, and their relationship to tetrapods (e.g., Rosen *et al.*, 1981; Long, 1985c; Schultze, 1987; Chang, 1989). Traditionally up to three major groups have been included in the 'rhipidistian' fishes; these have been termed the Osteolepiformes, Porolepiformes and Rhizodontiformes (e.g., Berg, 1940). All three are represented in the Aztec fauna. Within the Osteolepiformes of Jarvik (1942) two families have commonly been recognised: the Osteolepididae characterised by cosmine and rhomboid scales, and the Rhizodontidae lacking cosmine and with round scales (Jarvik, 1985). However Andrews & Westoll (1970a,b) used the latter term in a more restricted sense for several poorly known taxa from the Late Devonian and Carboniferous (*Rhizodus*, *Strepsodus*, *Sauripterus*), characterised by some special features of the shoulder girdle which distinguished them from the Eusthenopteridae. The latter group in their shoulder girdle structure closely resemble the Osteolepididae, even though they lack cosmine and rhomboid scales. Further evidence that presence or absence of cosmine, and scale structure, are not valid defining characteristics for high taxonomic categories is provided by Australian forms (Long, 1985a, 1987a), and some new taxa described below, which indicate that round scales and loss of cosmine were acquired in rhipidistians from the eastern part of Gondwana independently of these changes in Euramerican taxa.

We believe that many of the current uncertainties of higher classification of rhipidistians will be resolved when all regions of the world yielding Devonian vertebrates have been studied in comparable detail to the faunas of Europe and North America. The erection of new higher taxa is therefore premature, even though new information is provided below, casting doubt on the monophyly of some groups. Accordingly, in the systematic descriptions we retain the three major groups mentioned above (osteolepiforms, rhizodontiforms, porolepiforms), and within the Osteolepiformes we recognise four named subgroups, for which familial rank seems appropriate: Canowindridae n.fam., Osteolepididae, Megalichthyidae and Eusthenopteridae. The Megalichthyidae has previously been included as an osteolepid subfamily, while the new family Canowindridae includes both cosmine-covered and non-cosmoid taxa, and thus could be given higher rank, equivalent to the osteolepids and eusthenopterids together. We have avoided this, preferring to formalise groups at a level for which there is little disagreement about monophyly, to retain some nomenclatural stability given the many competing hypotheses about phylogenetic relationships stimulated in recent years by the adoption of cladistic methods. Our views on rhipidistian inter-relationships are considered in more detail and analysed cladistically in the discussion. The characters used and their distributions are summarised in Table 2 (Appendix 1) and Figure 47B. In the systematic section we mention these characters

(e.g., A1, B2) in our definitions without comment; character polarity is considered in detail in the discussion.

Materials and Methods

Most of the fish material from the Aztec Siltstone is preserved as bone in a siltstone or fine sandstone matrix. Much of the osteolepid material dealt with below has been prepared by mechanical removal of matrix, to retain the bone, which is generally well preserved. In other material most of the bone had weathered away to leave impressions in sandstone or siltstone. In cases where the enclosing matrix was non-calcareous (e.g., the holotype of *Notorhizodon mackelveyi*) the material was prepared by etching in hydrochloric acid to remove badly preserved bone, and the resulting clean impressions cast with latex rubber. All specimens were whitened with ammonium chloride to emphasise surface detail before study under the microscope, and most of the illustrations are based on detailed camera lucida line drawings. Crushing in some specimens (e.g., the holotype of *Koharalepis jarviki*) resulted in many fine cracks through the bone, but detailed study under the microscope generally permitted bone sutures to be distinguished unambiguously from surface fractures.

Most students of rhipidistian fishes have accepted the view that the anterior pair of large dermal bones in the skull bordering the pineal opening are homologous to the parietals of tetrapods, even though they correspond topographically to bones in actinopterygians commonly referred to as 'frontals'. We have chosen here to follow Jarvik (1944-1985) and Gardiner & Schaeffer (1989: 139) in retaining the more straightforward fish terminology of 'frontal' and 'parietal' for the anterior and posterior large paired bones of the skull table, which facilitates comparisons with other groups of fishes. At the same time it is recognised that a phylogenetic position of tetrapods as a sister-group to rhipidistians, or to a rhipidistian subgroup, or to some other osteichthyan group, would imply the homologies stated above. Skull roof measurements used in the descriptions follow the scheme of Jarvik (1948: fig.12; 1985: fig.2). Jarvik (1985: 10) advocated omitting duplication of the 'id' in taxonomic names based on genera ending in 'aspis' or 'lepis' (e.g., 'Osteolepidae'), but this is not in accordance with the rules of zoological nomenclature (Steyskal, 1980), and we use here the formal name 'Osteolepididae' for this well-known family. Since subfamilies are not utilised the informal term 'osteolepid' refers to members of this family.

Material described or mentioned here is housed in the following institutions: AMF – Australian Museum, Sydney, CPC – Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Canberra, WAM – Western Australian Museum, Perth, BMP – Natural History Museum, London, AF – Canterbury Museum, Christchurch, GS – New Zealand Geological Survey, Lower Hutt.

Tables 1 and 2 are listed in Appendix I.

Geographic and Stratigraphic Distribution

The modern stratigraphic subdivision of the Beacon Supergroup recognises two groups (Harrington, 1965); the lower Taylor Group of Devonian age or older, which is unconformably overlain by the Victoria Group (Permo-Triassic). The two formations (Beacon Heights Orthoquartzite, Aztec Siltstone) from which fish remains have been recorded are the uppermost formations of the Taylor Group. They are formally defined by McKelvey *et al.* (1977: 832-836). Remains of rhipidistian fishes described here are only known from the Aztec Siltstone.

The Aztec Siltstone is up to 220 m thick in the southern Boomerang Range (Figs 2,3), but thins to the north, where only the lower beds are preserved. The Metschel Tillite overlies the Taylor Group in some sections, where it may erode into the upper part of the Aztec Siltstone, and in some areas has apparently removed it altogether (McPherson, 1978).

The Aztec Siltstone is interpreted as an alluvial plain deposit, with various biological and non-biological parameters indicating a non-marine depositional environment (see Barrett & Kohn, 1975; McPherson, 1978, 1980; Barrett, 1980). Most of the major fish groups in the Aztec fauna have marine representatives of Devonian age, but the overall assemblage is similar to those from other red bed sequences (e.g., the Old Red Sandstone facies of Europe) traditionally regarded as fluvial deposits. This does not exclude the possibility that any or all of the taxa in the fauna were capable of tolerating or dispersing through normal marine environments.

Devonian fish localities are known over the entire area of exposure of the Aztec Siltstone. Material dealt with in this study has a wide provenance, from the Warren Range and the Boomerang Range in the south, to the region of the Mackay Glacier in the north (Fig.2). A new locality which includes indeterminate osteolepid and rhizodontid remains has recently been found near Mount Hughes in the Cook Mountains (Woolfe *et al.*, 1990), over 100 km south of the previously known southern limit of outcrop of the Aztec Siltstone. At Mount Fleming (locality 4) fish remains are recorded with plants from the top of the Beacon Heights Orthoquartzite, but otherwise all the material has been collected from the Aztec Siltstone, or from moraine or tillite assumed to be derived from this formation (cf. Grande & Eastman, 1986). Localities are numbered in Figure 2 according to the scheme of Young (1988). MS and RS numbers cited are registered fossil localities in the 'Ross Sea Environs' Fossil Record File of the New Zealand Geological Survey. Although fossil fish material has been recorded in the literature from Shapeless Mountain, Beacon Heights, Aztec Mountain, Alligator Peak (section A3), and the southern end of Mount Warren (localities 3, 5, 7, 18, 22, Fig.2), no material has yet been studied from these localities. Rhipidistian remains are known from all the remaining localities except for locality 1, but those from localities 2, 4, 9-12, and 16-23 are

currently indeterminable below ordinal level (Table 1).

Full details for these 24 fossil fish localities are given in Young (1988). Stratigraphic occurrence of rhipidistian remains from each locality where they have been recorded are summarised below, and indicated on stratigraphic columns in relation to the placoderm zonation of Young (1988) in Figure 3. Geographic distribution is summarised in Table 1.

2. GONDOLA RIDGE, MOUNT SUESS (MS4). This is the original locality where Devonian fish material was discovered in glacial moraine in 1911. The rhipidistian remains described by Woodward (1921) and White (1968) are revised below as indeterminate taxa. The original provenance of this fossil material is uncertain, but Young (1988) noted that the faunal assemblage (including thelodont scales) indicated derivation for at least some of the material from basal beds of the Aztec Siltstone.

4. MOUNT FLEMING (MS228-230; RS621, 622). Material collected from Mount Fleming by M.A. Bradshaw (1976-77, NZARP Event 33, Canterbury Museum) includes abundant thelodont scales, *Bothriolepis* plates (Young, 1988: pl.1 fig.4), and a single porolepiform scale described below. No other rhipidistian remains are recorded from Mount Fleming.

8. MOUNT CREAN (MS5, MS6; RS625-628). Fish remains collected from this locality by Gunn & Warren (1962) came from two levels 18 m apart, and were described by White (1968). The same outcrop was revisited in 1970-1971 (section L2 of Askin *et al.*, 1971; McPherson, 1978), and 1976-1977, and extensive new fossil collections were made. A detailed discussion of stratigraphic levels for seven collecting sites at this locality (MC1-7) was given by Young (1988: 12, 13). Localities for the various rhipidistians described from here are MC1 (*Mahalalepis* n.gen., osteolepids indet.); MC2 (*Koharalepis* n.gen., eusthenopterid indet.); MC 3 (osteolepid indet.); MC1,3,4, or 6 (*Platyethmoidia* n.gen., specimen associated with thelodont scales); MC5 (*Notorhizodon* n.gen.), MC7 (*Vorobjevaia* n.gen.). Specimen GS 7399/1 mentioned by White (1968: 7) as an 'indeterminate crossopterygian scale' is a round scale lacking an internal boss, and probably belongs to a dipnoan.

Most rhipidistian remains from this locality are assumed to come from the lower part of the Aztec Siltstone. Exceptions are *Koharalepis* n.gen. (approximating to the base of the *portalis* zone in the scheme of Young, 1988), *Notorhizodon* n.gen. (collected as a loose block which may have come from higher in the section), and *Vorobjevaia* n.gen. (assumed to be equivalent to the *karawaka* zone of Young, 1988).

9. LASHLY MOUNTAINS, SOUTH-EAST OF MOUNT CREAN (RS629-632). Fish remains from units 8-10 of section L1 of Askin *et al.* (1971; 15-30 m above the base of the Aztec Siltstone) include sharks and *Bothriolepis* already described (Young, 1982, 1988), and some indeterminate osteolepid remains described below. Also described is an indeterminate osteolepid from unit

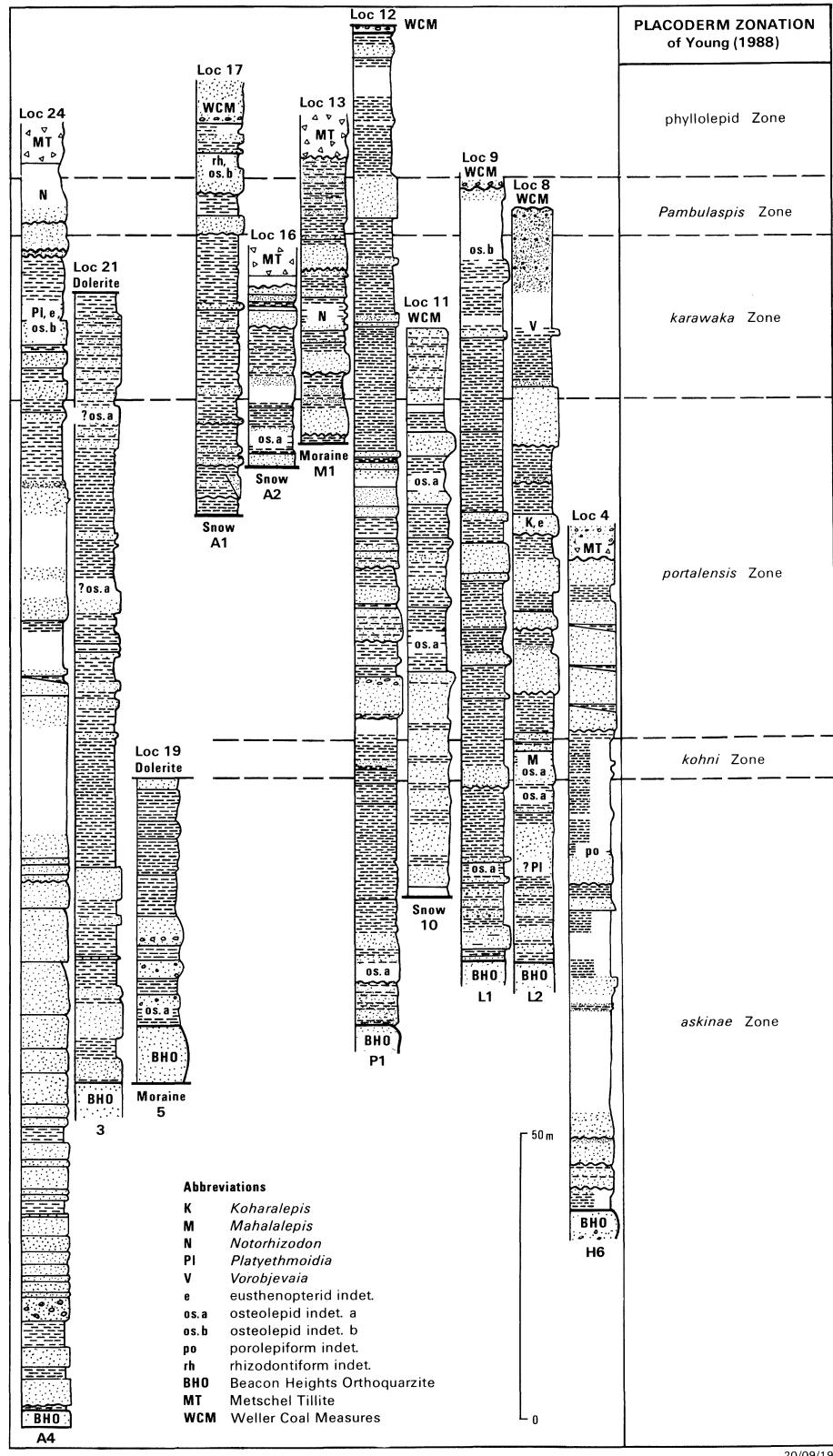


Fig.3. Approximate correlations of 11 sections through the Aztec Siltstone, containing rhipidistian remains at horizons indicated, shown against the placoderm biostratigraphic zones of Young (1988). Locality numbers (top of each measured section) are as in Figure 2. Numbers or letters at the base of each section refer to the sections of Askin et al. (1971) and Barrett & Webb (1973). Lithologies for stratigraphic sections modified after McPherson (1978).

34 (130 m above the base of the formation).

10. MOUNT FEATHER (MS7). White (1968) referred some osteolepid scales and bones to *Gyroptychius? antarcticus* (A.S.W.), but these are regarded here as indeterminate (see below).

11. PORTAL MOUNTAIN (MS232; RS633). Indeterminate osteolepid scales (e.g., AMF 55593) occur with *Bothriolepis portalensis* Young at its type locality (unit 17 of section 10 of Barrett & Webb, 1973, about 40 m above the lowest exposure of the Aztec Siltstone), and also in the higher horizon (unit 26, 70.8 m above lowest exposure). One of the latter is described below under osteolepid gen. et sp. indet.

12. PORTAL MOUNTAIN (RS634-637). One of the lowest recorded occurrences of osteolepid remains is in unit 4 of section P1 of Askin *et al.* (1971; 7-16 m above the base of the formation), which contains a diverse fauna including sharks, *Bothriolepis*, and thelodonts (Young, 1982, 1988; Turner & Young, 1992). These are described below as indeterminate osteolepid remains.

13. MOUNT METSCHEL (MS233; RS638-643). Both osteolepid and rhizodontid remains are recorded from the upper 31 m of the Aztec Siltstone, associated with four species of *Bothriolepis* (*B. alexi*, *B. karawaka*, *B. mawsoni*, *B. vuwae*; Young, 1988). Some of the rhizodontid remains are referred below to *Notorhizodon* n.gen. The osteolepid remains do not warrant description.

14. MOUNT METSCHEL, SOUTH-WESTERN END (RS644). Some rhizodontid bones and teeth referred below to *Notorhizodon* n.gen. occur at the top of the sequence at this locality in the fossiliferous horizon in section M2 recorded by Askin *et al.* (1971).

15. NORTHERN WARREN RANGE (MS234). The specimen of a rhipidistian jaw figured by McKelvey *et al.* (1972: fig.4) is described below under *Notorhizodon* n.gen.

16. NORTHERN BOOMERANG RANGE (MS235; RS645, 646). Osteolepid remains including isolated scales and a poorly preserved right lower jaw (AMF 55654) are noted here. They occur with *Bothriolepis* remains including *B. portalensis* Young in the upper 31 m of section A2 of Askin *et al.* (1971), but are insufficient to warrant description.

17. ALLIGATOR PEAK (MS236; RS647,648). Teeth and large scales with coarse ornament described by Ritchie (1972) as similar to *Holoptychius* belong to at least two taxa, dealt with below as indeterminate osteolepid and rhizodontid remains. The former is presumably the same as or closely related to the large osteolepid from slightly lower horizons at locality 24. The latter may include remains of *Notorhizodon* n.gen. but there is insufficient evidence to demonstrate this on the available specimens.

The material comes from unit 32 of section A1 of Askin *et al.* (1971), about 8 m below the Metschel

Tillite. This locality represents the uppermost phyllolepid zone in the biostratigraphic scheme of Young (1988: fig.5).

19. BOOMERANG RANGE, EAST OF ALLIGATOR PEAK (MS237). Fish remains in the basal 4 m of section 5 of Barrett & Webb (1973) were identified by Ritchie (in McKelvey *et al.*, 1972) to include articulated osteolepid rhipidistians. These are described below as osteolepids gen. et sp. indet. One of these specimens (AMF 54459) includes thelodont scales, not previously reported from localities south of Portal Mountain (Young, 1988).

20. ALLIGATOR PEAK, EASTERN SPUR (MS1, 2, 238, 239). Two specimens from MS2 of Gunn & Warren (1962; see White, 1968) are regarded below as indeterminate rhizodontid remains. This horizon is thought to be approximately equivalent to the fossiliferous level 70 m above the base of the Aztec Siltstone recorded in section 4 of Barrett & Webb (1973). No crossopterygian remains are recorded from the lower horizon (MS1, White, 1968).

21. ALLIGATOR PEAK, SOUTH-EASTERN SPUR (MS240, 241; RS652, 653). From the 81 and 111 m horizons in section 3 of Barrett & Webb (1973) Ritchie (in McKelvey *et al.*, 1972) noted large crossopterygian scales. Some indeterminate osteolepid scales from here are dealt with below.

23. SOUTHERN WARREN RANGE, WEST OF MOUNT RITCHIE (RS659). A few indeterminate osteolepid remains are associated with *Bothriolepis portalensis* at this locality (adjacent to section A5 of Askin *et al.*, 1971), but they are too poor for description. Young (1982) illustrated a shark tooth from this locality.

24. SOUTHERN WARREN RANGE, MOUNT RITCHIE (RS 660-663). Indeterminate osteolepid and eusthenopterid scales are described below from unit 54 of section A4 of Askin *et al.* (1971), 187 m above the Beacon Heights Orthoquartzite. From unit 62 (212 m above the base) comes the holotype of *Notorhizodon mackelveyi* n.gen., n.sp., associated with the antiarchs *Bothriolepis macphersoni* and *Pambulaspis antarctica* (Young, 1988).

Biostratigraphy and Age

Young (1988) suggested provisional age limits for the Aztec fish fauna of early Givetian to early Frasnian. Correlations with other sequences is rendered difficult by the fact that the Aztec succession is the only one known which preserves overlapping ranges of turiniid thelodonts and the antiarch *Bothriolepis* in its lower beds, and the first appearance of phyllolepid placoderms at the top of the sequence. The age assessment was based on a biostratigraphic scheme for the Aztec Siltstone which recognised six zones (Young, 1988: fig.5). As noted elsewhere (Young, 1991) rhipidistian remains occur right through the sequence, but based on the

systematic descriptions presented below some forms apparently have a restricted range. Rhipidistian occurrences in various correlated sections through the Aztec Siltstone are summarised in relation to the six placoderm zones in Figure 3. Taxa and localities referred to the six zones are summarised here:

1. *askinae* zone (localities 4,8,9,12,19). A specimen from locality 8 (Fig.3) tentatively referred to *Platyethmoidia antarctica* is associated with thelodont scales and therefore belongs in this zone, but the holotype occurs near the top of the sequence at locality 24, so this taxon may be wide-ranging. Otherwise only an indeterminate porolepiform (locality 4) and indeterminate osteolepids are known (associated with thelodonts at localities 8,9,12,19). The osteolepid scales are generally less than 15 mm across, and these fishes may have been of smaller size than the osteolepids higher in the sequence.

2. *kohni* zone (locality 8). The genus *Mahalalepis* n.gen. comes from this horizon, together with various isolated osteolepid remains. All observed scales are of small size.

3. *portalenensis* zone (localities 8,11,16,21,23). Accepting the stratigraphic interpretation at Mount Crean discussed by Young (1988: fig.4), the canowindrid *Koharalepis* from locality 8 can be tentatively assigned to this zone, since it comes from a horizon above the range of turiniid thelodonts. Also from this horizon at Mount Crean is an indeterminate eusthenopterid jaw. Otherwise only indeterminate osteolepid scales and teeth are known, including some from locality 21 in the Boomerang Range which are of comparable size to *Koharalepis*. *Bothriolepis portalensis* was identified from this locality by Young (1988). None of the scales observed from this horizon shows a peripheral zone of resorbed cosmine as is commonly seen in osteolepid material from the next highest zone.

4. *karawaka* zone (localities 8,9,13-15,21,24). Both eusthenopterid and rhizodontid scales and teeth are known, some of the latter tentatively referred to *Notorhizodon*. Associated are the osteolepids *Platyethmoidia* and *Vorobjevaia*, the latter placed in this zone on the basis of its association with *Bothriolepis barretti* Young (1988: fig.5). A common component is isolated large osteolepid scales (up to 30 mm across) which often show marginal cosmine resorption. Both features may distinguish these remains (listed as osteolepids indet. b in Table 1 and Fig.3) from indeterminate osteolepids in the lowest two zones (listed as osteolepids indet. a).

5. *Pambulaspis* zone (locality 24). The holotype of *Notorhizodon* occurs in this zone, with isolated large round scales also referred to this taxon.

6. phyllolepid zone (localities 17,?20). Material from here includes incomplete jaw and shoulder girdle remains and scales of a probable rhizodontid, and various indeterminate osteolepid remains.

Systematic Palaeontology

Class Osteichthyes

Subclass Sarcopterygii

Order Osteolepiformes Jarvik, 1942

Canowindridae n.fam.

Definition. Osteolepiforms in which the skull is very broad across the extratemporals (E1), the parietal, intertemporal, and supratemporal may be fused (E2), and the lateral extrascapular extends close to the midline. The median extrascapular has a broad posterior and narrow anterior margin. The main postorbital bone is excluded from the orbital margin by one or more small bones in a postorbital position. The jugal is at least twice as long as high (E3).

Remarks. Long (1985a, 1987a) has previously alluded to a higher osteolepiform taxon to contain the Australian genera *Canowindra* and *Beelarongia*, which we formalise here to include also the genus *Koharalepis* n.gen. Characters E1-3 are proposed below as synapomorphies of the group. Other resemblances included above are of uncertain status. Thus the small eyes of all known canowindrids is a feature also seen in porolepiforms, and may be a symplesiomorphy. The general shape of the extrascapulars resembles that in rhizodontids, and there is an additional postspiracular bone behind the orbit in porolepiforms. These features may be synapomorphies of some higher group (e.g., osteolepiforms or sarcopterygians), but evidence is equivocal, and their interpretation depends on phylogenetic position of the group. This is further considered below under discussion. The family as defined includes both forms with round scales which have lost their cosmine (*Canowindra*), and primitive forms with cosmine and rhomboid scales. Accepting monophyly of the group implies that these changes must have occurred within the group, independently of similar changes in other osteolepiforms and porolepiforms (Long, 1985a, 1987a).

Koharalepis n.gen.

Etymology. From the Maori word *kohara*, to shine, and the Greek *lepis*, a scale, an allusion to the shiny cosmine-covered scales and dermal bones of this form.

Diagnosis. A cosmine-covered canowindrid reaching a length of at least 1 m. Fronto-ethmoidal shield one and a third times as long as parietal shield; breadth/length indices of fronto-ethmoidal and parietal shields about 82 and 125 respectively. Three bones in lateral margin of fronto-ethmoidal shield behind orbit. Pineal plate situated well behind orbit. Pitlines on the

posterior dermosphenotic and the lateral extrascapular. Extratemporal broader than long. Median extrascapular slightly longer than broad with a convex posterior margin. Jugal about four times as long as high. Lachrymal reaching mouth margin. Maxilla over six times as long as high, with steep anterior margin. Opercular deeper than long, and subopercular about twice as long as high. Lower jaw with concave ventral margin. Scales rhombic with convex anterior, posterior, and ventral external cosmine margins. Each scale overlapped more by the scale anteroventral to it.

Remarks. *Koharalepis* n.gen. shows three special features not seen in any other osteolepid, which justify the erection of a new genus. There is an extra bone in the supraorbital - dermosphenotic series (here called the anterior dermosphenotic), the jugal is an elongate bone which excludes the postorbital from the orbital margin by contact with the posterior supraorbital, and the lachrymal apparently forms part of the mouth margin. It is suggested below that the 'accessory postorbital' previously described for *Beelarongia* may belong to the skull, to give a similar bone pattern to that of *Koharalepis*. However *Beelarongia* has a much shorter and broader fronto-ethmoidal and more elongate parietal shield, the latter of different shape, and it differs in the shape of various skull and cheek bones. *Canowindra* differs from *Koharalepis* in the absence of cosmine, round scales, the presence of two accessory postorbital bones, ratio of the fronto-ethmoidal to parietal shields, orbit shape, shorter, broader median extrascapular, and deeper opercular bone.

Koharalepis jarviki n.sp.

Figs 4-10, 11A, 12-14

'crossopterygian head and trunk' Askin *et al.*, 1971: 57.
'osteolepiform-like fishes from Antarctica' Long, 1985a: 98.
'undescribed form ... from Antarctica' Long, 1987a: 839.
'osteolepiform crossopterygian skull' Young, 1988: 12.
'crossopterygian osteichthyan ... from Mount Crean' Young, 1989b: 47.
'new genus' Long, 1990: fig.4B.
'new osteolepid' Young, 1991: 545.

Etymology. After Professor Erik Jarvik, Stockholm, in recognition of his major contribution to the study of crossopterygian fishes.

Holotype. AMF 54325, a complete skull and anterior part of the trunk, with part of the pectoral fin.

Locality. Mount Crean, Lashly Range (locality 8, Fig.2).

Horizon. Collecting site MC2 of Young (1988: fig.4), recorded as unit 8, section L2 of Askin *et al.* (1971), but actual level uncertain, although above the uppermost thelodont bearing horizon (see Young,

1988: 13).

Diagnosis. As for genus (only species).

Description. The holotype of *Koharalepis* comes from a relatively large fish (estimated length approximately 1 m), preserved as bone in a hard dark siltstone. The main piece shows the somewhat crushed and flattened skull roof, with both cheek units in dorsal view (Fig.4). Maximum preserved width across the operculum is approximately 220 mm. Behind is a portion of the body squamation extending approximately 300 mm from the tip of the snout. The counterpart of the posterior part of the right cheek includes the dorsal impression of the right pectoral fin. The ventral surface of the specimen has been prepared mechanically to show both lower jaws, the right lateral gular and subopercular, and scattered scales, some partly articulated (Fig.5). The shoulder girdle is displaced and largely embedded in the matrix, but the two halves are clear in a radiograph (Fig.6), which also shows images of marginal tooth rows, tusks of the left lower jaw and both vomers, the narrow posterior part of the ethmosphenoid, the thickened dorsal margin of the palatoquadrate (Pq), and a presumed image of the hyoid arch (Hy). The matrix of the specimen is generally devoid of microvertebrate remains, except for a patch inside the left lower jaw in which acanthodian scales are abundant, and could represent the last meal of this fish (acan, Fig.8). The broken posterior section (Fig.7B) shows imbricated scales wrapped around a thickened central portion which contained the vertebral column (not preserved). The ventral surface on the left side shows up to six scales overlapping each other.

Skull. The head was evidently rather flat and broad posteriorly, and our restoration suggests that much of the cheek was visible in dorsal view (see below). The bones of the skull roof are generally well preserved, although somewhat crushed, and some dermal bone sutures are evident. The fronto-ethmoidal and parietal shields and the cheek bones form three discrete units, as is normally the case in osteolepids. The extratemporals are slightly displaced on the specimen, and were presumably in loose connection with the rest of the parietal shield.

The fronto-ethmoidal shield is crushed, and only the left margin is clear. It is about 1.2 times as long as broad, which is thus more elongate than *Gyroptychius? australis*, and *Beelarongia* (Young & Gorter, 1981; Long, 1987a). The shield broadens anteriorly, and is almost twice the breadth of its posterior margin at the level of the postorbital corners. The preorbital and subnarial corners are obscured on both sides by the lower jaws. The left anterior naris is visible but poorly preserved (fe.exa, Fig.9A). It is just obscured in dorsal view, but this may be due to crushing. The lateral margin of the shield shows a slightly sinuous posterior section, then a conspicuous notch (n.Po, Fig.10A). These together represent the postorbital notch of

other osteolepids. Jarvik (1948: 40) noted that the postorbital notch may be subdivided into anterior and posterior sections, but in *Koharalepis* the deep anterior notch is unusual. The large postorbital plate is preserved in approximate position, and in dorsal view shows an anterodorsal process to fill this notch, as predicted by Young & Gorter (1981: 118) for *Gyroptychius?* *australis*, the only other osteolepid to show a similar configuration in this region. In front of the notch is a short anterolaterally directed margin (po.m, Fig.10A), again as in *Gyroptychius?* *australis*, followed by the orbital notch (orb, Fig. 10A), which is about 6 mm long on the left side, although its limits are not very clear. The right orbital notch is

obliterated by a crack, but the dorsal notch on the right lachrymal is about 8 mm long, although it is not clear that all of this formed the orbital margin (see below). In *Koharalepis* the orbit evidently was somewhat smaller (Fig.10C) than in *Gyroptychius?* *australis* (Young & Gorter, 1981: fig.25C).

Of the component bones of the fronto-ethmoidal shield, dermosphenotics, frontals, supraorbitals and posterior nasals can be inferred on the left side. There is a large ovoid pineal plate with a small foramen, placed some distance behind the orbit. In the snout region the dermal bone sutures are covered by a continuous sheet of cosmine.

The dermosphenotic (Ds2) is an elongate bone, about



Fig.4. *Koharalepis jarviki* n.gen., n.sp. Holotype (AMF 54325) in dorsal view (from Mount Crean). Specimen whitened with ammonium chloride.

one third as broad as long, with an acutely pointed anterolateral corner, much as in *Gyroptychius* (Jarvik, 1948: fig.13F,G). Its surface is covered with numerous laterosensory canal pores, and a short pitline is seen on the left plate near the posterior margin (pl. Fig.7A). The pores are near the lateral edge of the skull at the anterior end of the dermosphenotic, but also continue on the bone in front, so it is not clear which bone carried the branch of the infraorbital canal. If on the posterior bone, it is at a point very close to the anterior margin, as shown on the right side of Figure 10A.

Sutures reaching the skull margin in the postorbital

and orbital notches show that there are two bones between the dermosphenotic and the orbit. The anterior bone (So2, Figs 7A, 10A) has all margins clearly defined, and includes the posterior part of the orbit, the postorbital corner and postorbital margin. Its posterior margin lies in the deepest part of the postorbital notch. Unlike adjacent bones it is devoid of sensory pores. Anteromesially its margin is notched, suggesting two bones of the nasal series on its mesial side. Both carry scattered sensory pores (Fig.10A), and the anterior also has a group of pores for a sensory organ (gp.so, Fig.9A), in a similar position relative to the orbit to that figured for a generalised osteolepid by Jarvik (1948: fig.36A).



Fig.5. *Koharalepis jarviki* n.gen., n.sp. Holotype (AMF 54325) in ventral view. Specimen whitened with ammonium chloride.

In front is another supraorbital (So1, Fig.10A). The bone behind the posterior supraorbital (Ds1) has a poorly defined mesial margin, but appears to extend as far back as the anterior end of the frontal pitline (pl.Fr). The corresponding bones on the right side are obscured by crushing (Fig.7A). Separate anterior and posterior dermosphenotic have previously been illustrated by Jarvik (1948: fig.17) in a composite showing the largest number of bones found by him in the cranial roof of the Scottish Middle Devonian osteolepids, but in fact this condition is recorded in only a single specimen of *Osteolepis macrolepidotus* (Jarvik, 1948: 58). We therefore consider it most unlikely that the observed condition in the holotype of *Koharalepis* is an individual variation.

The frontal (Fr, Fig.7A) is three times as broad as the dermosphenotic, and the largest bone of the fronto-ethmoidal shield. Its anterior suture is obscured by cosmine, but the median suture extends anteriorly in front of the pineal bone, to give an indication of frontal length. The posterior margin of the frontal is gently convex. The mesial margin of the anterior

dermosphenotic is not clear, so it is uncertain whether the supraorbital sensory canal crosses the frontal before passing onto the nasal series, the normal condition in osteolepids, or whether it remained in the lateral series of bones. Two alternatives are shown on left and right sides in Figure 10A. The frontal pitline is clear on both sides (pl.Fr).

The remaining fronto-ethmoidal bones cannot be distinguished as separate elements, but the termination of the median suture some distance behind the snout might suggest a large median postrostral bone (?Ptr).

The parietal shield (PaS, Fig.7A) has strongly concave anterolateral and lateral margins, embayed respectively for the posterodorsal margin of the postorbital bone (Po), and for the spiracular notch (n.spir) and convex dorsal margin of the squamosal (Sq). The anterior margin of the shield is gently concave, and there is no significant gap between the two shields as occurs in some porolepiforms (e.g., *Glyptolepis*, Jarvik, 1972) and rhizodontiforms (Long, 1989). The posterior margin is slightly pointed posteriorly, and gently notched for the lateral extrascapulars. There are no visible sutures

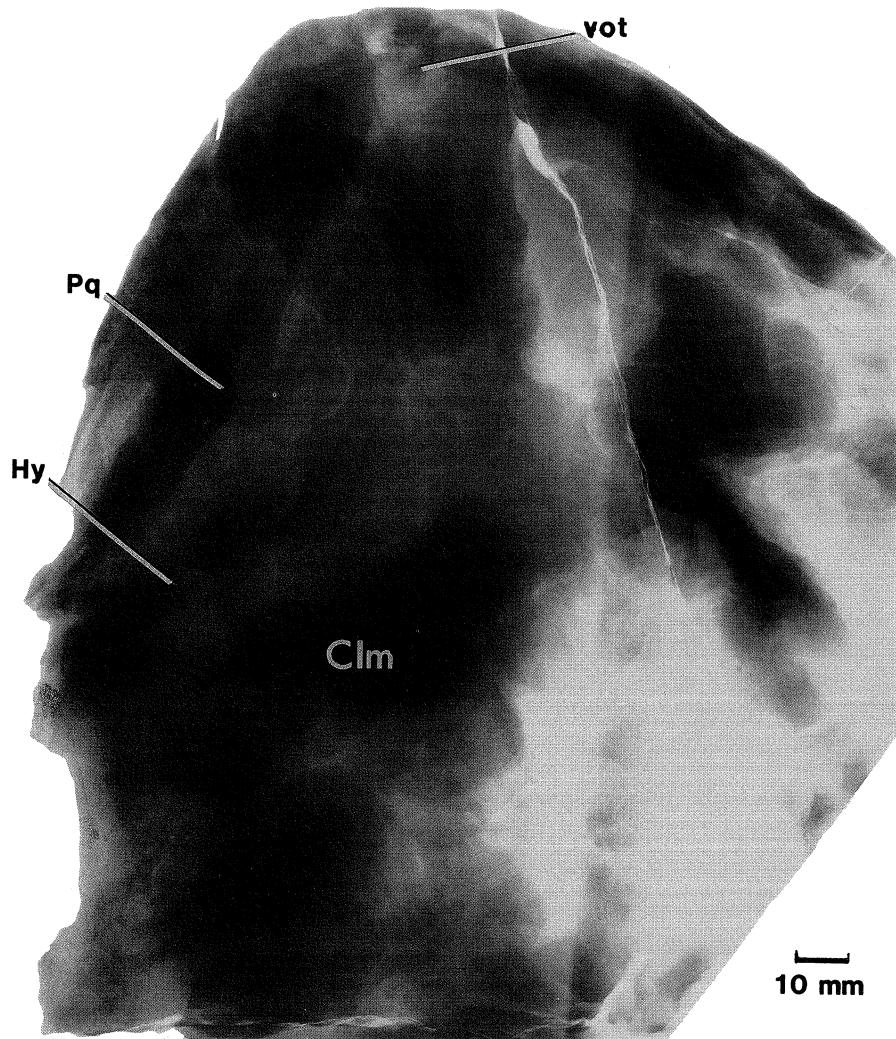


Fig.6. *Koharalepis jarviki* n.gen., n.sp. X-radiograph of the holotype (AMF 54325).

apart from the median parietal suture, and the mesial suture of the extratemporal bone (Et). The median parietal suture is sinuous posteriorly, but indistinct anteriorly.

The course of the main lateral line canal is indicated by sensory pores forming a double row running straight back from the anterolateral corner of the parietal shield, then passing laterally toward the spiracular notch, and posteriorly onto the lateral extrascapulars close to the lateral edge (lc, Fig. 10A). The long transverse (middle) pitline and shorter posterior pitline (pl.tr, pl.p) have a posterior position,

indicating a centre of ossification in the posterior third of each parietal, as in other osteolepiforms. The broad triangular extratemporal bones (Et) are broken and displaced on both sides, but enough is preserved for a reliable reconstruction of their shape. The extratemporal is about one third as broad as each side of the shield, and extends anteriorly for about one quarter of its length.

The extrascapulars are slightly displaced but well preserved. The median extrascapular (m.Esc) has a pointed anterior and broadly convex posterior margin. The larger lateral extrascapulars (l.Esc) are of

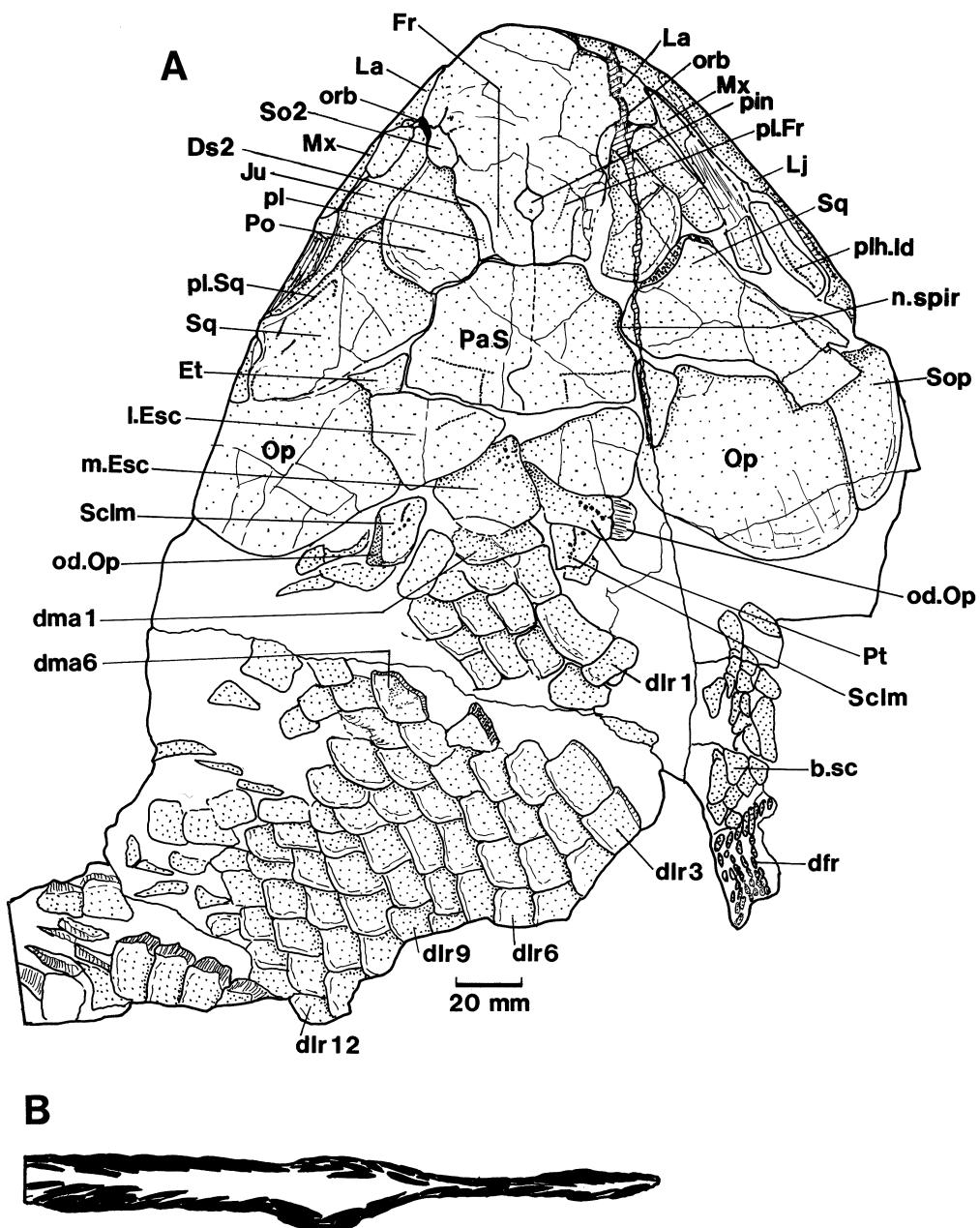


Fig.7. *Koharalepis jarviki* n.gen., n.sp. Holotype (AMF 54325). A, whole specimen in dorsal view showing general features of the dorsal surface (for details of suture pattern on skull roof and cheek see Figs. 9, 10); B, scale arrangement in a sectional view of the posterior preserved edge of the holotype.

triangular shape, and overlap the median extrascapular, but without the clear overlap flange seen in *Eusthenopteron* (e.g., Jarvik 1944a: fig.9). Anteriorly they almost meet in the midline, where they are excluded from the posterior margin of the parietal shield by the narrow anterior margin of the median extrascapular. This configuration is reminiscent of the extrascapulars of rhizodontids (Andrews, 1973, 1985; Long, 1989). Sensory pores pass back across the lateral extrascapular to its posterior corner, with a mesial branch for the occipital cross commissure, and a short anteromesially directed pitline (stcc, pl.Esc, Fig.10A).

The cheek of *Koharalepis* is composed of seven elements as in other osteolepiforms. The left cheek is preserved with the postorbital and squamosal essentially in position against the skull (Po, Sq, Fig.7A). The postorbital is of large size, and carries scattered sensory pores on its anterodorsal process (pr.ad, Fig.9A). The squamosal-preopercular-quadratojugal unit appears relatively complete, although its dorsal margin is broken.

The squamosal pitline (pl.Sq, Fig.9B) is long, with a strong loop at the anterior end, as in *Osteolepis*. The ventral margin of the bone shows a notch adjacent to the clearly defined posterior margin of the jugal (Ju). Another notch further back coincides with a fracture which might be the squamosal-quadratojugal suture. Posteriorly the bone is fragmented, but two pitlines are clear (pl.Qj, pl.Pop), although no bone sutures are visible. Scattered sensory pores extend dorsally from the squamosal pitline for the jugal canal (juc). Pores along the ventral margin of the squamosal, and of the jugal on the right side (Fig.9C), presumably relate to the same canal.

The whole of the jugal bone is well displayed on the left side (Ju, Fig.7A). It is a long low bone (length 47 mm) of fairly constant height; with a L/B index 3.6 it is more elongate than the jugal of *Porolepis* (e.g., Jarvik, 1980a: fig.186). Dorsally there is a short anterior contact with the skull roof behind the orbit, although the anterodorsal corner is obscured by the skull (So2). Behind is a long slightly undulating dorsal margin with

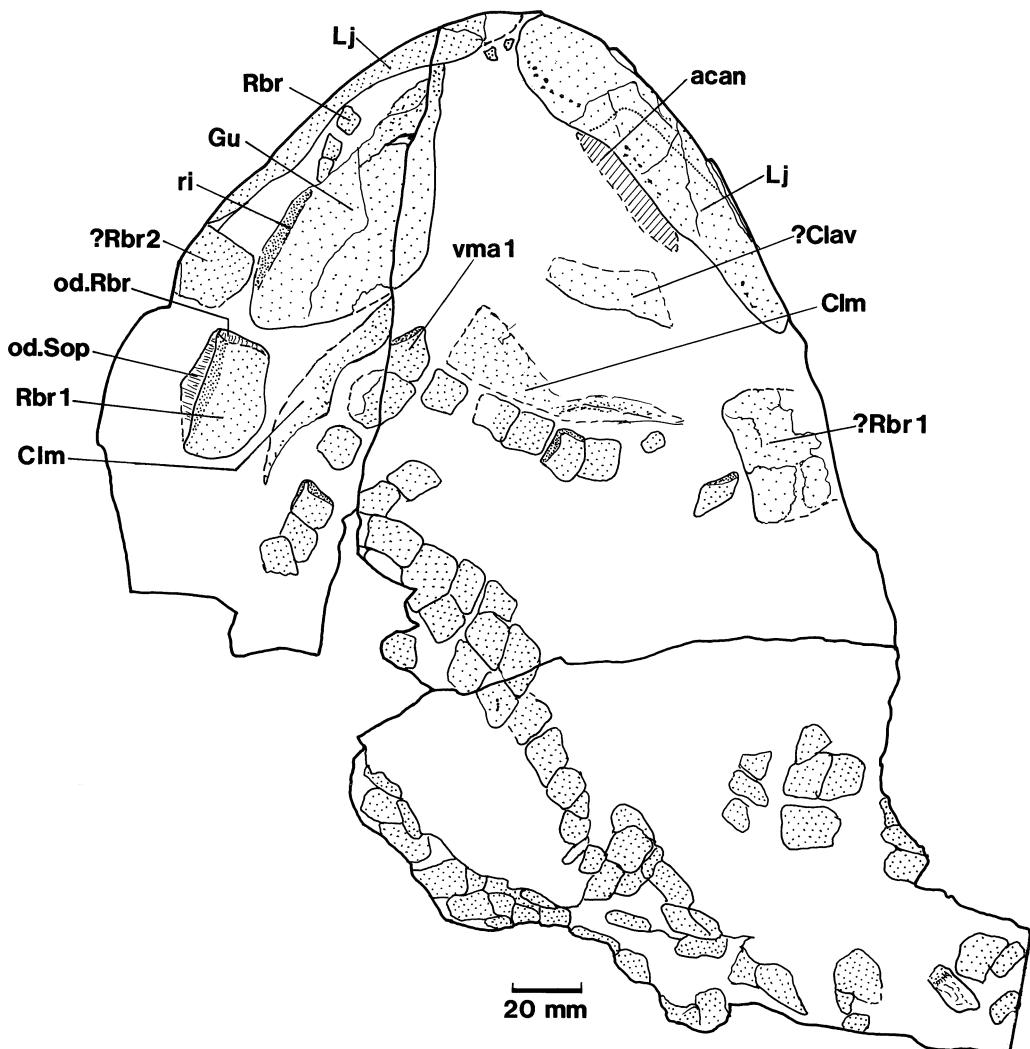


Fig.8. *Koharalepis jarviki* n.gen., n.sp. Holotype (AMF 54325) in ventral view.

the postorbital. The margins in contact with the lachrymal and maxilla are as preserved on the right side, the anterior with a narrow overlap area (od.La, Fig.9A). The lachrymal is preserved with a complete ventral border which is displaced over the maxilla and lower jaw. There is a central group of fine pores (gp.so, Fig.9A), and larger pores for the infraorbital canal (ioc), just as illustrated by Jarvik (1948: figs 32, 36A). The ventral margin is slightly concave, but the dorsal is incompletely preserved. The anterior part of the left maxilla (Mx) shows some sensory pores of the infraorbital canal as described in other forms (Jarvik, 1944a, 1966), and a distinct angle on its dorsal margin at the lachrymal-jugal contact.

The right cheek has been flattened upward and is largely visible in dorsal view, but with its ventral margin partly obscured by the lower jaw (Figs 7A, 9C). The right lachrymal (La, Fig.9C) shows a concave dorsal margin, assumed to be part of the orbital margin, although a notch of corresponding size on the skull roof is not clearly seen on either side. The convex ventral margin abuts against and partly overlaps the

lower jaw. The posterior margin is displaced from its contact with the jugal (Ju). The anterior end of the maxilla is well preserved (Mx), again with a clear angle in its dorsal margin where the jugal and lachrymal meet, as seen on the left side. Also like the left side, the bone decreases in height anteriorly toward a point. Although slightly obscured by the lachrymal, it seems clear that the maxilla did not exclude the lachrymal from the mouth margin, at least externally. It must be assumed that dental laminae of the premaxilla and maxilla were in contact within the mouth, presumably a necessary condition to provide a continuous marginal tooth row, but this cannot be seen on the specimen, nor is it shown on the x-rays. One illustration of *Megalichthys* (Jarvik 1966: fig.14D) shows the lachrymal in point contact with the jaw margin, but no previously described rhipidistian shows the condition displayed by *Koharalepis*. However, a tooth-bearing lachrymal occurs in some palaeoniscoids (e.g., *Glaucolepis*, in which it is interpreted as a fused bone, the 'lacrimo-maxillary'; see Nielsen 1942: fig.27).

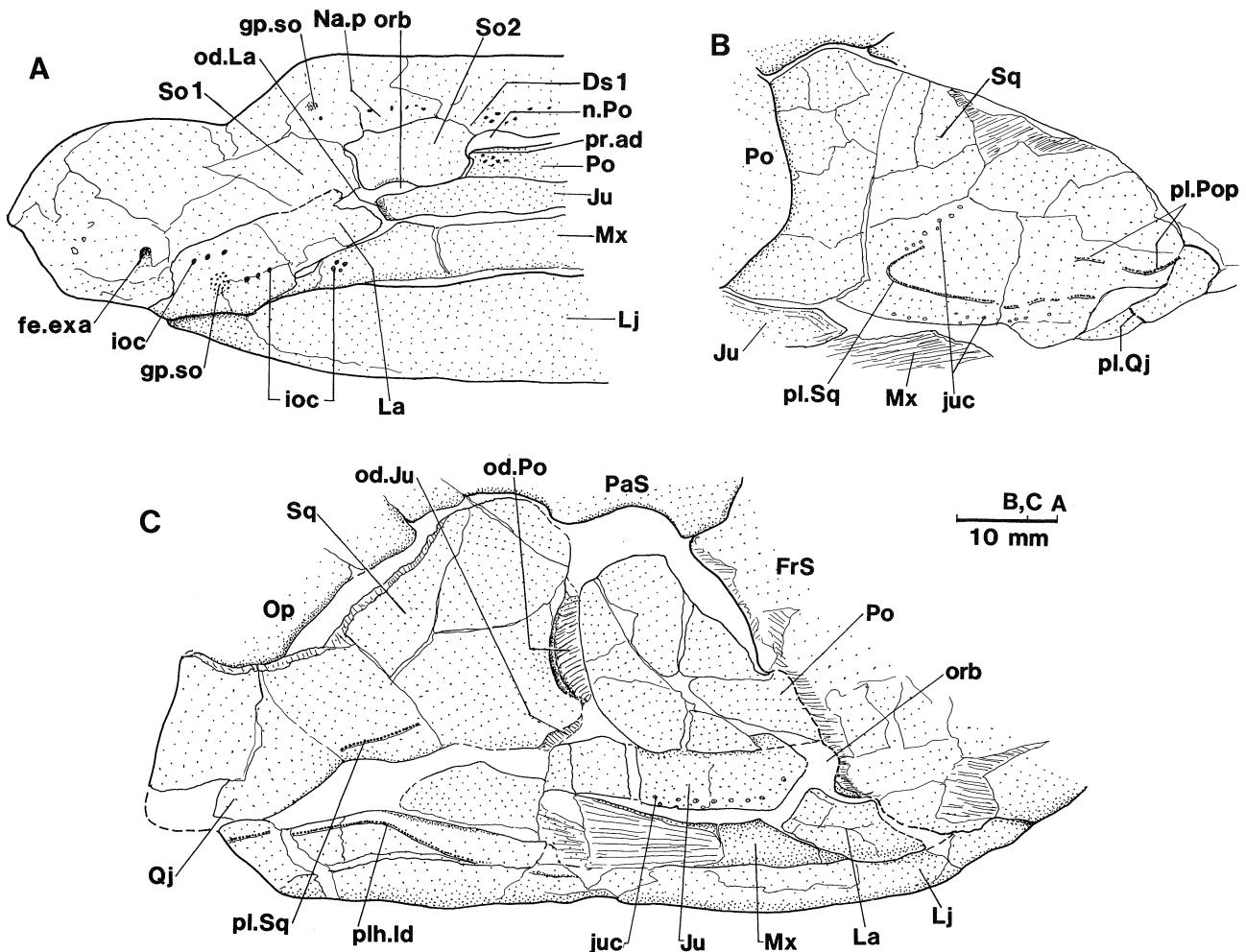


Fig.9. *Koharalepis jarviki* n.gen., n.sp. Camera lucida drawings showing details of the bones of the cheek as preserved on the holotype (AMF 54325). Many cracks and fractures omitted. A, left orbital region in lateral view; B, posterior part of left cheek in lateral view; C, right cheek in dorsal view.

The ventral margin of the maxilla in *Koharalepis* abuts against the lower jaw, as does the lachrymal. Pores of the infraorbital canal are seen on both the lachrymal and anterior end of the maxilla (ioc, Fig.9A), as in other forms (e.g., *Latvius*; Jessen, 1966: pl.3). The abraded middle section of the maxilla shows radiating striations from the ossification centre, anteriorly placed as in other forms (e.g., Jarvik, 1948: fig.25). The posterior end shows another slight angle on the dorsal margin which fitted into a notch at the presumed quadratojugal-squamosal suture, which is displaced posteriorly. The anterior margin of the jugal against the lachrymal is clear; its anterodorsal margin shows no obvious orbital margin, but is partly obscured by the large crack running from the back of the specimen to the snout (Figs 4, 7A). Its long ventral edge carries pores of the jugal canal

(juc, Fig.9C), and closely matches the posterior section of the dorsal margin of the maxilla. The posterior extremity of the jugal is truncated by a fracture, but the adjacent squamosal shows the normal overlap area (od.Ju).

The postorbital (Po, Fig.9C) is partly displaced over the jugal, and its dorsal edge is incomplete and obscured by the skull roof. Its convex posterior margin sits adjacent to a large overlap area on the anterior margin of the squamosal (od.Po). The squamosal is fractured and the posterodorsal margin of the cheek unit is broken just in front of the anterior border of the opercular plate (Op), so the preopercular plate is missing. The quadratojugal (Qj) is displaced to overlie the opercular and subopercular bones (Figs 7A, 9C), and its suture with the squamosal is assumed to be indicated by a notch in the ventral margin of the cheek

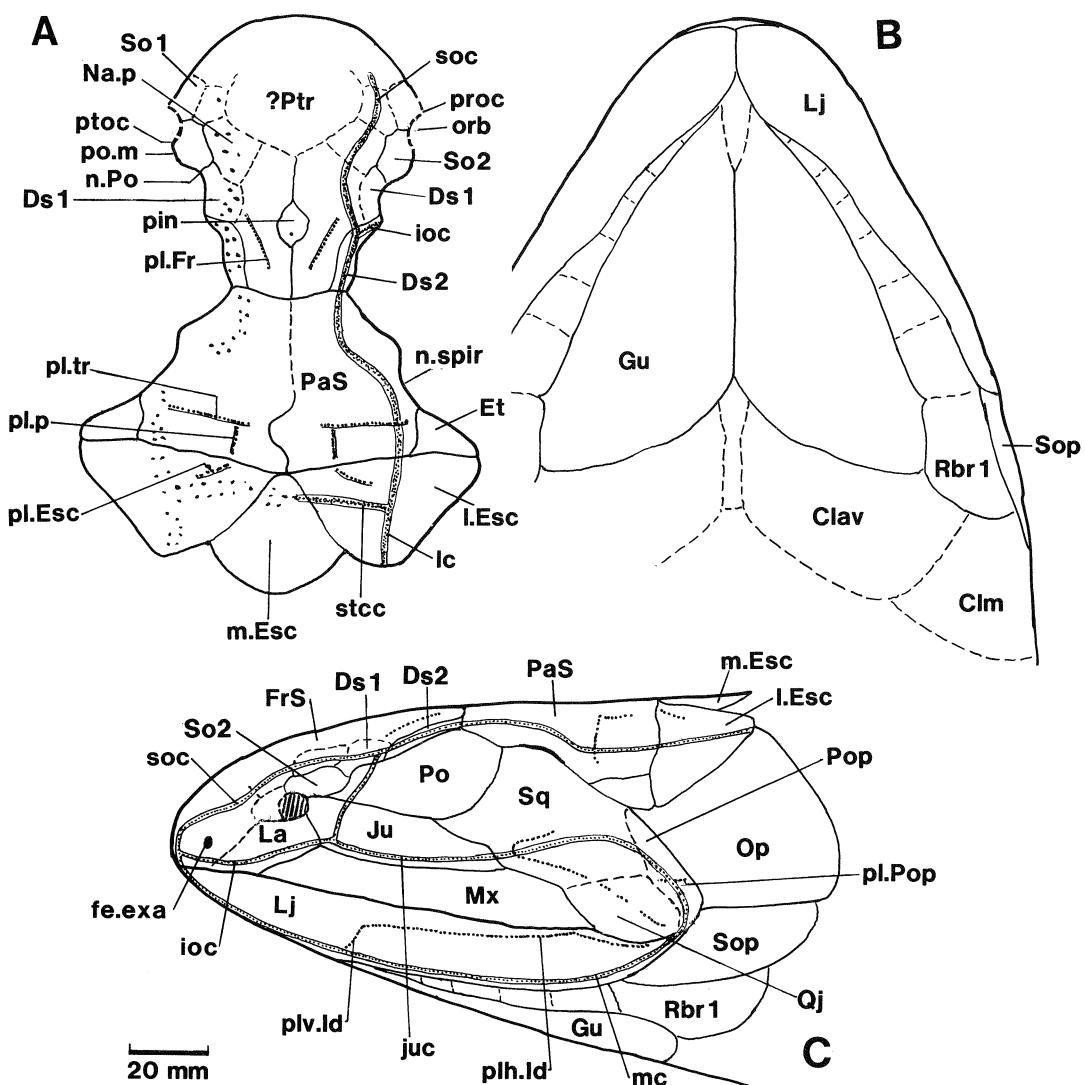


Fig.10. *Koharalepis jarviki* n.gen., n.sp. A, restoration of the skull roof in dorsal view, with distribution of laterosensory pores shown on the left side, and sensory canals on the right. Some pitlines not shown. Size and shape of the orbit uncertain (see text for discussion); Alternative interpretations of the anterior dermosphenotic and supraorbital sensory canals shown on each side; B, restoration of the head in ventral view; C, restoration of the head in left lateral view. After the holotype (AMF 54325).

unit beneath the squamosal pitline (pl.Sq).

A reconstruction of the cheek is given in Figure 10C. Special features are the large size of the postorbital, which does not reach the orbit, the long low jugal, and the termination of the maxilla behind the lachrymal. The size of the orbit cannot be reliably determined, but it seems to have been small; the notch on the right lachrymal suggests a diameter of 6 to 8 mm, but the corresponding poorly preserved notch on the skull roof seems smaller, and the orbit may have been only half this size, with only part of the lachrymal notch forming the orbital margin. The suture for the preopercular bone is unclear, but was presumably bar-like as in other osteolepiforms (Long, 1985a), and carried the preopercular sensory canal towards the lower jaw.

Only the dorsal part of the operculo-gular series is well preserved. The operculum (Op, Fig.7A) is large, and deeper than long, in contrast to other osteolepiforms in which it is generally longer than deep (Jarvik, 1948). Its strong anterodorsal corner and margins are well exposed on the right side. The anterior margin is straight to slightly concave, and the posterior margin is strongly convex. The subopercular bone is also well exposed on the right side, except for its anterodorsal corner. It is almost twice as long as deep, and deepest at the anterior margin. It is slightly shorter than the operculum, and less than half its height. The right side of the holotype shows that the anterior part of the opercular and subopercular bones were overlapped by the cheek unit, and reached about as far forward as the front of the preoperculum. The left suboperculum is folded onto the ventral surface and badly fractured, so shape is uncertain (Fig.8).

On the ventral surface (Figs 5, 8) only the right lateral gular is preserved, although the full extent of its anterior end cannot be determined. It is broad with a

convex posterior and relatively straight mesial margin, which is broken anteriorly but possibly indicates a shallow notch for a slender median gular (Fig.10B). The cosmine surface is depressed laterally across a slight ridge (ri, Fig.8) which defines a narrow marginal zone, but the overlap for the branchiostegals is not preserved. The lateral gular pit-line is either not developed or obscured by the left lower jaw. The first branchiostegal ray of the right side is also well exposed (Rbr1). It is of similar shape to the suboperculum but deeper posteriorly. The exposed dorsal margin is slightly convex, and overlap areas for the suboperculum and next branchiostegal (or submandibular) are well developed (od.Sop, od.Rbr). In shape this bone resembles that of *Gyroptychius? australis* (Young & Gorter, 1981) rather than *Osteolepis* (Jarvik, 1948). It is almost as deep (or broad) as the suboperculum, but only three quarters its length. Anterior branchiostegal elements can be partly seen lateral to the right lateral gular (Rbr), but details of their shape and relative sizes cannot be determined. On the left side a poorly preserved large element could be the suboperculum (not preserved in dorsal view; Fig.7A), but its shape suggests it may be the first branchiostegal (?Rbr1).

The lower jaw is preserved but crushed on both sides on the holotype. Most of the left jaw is exposed in ventral view, but is broken such that the biting margin is only seen on the dorsal side. The right jaw is badly fractured, but the posterior part of the horizontal pitline is seen in dorsal view (plh.Id, Figs 7A, 9C). The posterior margin is unclear on both sides, but jaw length is estimated at about 130 mm, with the jaw about 4.3 times as long as deep, and deepest at the anterior end. Sutures for the dentary and infradentaries are completely obscured by cosmine. The ventral margin on both sides

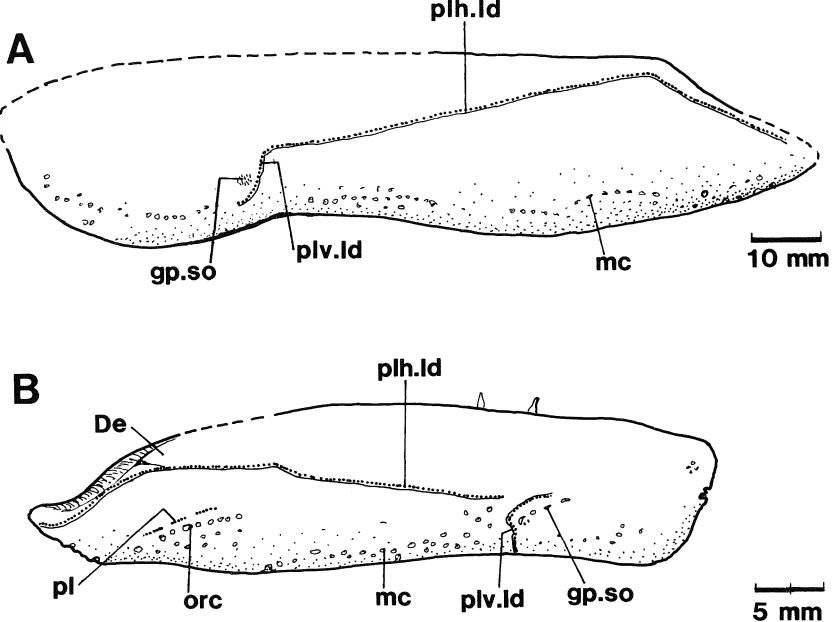


Fig.11. A, *Koharalepis jarviki* n.gen., n.sp. Left lower jaw in lateral view, restored after the holotype (AMF 54325); B, *Platyethmoidia antarctica* n.gen., n.sp. right lower jaw in lateral view (AF 266).

has a strongly concave central division (Fig.11A), in contrast to the lower jaw described below from Mount Crean (Fig.11B). Apart from a possible tusk seen in x-rays in front of the vomerine tusk at the anterior end of the right lower jaw (Fig.6), there is no information on the lower dentition or morphology of the inner surfaces of the lower jaw.

Pectoral girdle. The pectoral girdle is not well known. The post-temporal is preserved on the right side (Pt, Fig.7A) approximately in position between the median and lateral extrascapular, with the latter obscuring its anterior margin. It was apparently higher than long, but the posterior margin is incomplete. A ventral area can be seen which was overlapped by the operculum (od.Op), as in *Osteolepis* (e.g., Jarvik, 1948: fig.25). Immediately behind is the incomplete supracleithrum (Sclm), which carries a short pitline. Both bones have pores for the lateral line canal. The supracleithrum is better exposed on the left side, again with a pitline and sensory canal pores, and a prominent overlap area

presumably for the operculum (od.Op). This bone has evidently been rotated from its articulated position, as its broader end should be dorsomesially placed, as in other osteolepids (e.g., Jarvik, 1948: fig.25). Part of the cleithrum and a possible clavicle are seen on the ventral surface (Clm, ?Clav, Fig.8), but they are too incomplete for description. The anterior region of the right cleithrum shows fine reticulate ornament, as is normal in osteolepiforms.

Body squamation. The scales of the first 12 rows behind the extrascapular are partly preserved in articulation, and seen in dorsal view (Fig.4). The median extrascapular is displaced posteriorly to overlap and partly obscure the anterior scale of the dorsal median scale row, but it is assumed (from their large size) that the first row is that preserved on the right side (dlr1, Fig.7A). This and the second scale row originate from a single large median dorsal scale (dma1), as in *Osteolepis* (Jarvik, 1948: fig.26A). The posterolateral margin of the specimen on the right side is seen from the section to be the edge of scales in dorsal view. The dorsal median scales have a sector shape, with strongly convex posterior and slightly concave anterior margins (dma6). The large size of the median scales is also seen in osteolepids (e.g., Jarvik, 1948: fig.26A). Typical body scales are thick, with the normal cosmine-covered exposed area, surrounded by a well-defined groove and overlap area as in other osteolepids. In contrast to *Gyroptychius* (Jarvik, 1948: fig.28), the anterior overlap area on each scale is overlapped more by the scale anteroventral to it than by the scale anterodorsal to it, giving the arrangement described for eusthenopterids by Jarvik (1985: fig.17). The anterodorsal scale overlap area is clearly seen on individual scales as a short, concave dorsal margin to the exposed scale area. There is a high articular process on each scale, as noted in the Mount Howitt form *Beelarongia patrichae* (Long, 1987a). As far as can be seen on the holotype the basal surface of the scales shows typical osteolepid development, with a thickened vertical ridge.

Scale rows on the ventral surface are much less complete (Fig.5). The first row is in position on both sides behind the shoulder-girdle, with a large possible median scale (vma1, Fig.8), and other scales poorly exposed back along the midline.

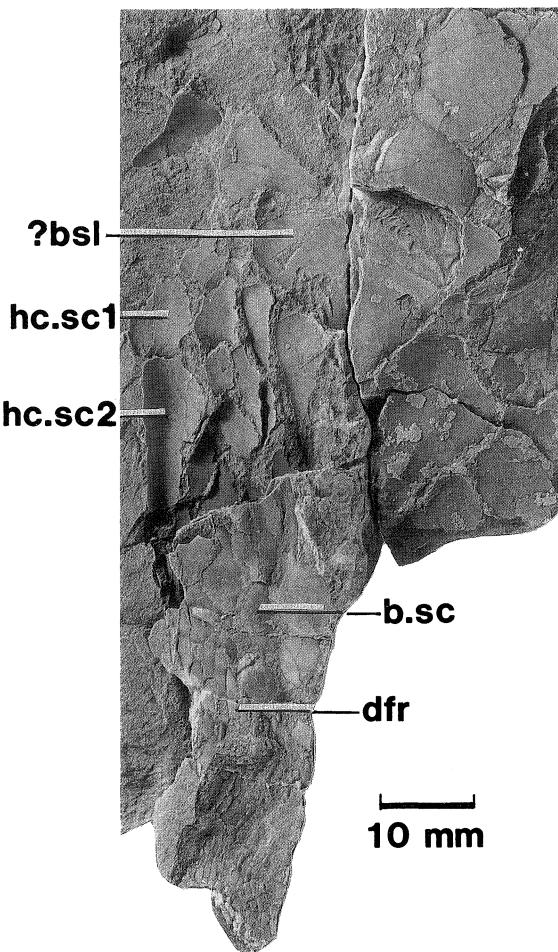


Fig.12. *Koharalepis jarviki* n.gen., n.sp. Detail of the right pectoral fin of the holotype (AMF 54325), the proximal part as an impression of the dorsal surface, the distal part showing scales and dermal fin rays of the ventral surface. Specimen whitened with ammonium chloride.

Pectoral fin. The proximal part of the right pectoral fin is preserved as an impression of its dorsal surface on the counterpart, and a small detached piece preserves a more distal portion, including both dorsal and ventral surfaces. The leading edge on the impression (Fig.12) shows adjacent proximal equidimensional (hc.sc1), and distal elongate impressions (hc.sc2), apparently corresponding closely in shape to the hemicylindrical scales protecting the leading edge of the fin in *Osteolepis* as illustrated by Jarvik (1948: fig.30A). The detached piece shows various rhombic or rounded basal scales of the fin lobe up to 8 mm across (b.sc), and

distally on the ventral surface up to ten rows across of the dermal fin rays (dfr). These are elongate, up to 1 mm wide, and about five times as long. They are cosmine covered, and a few at the distal end show the grooved inner surface as described by Jarvik (1959: 23). A broken impression of an apparently elongate element may represent the basal scute of the fin (?bsl, Fig.12), but margins are unclear. In Figure 14 the basal scute of the fin is restored after *Osteolepis*.

Restoration. The right pectoral fin as preserved has the correct position with respect to the skull roof when the scale rows are restored (Fig.13), indicating that the right cheek unit has been displaced forward and outward during flattening. In other forms the dorsolateral scale rows have up to seven (*Osteolepis*) or ten (*Gyroptychius*) scales running over the flank above the pectoral fin (Jarvik, 1948: figs 26, 27). As noted above the broad gular plate of the holotype suggests a relatively broad head, and a restoration in ventral view (Fig.10B), based on actual breadth of the gular

and branchiostegals, gives a width across the posterior part of the gulars which is about 70% of the preserved width. This degree of flattening has been assumed in the restorations (Figs 13, 14), which are nevertheless only an approximation given the crushed preservation of the specimen.

Family Megalichthyidae

Definition. Cosmoid osteolepiforms in which the external naris may be elongate or slit-like (D6), and partly enclosed by a posterior tectal bone (D2), there is an interpremaxillary process with teeth on the premaxilla (D7), the vomers are short and broad, sometimes with a strong mesial process (D1), the pineal foramen is closed (D4), the frontal bones are notched to receive the posterior nasals (D3), and the lachrymal notch is well-developed.

Remarks. As noted by Long (1985b: 374) the Late

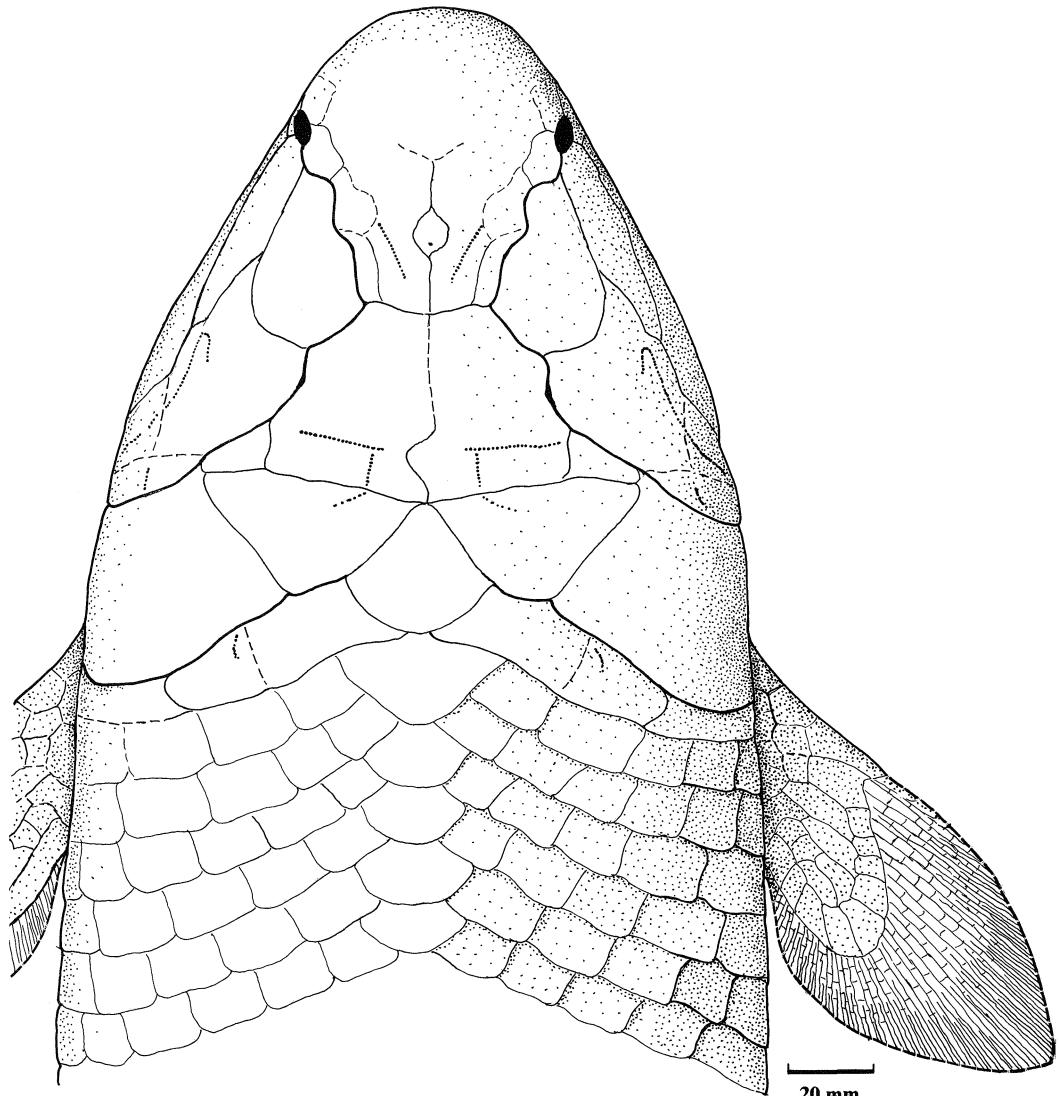


Fig.13. *Koharalepis jarviki* n.gen., n.sp. Restoration of fish in dorsal view, based on the holotype.

Palaeozoic genera *Megalichthys* and *Ectosteorhachis* are united by several specialised features, which we formalise here in the above definition to include the new genus described below, and *Megistolepis* Vorobjeva, 1977. Some disagreements about differences of structure between *Megalichthys* and *Ectosteorhachis* (e.g., the shape of the naris) are discussed by Jarvik (1985: 8). Vorobjeva (1977) previously proposed subfamilial rank for *Megistolepis*, and for megalichthyids, but this implies a scheme of relationships which at present is not strongly supported. Other possible specialisations of the group or some of its members include the structure of the cosmine (Thomson, 1975), the deep maxilla (Jarvik, 1966), the complex dermal articulation between the parietal and fronto-ethmoidal shields, and the extensive branch of the lateral line canal into the parietals (Bjerring, 1972). Character distributions are considered below in a discussion of the inter-relationships of megalichthyid genera, and their relationships to other osteolepids.

Mahalalepis n.gen.

Etymology. After Dr S. Mahala Andrews, Edinburgh, in recognition of her major contribution to the study of rhipidistian fishes.

Diagnosis. A megalichthyid with a narrow blunt snout, pronounced subnarial corners, two large supraorbitals, and a pronounced orbital notch about half way along the length of the fronto-ethmoidal shield. Posterior tectal bone has a longer supranasal than infranasal process, the frontal bone has a short contact with the posterior supraorbital, and the posterior nasal is long and narrow.

Remarks. This form is only known from a single specimen, but it differs clearly from other cosmine-covered Antarctic osteolepids. The fronto-ethmoidal shield was evidently much more elongate than in *Platyethmoidia*, and less broad across the nasal region than in *Koharalepis*, with the orbits placed much farther to the posterior, only one dermosphenotic, and a different shape to the postorbital notch, and frontal and posterior nasal bones. The latter two characters serve to distinguish *Mahalalepis* from all previously described cosmoid osteolepids. The possibility that this form belongs with the jaw described below as *Vorobjevia* cannot be excluded, but is considered unlikely because of the difference in stratigraphic level of the two specimens. The presence of a posterior tectal bone forming the posterior boundary of the external naris, the probable absence of a pineal foramen, the nasal bone notched into the frontal, and possibly the elongation of the shield, are characters indicating the megalichthyid affinities of

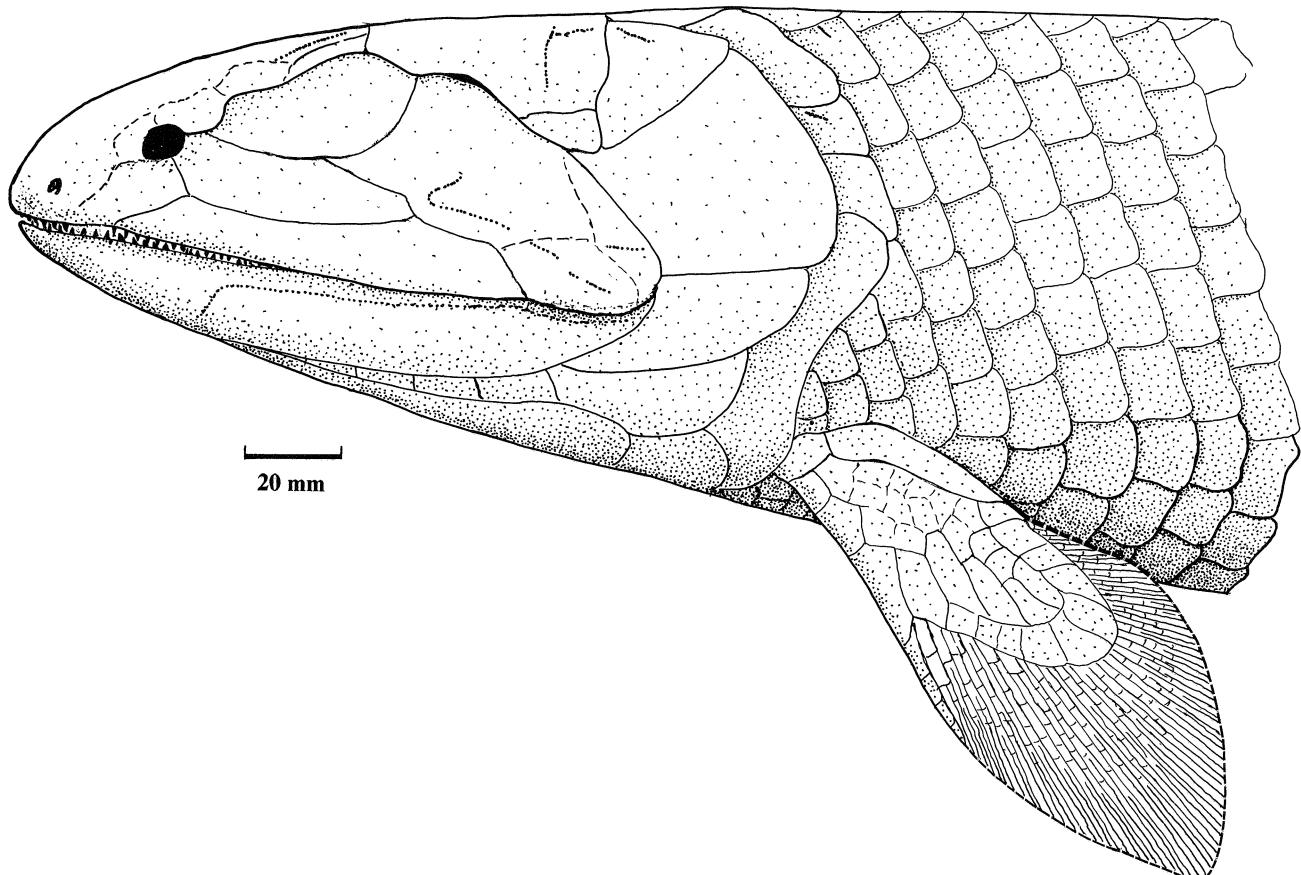


Fig.14. *Koharalepis jarviki* n.gen., n.sp. Restoration of fish in left lateral view, based on the holotype.

this form. However, it differs strongly from *Megalichthys* in the narrow snout, and the presence of large supraorbitals, but these may be primitive features for the group. The form of the vomers and premaxillae is unknown, and must be assumed for the present to be consistent with the above familial definition.

***Mahalalepis resima* n.sp.**

Fig.15

'osteolepid jaw fragments' Young, 1988: 12.
'osteolepiforms gen. et sp. nov.' (pars) Young, 1991: 543.

Etymology. After *resimus* (Latin), turned up, with reference to the shape of the snout in lateral view.

Holotype. CPC 27839, an incomplete fronto-ethmoidal shield.

Locality. Mount Crean, Lashly Range (MC1, locality 8, Fig.2).

Horizon. Collecting site MC1 is referred to unit 3 of section L2 of Askin *et al.* (1971), although precise stratigraphic position is uncertain (Young, 1988). Associated thelodont scales indicate a low level in the

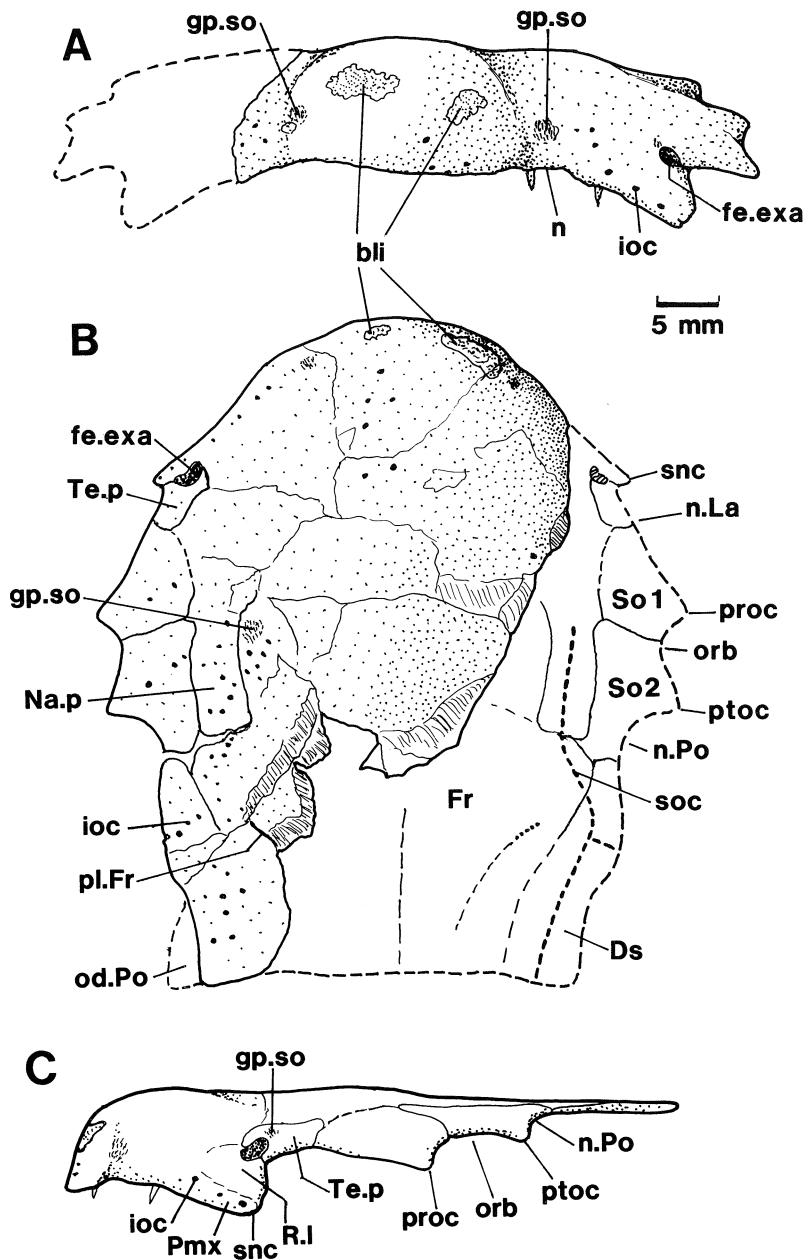


Fig.15. *Mahalalepis resima* n.gen., n.sp. Holotype from Mount Crean (CPC 27839), an incomplete fronto-ethmoidal shield partly restored in anterior (A), dorsal (B), and left lateral (C) views.

Aztec Siltstone. The species *Bothriolepis kohni* Young comes from the same unit.

Diagnosis. As for genus (only species).

Description. This specimen is the left side of a cosmine-covered fronto-ethmoidal shield with a preserved length of 60 mm, but too incomplete for proportions to be determined. The pineal foramen is not preserved, and the outline restoration (Fig.15B) is based on midline braincase structure preserved on the broken posterior margin. The left lateral and anterior margins are entire, with postorbital, orbital and lachrymal notches well displayed (n.Po, orb, n.La, Fig.15).

The preserved part of the cosmine surface shows evidence of bone sutures and the course of sensory grooves. The left posterior corner comprises the dermosphenotic (Ds, Fig.15B), with the normal wide overlap for the postorbital seen in section on its broken posterior end (od.Po). The sensory pores run laterally off the bone as the infraorbital canal (ioc), and mesially across the anterolateral margin of the frontal (Fr). At its anterior end near the postorbital notch (n.Po) the bones have come slightly apart to reveal the sutures, traceable forward around the orbit. Posterior and anterior supraorbitals (So2, So1) form the post- and preorbital corners respectively. Compared to the dermosphenotic the supraorbitals have only a few scattered sensory pores. The suture between the frontal (Fr) and the posterior element of the nasal series (Na.p) shows a notch through the broken cosmine surface for the passage of the sensory canal. The posterior nasal is an elongate bone, and its mesial suture may have been with a large median postrostral, although the cosmine cover obscures other margins of this element, if present. Alternatively, the frontal may have extended much further forward mesial to the nasal series than in other osteolepiforms. The presence of a group of pores for a cutaneous sensory organ (gp.so, Fig.15B), which may correspond to that on the osteolepid frontal as described by Jarvik (1948: fig.36), supports the second interpretation. The nasal forms a right-angled notch into the margin of the frontal, behind which the distribution of sensory pores indicates the normal osteolepiform course for the supraorbital sensory canal (soc). The frontal has an unusually short contact with the posterior supraorbital compared to other genera, which together with the elongate posterior nasal gives a distinctive skull roof pattern.

The left nasal opening is well preserved (fe.exa), but surrounding bones are not absolutely clear because of cracking. Following Jarvik (1966: fig.14) the subnarial corner (snc) must be on the premaxilla, where pores of the infraorbital sensory canal are clear (Pmx, ioc, Fig.15C). The bone in the anterior part of the lachrymal notch (Te.p) has an anteroventral process enclosing the nasal opening laterally, and apparently extends around the posterodorsal half of the opening, as does the posterior tectal of *Megalichthys*. A group of pores on this bone for a cutaneous sensory organ (gp.so, Fig.15C) has the same position as that illustrated for *Gyroptychius*

by Jarvik (1966). The bone forming the anterior margin of the nasal opening is presumably a lateral rostral (R.l), and like *Megalichthys* there is no sign of a suture with the premaxilla. The posterior tectal is a slightly more elongate bone than in *Megalichthys*, and differs in having a longer process dorsal to the nar. In *Ectosteorhachis* on the other hand the ventral (infranasal) process of this bone is longer than the dorsal.

The snout has a rather blunt profile in lateral view (Fig.15C). In anterior view two slight notches are evident in the mouth margin (n, Fig.15A). There are scattered pores for the infraorbital sensory canal, and above these, pore clusters for paired cutaneous sensory organs (gp.so), and blisters of resorbed cosmine (bli) as described by Jarvik (1948).

Family incertae sedis

Platyethmoidia n.gen.

Etymology. From *platys* (Gk), broad, with respect to the broad ethmoidal region of the skull.

Diagnosis. A cosmine-covered osteolepiform with a short broad fronto-ethmoidal shield (breadth/length index 125), a pronounced preorbital and slight postorbital corner, and external nares partly visible from above. Lower jaw 4.5 times as long as deep. Clavicle with a broad ascending process and anterior margin.

Remarks. *Platyethmoidia* n.gen. is distinguished from *Koharalepis*, and all other osteolepids, by its broader fronto-ethmoidal shield, larger orbits, less pronounced postorbital corner, and shape of the lower jaw. The slit-like nares and closed pineal foramen are possible resemblances to megalichthyids, but the nares have a different orientation, and there is no evidence of a posterior tectal, so these characters further distinguish the new genus from *Mahalalepis* described above. *Gyroptychius?* *australis* Young & Gorter (1981) also had a short broad fronto-ethmoidal shield, and similarly shaped lower jaw, but *Platyethmoidia* differs in the greater breadth of the fronto-ethmoidal shield, the less pronounced orbital notch, and nares partly visible from above, with the snout not folded under toward the mouth margin. *Gyroptychius?* *australis* has a similar postorbital notch to *Koharalepis* as described above, and it is possible that both this form and *Platyethmoidia* are canowindrids as defined above, but additional material is needed to substantiate this.

Platyethmoidia antarctica n.sp.

Figs 11B, 16, 17

'osteolepiforms gen. et sp. nov.' (pars) Young, 1991: 543.

Etymology. After *antarcticus* (L), southern.

Holotype. AMF 54405, an incomplete fronto-ethmoidal shield.

Other material. Provisionally included is AF 266, comprising a right lower jaw, incomplete clavicle, and associated scales.

Localities. The type locality is Mount Ritchie (locality 24, Fig.2), southern Warren Range (AMF 54405). The other specimen (AF 266) is from Mount Crean, Lashly Range (locality 8, Fig.2).

Horizon. The holotype comes from unit 54, section A4 of Askin *et al.* (1971), 5-30 m below the top of the Aztec Siltstone. AF 266 is recorded from units 5-8, section L2 of Askin *et al.* (1971), and thus equivalent either to MC2 or MC3 of Young (1988: 12). However the sample contains thelodont scales, which are not known from MC2, while the lithology is much darker than that typical of MC3. The presence of thelodonts indicates either the *askinae* or *kohni* zones of Young (1988), probably in the lower 80 m of Aztec Siltstone.

Diagnosis. As for genus (only species).

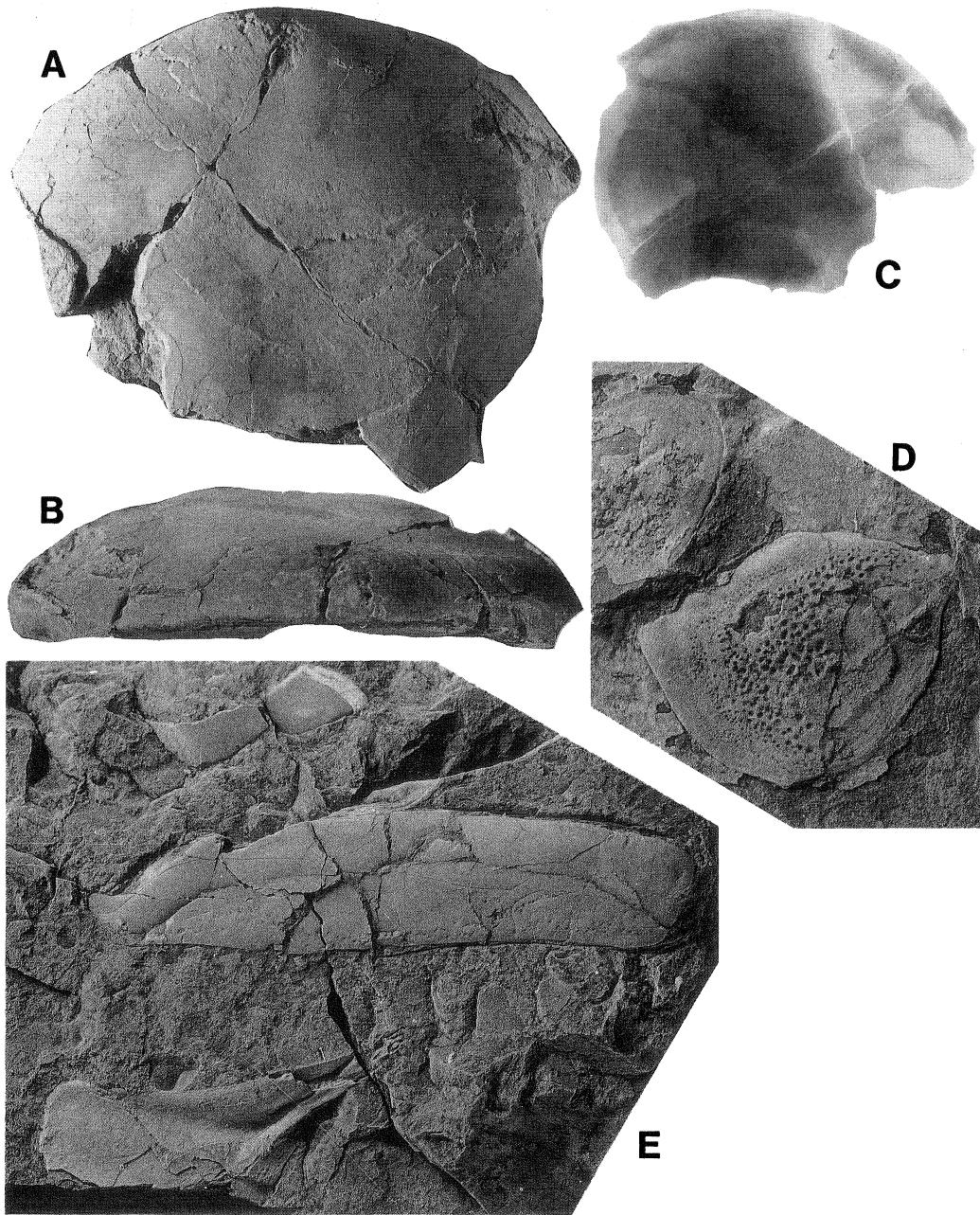


Fig.16. *Platylethmoidia antarctica* n.gen., n.sp. A-C, holotype from Mount Ritchie (AMF 54405), a fronto-ethmoidal shield in dorsal (A) and anterior (B) views; C, x-radiograph in ventral view; D, scales, and E, right lower jaw, clavicle and associated scales of AF 266 (from Mount Crean). (A,C x1.5; B x1; D x4; E x2; all specimens except C whitened with ammonium chloride.)

Remarks. The holotype comes from a similar stratigraphic level to the lower jaw described below as *Vorobjevaia*, but that form evidently had a much narrower snout. The second specimen is provisionally included on the following tentative evidence: the shape of its lower jaw resembles that of *Gyroptychius? australis* Young & Gorter (1981), which also had a short broad fronto-ethmoidal shield as in the holotype of *P. antarctica* n.sp., and may be closely related. (As noted by Long, 1987a, *Gyroptychius? australis* needs redescription, and probably represents a new genus.) Since there is no overlapping morphology, the provisional association of these two specimens in one taxon is subject to confirmation when further material is discovered.

Description. The holotype is an incomplete fronto-ethmoidal shield preserved as bone (Fig.16A-C), which is noteworthy for its flat development. It was apparently very short and broad in proportion, but the reconstruction (Fig.17) needs confirmation with other material as the posterior edge of the specimen is broken. Nevertheless this seems to approximate the natural margin, judging by the right posterolateral corner of the shield, which is preserved as an impression of the inner surface.

The right side of the specimen includes the frontal,

as indicated by the frontal pitline (pl.Fr, Fig.17A) and a group of sensory pores (gp.so) as described in a similar position in Scottish osteolepids (Jarvik, 1948). Together with the nasal openings this pitline gives a reliable indication of the midline, by which the left posterolateral corner of the specimen has been reconstructed. The left nasal opening has been exposed by grinding the bone surface, and the right is complete. They are slightly visible in dorsal view (fe.exa). In anterior view the biting margin of the mouth is slightly concave (Fig.16C), with the nasal openings as teardrop-shaped slits close to the margin, which are angled upward toward the midline, rather than rostrocaudally as in *Megalichthys*.

Pores for sensory canals are not well developed, but those for the supraorbital canal are clear on both sides (soc, Fig.17A). There is no sign of the pineal foramen, which may have been just behind the preserved portion, or closed over (in *Gyroptychius? australis* it is positioned just in front of the frontal pitline), nor of any bone sutures except for one on the left side running anteromesially from the region of the orbital notch, which may be the anterior suture of the anterior and posterior supraorbital bones.

In lateral view (Fig.17B) the subnarial (snc) and preorbital corners (proc) are well developed, the latter very broad in dorsal view compared to other taxa. The

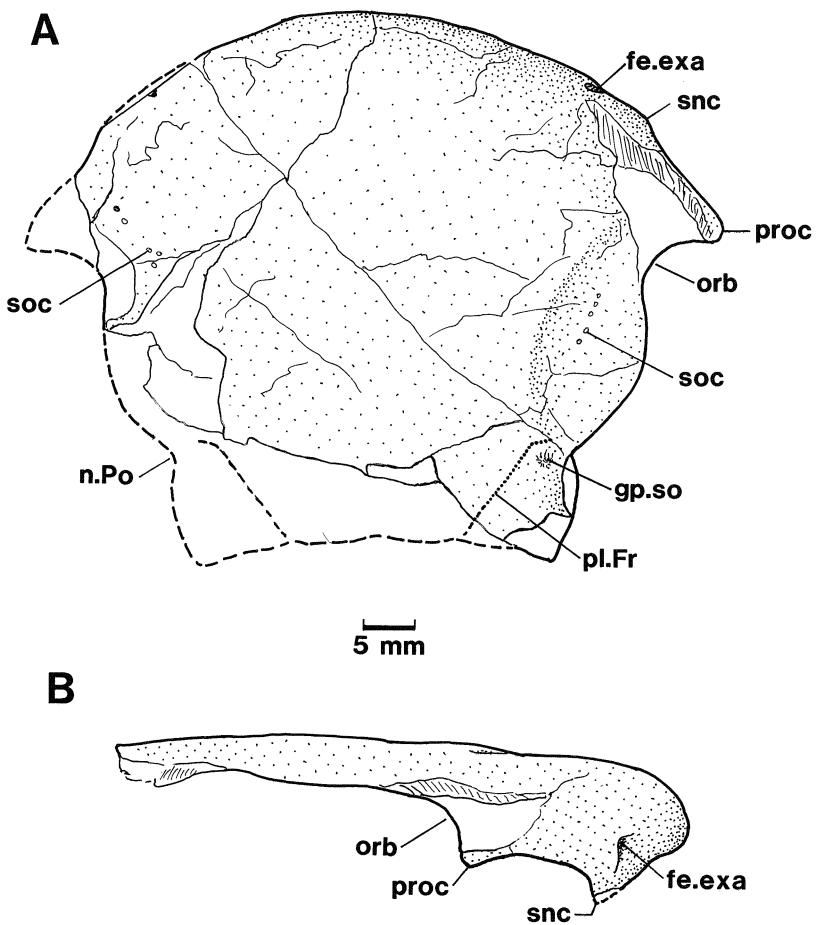


Fig.17. *Platyethmoidia antarctica* n.gen., n.sp. Fronto-ethmoidal shield in dorsal (A) and right lateral (B) views. After the holotype (AMF 54405).

bone is missing from the orbit on the right side, but the shape of the orbital notch (orb) is clearly preserved as an impression.

Compared to *Koharalepis* (Fig.10) the shield is much broader across the preorbital corners, the orbits are larger, the postorbital corner is less pronounced, and the shield is much shorter and broader in overall proportion.

The second specimen tentatively referred to the species (AF 266) includes a right lower jaw, incomplete clavicle, and associated scales (Fig.16D,E). The jaw is 54 mm long and deepest posteriorly (12 mm). It differs from that of *Koharalepis* in having a less concave ventral border. Its posterior region shows a smooth overlap flange for the cheek plates, and a prominent posterior process ventral to the point of jaw articulation. A short suture leading from the overlap area to the horizontal pitline defines the posterior end of the dentary (De, Fig.11B). This jaw is distinguished from that of many osteolepids by the ventral position of the articular region relative to the dorsal margin of the jaw. This is also a feature of *Gyroptychius? australis* described by Young & Gorter (1981), which has a jaw of similar proportions. In most osteolepidids the pars articularis is at about the same level as the biting margin of the jaw (*Osteolepis*, *Thursius*, *Gyroptychius*; Jarvik, 1948: fig.23A), but a deeper posterior notch has been described in some osteolepidid jaws from the Upper Devonian Bergisch-Gladbach fauna (Jessen, 1966: pls 1, 8-10), and in the genera *Shirolepis* and *Greiserolepis* by Vorobjeva (1977). Noteworthy on AF 266 is the long horizontal infradentary pitline (plh.Id), which runs from below the articular region anteriorly for almost three quarters the length of the jaw, comparable to that on some osteolepidids (*Osteolepis*, *Gyroptychius*, Jarvik, 1948). The vertical infradentary pitline (plv.Id) is as developed in other osteolepids. A row of pores (gp.so) may correspond to those for a cutaneous sensory organ described by Jarvik (1948), and there is a small cluster of laterosensory pores close to the anterodorsal margin of the jaw, and another on the anterior margin. The course of the mandibular sensory canal is clearly shown by numerous large pores close to the ventral margin of the jaw (mc), and a dorsal row represents the oral canal (orc). Just above this canal is another pitline in three short sections (pl), not previously recorded as a separate line in osteolepids. A few marginal teeth are exposed on the biting margin but otherwise the dentition and the mesial surface of the jaw are not visible on the specimen.

The associated right clavicle as far as preserved shows normal development. Preserved length is 33 mm. The ascending process appears broader and more laterally directed than in *Eusthenopteron* (Jarvik, 1944b: fig. 4E), perhaps reflecting a more depressed body shape. The mesial margin of the ventral lamina is broken off, but the preserved lateral part of the anterior margin is less pointed than in some previously figured clavicles (e.g., Jarvik, 1944b, 1948: fig.25E; Young & Gorter, 1981: fig.28C).

The two types of scales on the specimen are closely associated, and it is assumed that they come from the same fish. As well as normal cosmoid scales (Fig.16E), two scales with an ornament of irregular ridges have evidently lost their cosmine by resorption (Fig.16D). This condition is well known in osteolepids (e.g., Jarvik, 1948: fig.6).

Vorobjevaia n.gen.

Etymology. After Dr Emilia Vorobjeva, Moscow, in recognition of her major contribution to the study of rhipidistian fishes.

Diagnosis. An osteolepiform in which the lower jaw has a posterolateral division of the parasymphysial dental plate reaching the coronoid lamina, a sigmoid dentary tusk twice as long as the coronoid tusks, a rounded dorsal process in front of each coronoid tusk, and the parasymphysial dental plate elevated as a high rounded tuberculate process. The lower jaw is about 4.5 times as long as deep, and deepest posteriorly.

Remarks. The new genus is distinguished from all other rhipidistians in which the lower jaw is known by the strong dorsal processes on the coronoid lamina and supporting the parasymphysial dental plate. The parasymphysial dental plate includes a narrow posterolateral portion reaching back to the coronoid lamina, a feature used by Jarvik (1972: fig.50) to distinguish osteolepids from rhizodontids (including eusthenopterids as used here). On this evidence it is assumed for the present that *Vorobjevaia* retained cosmine on the dermal bones, although this needs confirmation with new material. Other cosmoid osteolepids with a dentary tusk include *Megalichthys* and *Thysanolepis* (Jarvik, 1966; Vorobjeva, 1977), and the large size of the tusk and recurved teeth of the latter might indicate a close relationship to *Vorobjevaia*. *Platyethmoidia antarctica* n.gen. n.sp., which comes from an equivalent high level in the Aztec Siltstone, has a broad rounded snout which is quite different from the long narrow snout suggested by the shape of the jaw in *Vorobjevaia*. The lower jaw provisionally referred above to *P. antarctica* is also very different in preserved morphology.

Vorobjevaia dolonodon n.sp.

Figs 18A,B, 19A

'crossopterygian jaw' Young, 1988: 13.

'osteolepiforms gen. et sp. nov.' (pars) Young, 1991: 543.

Etymology. After the Greek *dolon*, dagger, and *odon*, tooth.

Holotype. AMF 54328, a left lower jaw in internal

view, preserved as an impression in sandstone.

Locality. Mount Crean, Lashly Range (locality 8, Fig.2).

Horizon. MC7, unit 28 of section L2 of Askin *et al.* (1971), associated with *Bothriolepis barretti* Young.

Diagnosis. As for genus (only species).

Description. This left lower jaw is preserved as an impression of its inner surface. It is about 90 mm long and 20 mm deep posteriorly, and shows some unusual features. There is a very long slightly sigmoid dentary tusk (Fig.18A), which in its large size is reminiscent of some rhizodontids (e.g., Andrews, 1985), or the osteolepid *Thysanolepis*, which also has sigmoid teeth (Vorobjeva, 1977: fig.36). Behind are three much shorter coronoid tusks, each with a distinct replacement socket. The tusks are round in section. Noteworthy is the bulbous parasympathetic dental plate (Ps.dp), which sits on a high prominence mesial to the dentary tusk. The surface of the dental plate is poorly preserved, but was

apparently covered with small rounded tubercles. It is convex upward, and in dorsal view has a triangular shape with a straight lateral margin (Fig.18B). A narrow ridge extends posterolaterally to the coronoid lamina adjacent to the first coronoid tusk (plPs). Its surface is also poorly preserved, but a few indistinct tubercles can be discerned. This corresponds to the posterolateral division of the parasympathetic dental plate figured by Jessen (1966), and used by Jarvik (1972: fig.50) to distinguish the parasympathetic dental plate of osteolepids from the reduced plate of eusthenopterids.

Behind the first coronoid tusk (t.Co1) the thickened coronoid lamina decreases in height posteriorly, but is elevated as another bulbous prominence in front of the socket for the second tusk (pr.Co), and a similar structure is developed in front of the third tusk. Such structures have not previously been reported in rhipidistians.

The lateral tooth bearing lamina of the dentary is poorly preserved lateral to the coronoid, and continues posteriorly as a faint impression near the anterior end of the adductor fossa, also poorly preserved. On the mesial surface the prearticular dental plate is well preserved, with a covering of fine tubercles, coarser dorsally, and interspersed in the middle part of the plate

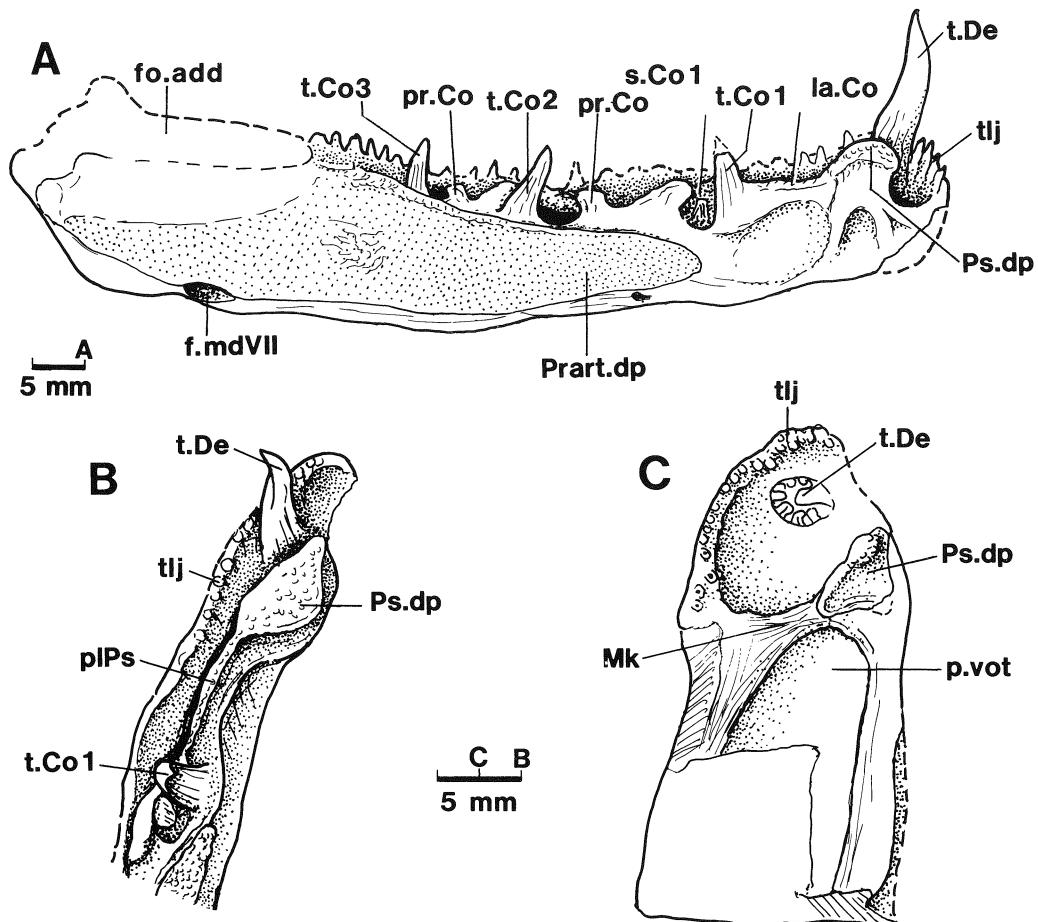


Fig.18. A, B. *Vorobjevaia dolonodon* n.gen., n.sp. Holotype (AMF 54328), based on a latex cast from the impression of the left lower jaw in mesial (A) and dorsal views (B, anterior part of jaw only); C, eusthenopterid gen. et sp. indet. Anterior part of left lower jaw in dorsal view (AMF 54332).

with a fine vermicular ornament. Sutures between the coronoids and infradentaries are unclear, but the infradentaries did not have the broad ventral expansion of *Notorhizodon* n.gen. (see below). Posteriorly a large opening probably carried the mandibular ramus of the facial nerve (f.mdVII). The jaw is deepest posteriorly, and the mandibular joint was evidently well developed, but its structure is unclear. There is no indication of a retroarticular process.

osteolepid gen. et sp. indet.

Remarks. Apart from the specimens already described there are many isolated scales and bones which can be assumed to be osteolepids by their cosmine, but are too incomplete, poorly preserved, or intractable to be referred with any reliability to the taxa described above. Included here is the original material described by Woodward (1921) and White (1968). Representative examples of this material, and some previously described specimens, are dealt with below in order of locality.

GONDOLA RIDGE, MOUNT SUESS (locality 2)

Holoptychius antarcticus Woodward, 1921: 58.
'osteolepid' Woodward, 1921: 59.
Holoptychius antarcticus, Osteolepidae indet. Gross, 1950: 72.
Gyroptychius ? antarcticus (pars) White, 1968.

Material. BMP 12573, 574, 576, 579, 581, 583, 588, 40570, 49169, 170, 171, 176, GS 7397/3,6

Description. Woodward (1921: 59) noted the large size of the osteolepid scales in the Granite Harbour material compared to the Middle Devonian osteolepids from Europe ('at least equal in size to those of the Lower Carboniferous *Megalichthys*'). White's lectotype (BMP 12573) shows the shiny cosmine surface and extensive overlaps, just as observed on the scales of *Koharalepis* described above, and many examples from other localities (see below).

BMP 12588 is a specimen about 35 mm high with a partly abraded shiny cosmine surface, and a convex margin presumed to be posterior. It was identified by Woodward (1921) as a possible left suboperculum, but we consider it too incomplete for definite determination.

BMP 49169 is listed by White (1968: 6) to include scales and part of a left lower jaw. The latter is a concave impression about 30 mm long and 10 mm high, which may be a jaw fragment but shows no reliable distinguishing features.

The GS specimens listed above were not located in the collections of the NZGS.

Remarks. Rhipidistian crossopterygians of two types were identified by Woodward (1921) from the original locality at Mount Suess. Some scales and a possible

clavicle were referred to a new species of the porolepiform *Holoptychius*, and other scales and an incomplete cheek plate identified as an osteolepid. Later, White (1968) found with further preparation that Woodward's supposed '*Holoptychius*' scales had a smooth cosmine surface, and he correctly identified Woodward's specimen 'with delicate reticulate ornament suggesting the clavicle of *Holoptychius*' as a pectoral fin element of the antiarch *Bothriolepis*. Except for a possible 'rhizodont' tooth from the Boomerang Range, White referred all the rhipidistian remains to the osteolepid, which he renamed *Gyroptychius?* *antarcticus* (Woodward), the specimen chosen as lectotype being a scale preserved as an impression (BMP 12573). With the new taxa described above it is now clear that such remains are indeterminable, and since the material was collected from moraine and may have come from several localities, it is unlikely that a single taxon is represented. We propose therefore that Woodward's specific name be regarded as a *nomen nudum*. Some comments on certain described specimens are given below.

MOUNT CREAN (locality 8, MC1)

Fig.19D

'osteolepid scales and jaw fragments' Young, 1988: 12.

Material. AMF 55911, CPC 27840.

Horizon. Unit 3 of section L2 of Askin *et al.* (1971), which may be equivalent to MS 6, the lower horizon of Gunn & Warren (1962; see discussion in Young, 1988).

Description. In addition to the holotype of *Mahalalepis resima* n.gen., n.sp., the material from collecting site MC1 of Young (1988: fig.4) includes several other samples with indeterminate osteolepid scales and bones, of which two are mentioned here. AMF 55911 has many scales visible in section, with a larger bone which may be part of a cheek plate or lower jaw. The cosmine surface is richly supplied with laterosensory pores. CPC 27840 (Fig.19D) is a cosmoid scale 18 mm high by 12 mm across, and well preserved in external view. The green siltstone matrix contains thelodont scales. This is one of the largest scales of its type observed in the lower beds of the Aztec Siltstone. These specimens could belong to *Mahalalepis*, but with no specific evidence supporting this they are left for the present in open nomenclature.

MOUNT CREAN (locality 8, MC2)

Gyroptychius ? antarcticus (A.S.W.) White, 1968: 7, 8.

Material. GS 7398/4,5,8,9,17,19,27.

Horizon. Unit 8 of section L2 of Askin *et al.* (1971), which may be equivalent to MS 5, the upper horizon of Gunn &

Warren (1962; see discussion in Young, 1988).

Description. The Gunn & Warren collection may have come from the equivalent horizon to that of *Koharalepis*, but the specimens provide no evidence of this. GS7398/17 includes an unprepared scale or bone preserved in visceral view, which appears almost symmetrical, with a short anterior median ridge on the inner surface. It may be from the median dorsal or median ventral scale row, or a small bone from the head (e.g., median gular). The other specimens listed by White

(1968) were not located.

MOUNT CREAN (locality 8, MC3)

Fig.19C

'osteolepids' Young, 1988: 12.

Material. CPC 27841, 842.

Horizon. This collecting site at locality 8 (MC3, Young,

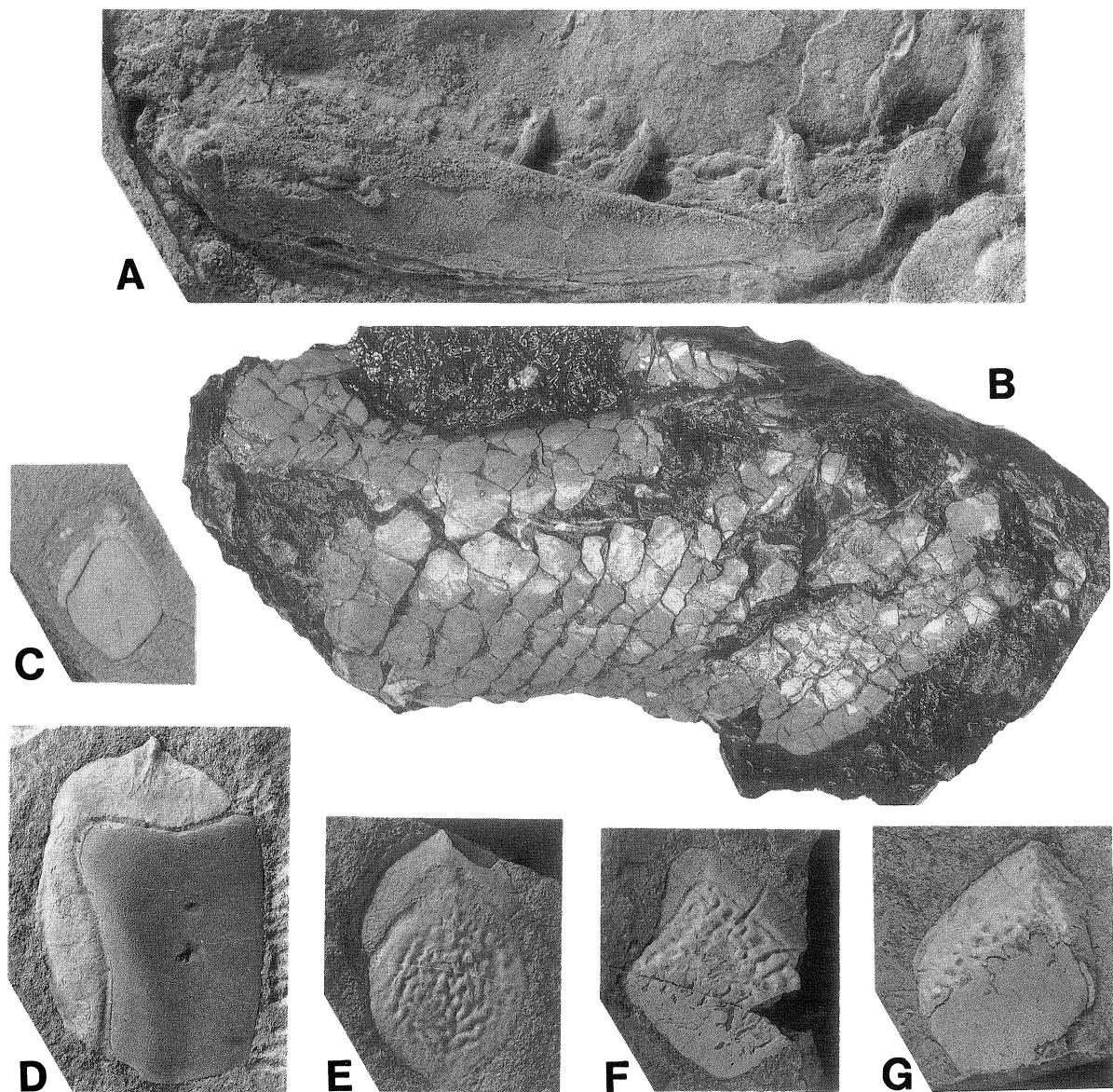


Fig.19. A. *Vorobjevaia dolonodon* n.gen., n.sp. Holotype from Mount Crean, latex cast of the impression of the left lower jaw in mesial view (specimen whitened with ammonium chloride); B, portion of the body squamation of an undetermined osteolepid from Boomerang Range, locality 19 (AMF 54459), photographed under alcohol. C-G, isolated indeterminate osteolepid scales from various localities, all whitened with ammonium chloride; C, CPC 27841; D, CPC 27840 (both locality 8, Mount Crean); E, CPC 27847 (locality 12, Portal Mountain); F, AMF 54385; G, AMF 54384 (both from locality 24, Mount Ritchie). (A,C,F,G x1.5; B x0.8; D,E x3)

1988: fig.4) is the type locality for *Bothriolepis askinae*, assigned to unit 5 of section L2 of Askin *et al.* (1971), although stratigraphic position is uncertain (see Young, 1988: 12). The presence of thelodont scales suggests a lower level than the type locality for *Koharalepis*. CPC 27842 comes from scree between MC3 and MC4, but lithology suggests origin near this level.

Description. Of various isolated scales and plates CPC 27841 is a well preserved example, some 17 mm long with a short sensory groove (Fig.19C). The cosmine adjacent to the overlap areas (mainly enclosed in the matrix) is separated off by a deep line reminiscent of the Westoll-lines of diploans. CPC 27842 is the posterior portion of a right osteolepid jaw about 60 mm long and 30 mm high. The mandibular joint is preserved partly enclosed in matrix, and the broken anterior section shows the prearticular enclosing the meckelian space. The external cosmoid surface is badly fractured and abraded, but where preserved shows a marked degree of blister-like development, suggesting several generations of cosmine resorption.

LASHLY MOUNTAINS, SOUTH-EAST OF MOUNT CREAN (locality 9)

Material. CPC 27843, 844.

Horizon. Units 8 or 10 (CPC 27843) and 34 (CPC 27844) of section L1 of Askin *et al.* (1971).

Description. CPC 27843 is a curved portion of cosmoid bone 35 by 70 mm in size, and thus from a large fish. It shows several areas of sensory pores and a short segment which appears to be suture, but cannot be followed due to bad fracturing of the cosmine surface. It may be the posterior part of the left cheek unit of a large osteolepid, but provides insufficient information for reliable identification.

CPC 27844 comprises four associated samples containing osteolepid remains, the largest a piece of siltstone about 240 mm across with many large osteolepid scales, some showing imbrication, and presumably all from one large fish. The scales are up to 30 mm across. Many show blister-like variations in the cosmine, and most exposed in external view have a marginal resorbed zone showing the underlying coarsely ornamented surface. This same feature occurs in osteolepid scales from the top of the sequence at Mount Ritchie (see below).

MOUNT FEATHER (locality 10)

Gyroptychius ? antarcticus (Woodward) pars White, 1968: 22, 23.

Material. GS 7400/2+5+13, and counterpart (BMP 49171); GS7400/3,6-12.

Horizon. Possibly some 90 m above the base of the Aztec Siltstone, but precise stratigraphic position uncertain. The greenish siltstone matrix is similar to that from locality MC2 at Mount Crean.

Description. BMP 49171 was figured by White (1968: fig.16) as a suboperculum, but if correct it is very different from this bone in *Koharalepis*. Two of its margins are broken, and the anterior margin is slightly inflected. The plate is flat longitudinally, with a slight dorsoventral curvature, but it seems too flat to be a subopercular, and is not an extrascapular because there is no sign of a sensory canal, which should be visible on the abraded external surface. We consider this specimen too incomplete for reliable determination.

PORTAL MOUNTAIN (locality 11)

'rare osteolepids' Young, 1988: 13.

Material. CPC 27845.

Horizon. Unit 26, section 10 of Barrett & Webb (1973).

Description. This specimen comprises numerous scales and plates closely associated in a friable green mudstone, presumably all from one individual. However preparation has been hampered by the friable nature of the sample, which for the present remains indeterminate.

PORTAL MOUNTAIN (locality 12)

Fig.19E

'crossopterygians' Young, 1988: 13.

Material. CPC 27846 - 857.

Horizon. Unit 4, section P1 of Askin *et al.* (1971).

Description. As noted by Young (1988) this lowest horizon in the P1 section contains a diverse fauna including arthrodires, acanthodians, palaeoniscoids, elasmobranchs and thelodont scales. All observed crossopterygian remains are osteolepids. CPC 27850 and 27852 are exposed in internal view to show the scale ridge, just as illustrated for *Gyroptychius* by Jarvik (1948: fig.28C). However, the ridge terminates in about the middle of the height of the scale due to the more extensive ventral overlap. CPC 27847 (Fig.19E) has an external ornament of low irregular ridges reminiscent of *Glyptopomus* (Jarvik, 1950b), and resembles the scales from which cosmine has been resorbed which Jarvik (1948: fig.6) illustrated from the Middle Devonian osteolepid fauna of Scotland.

ALLIGATOR PEAK (locality 17)

'large scales and teeth of a crossopterygian [with] a coarse ornamentation' (pars) Ritchie, 1972: 352.

Material. AMF 55446.

Horizon. Unit 32 of section A1 of Askin *et al.* (1971), about 8 m below the top of the formation, corresponding to MS236, section 6 of Barrett & Webb (1973).

Description. This specimen includes a large tooth and associated rhomboid scales from which most of the cosmine has been resorbed to reveal the underlying coarsely ornamented bone. This is clearly an osteolepiform scale, and not to be confused with associated coarsely ornamented crossopterygian remains which belong to a rhizodontid (see below).

BOOMERANG RANGE, EAST OF ALLIGATOR PEAK
(locality 19)

Figs 19B, 20

'articulated crossopterygian fish' Ritchie, 1972: 352.

'articulated but incomplete osteolepid' Turner & Young, 1992: 98.

Material. AMF 54381-383, 54452, 454-460, 463.

Horizon. MS237, in the basal 4 m of section 5 of Barrett & Webb (1973).

Description. AMF 54382 is interpreted in Figure 20 as a partly articulated caudal region preserved in left lateral view (counterpart AMF 54383) showing the second dorsal fin (sdf), posterior part of the median

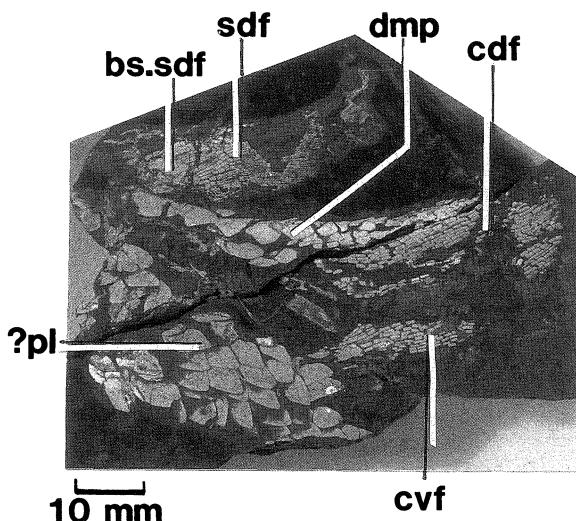


Fig.20. Incomplete tail of an undetermined osteolepid from the Boomerang Range; left lateral view (AMF 54383). Photographed under alcohol.

dorsal scale row (dmp), and the dorsal lobe of the caudal fin. All fins are incomplete, and the scales are somewhat displaced with respect to each other. Thus it is not clear how accurately patches of squamation reflect body shape, and an alternative interpretation is that the two preserved fins are first and second dorsals rather than second dorsal and caudal. If so then the second dorsal fin would have been about twice as large as the first, with both much closer together than in other osteolepids (e.g., Jarvik, 1948: fig.27). A relatively large but badly fragmented plate may be the basal scute of the second dorsal fin (bs.sdf). The dorsal part of the caudal fin lobe (cdf) is largely obscured by matrix. The ventral portion (cvf) is represented by patches of elongate cosmine-covered dermal fin rays similar to those on the pectoral fin of *Koharalepis*. The narrow section of body squamation beneath the fin might indicate similar shape to the caudal fin of *Gyroptychius* (Jarvik, 1948: fig.27F) or *Latvius niger* (Jessen, 1973: fig.2A). In front of the caudal fin a rostrocaudally elongated scale on the flank of the body with an anterior overlap area exposed carries a short horizontal pitline (pl), which could represent the accessory or ventrolateral body pitline of Jarvik (1948).

AMF 54381 is a flattened fragment 20 by 28 mm in size showing both sides of the body squamation. Scales are about 10 mm across, and three on one side show pitlines. AMF 54459 is a larger piece (preserved length 135 mm) showing about 14 scale rows, arranged in the normal dorsolateral and ventrolateral oblique rows (Fig.19B). The last preserved of the presumed dorsolateral rows contains eight scales. Anteriorly on the presumed ventral surface is a large basal scute, most likely for the anal or pelvic fin. However, no fin rays are preserved so position on the body is uncertain.

AMF 54452 comprises fragments of squamation which may have come from one of the previous specimens, AMF 54463 is a ridge scale, and the remaining specimens are isolated scales similar in size and morphology to those on the articulated specimens.

ALLIGATOR PEAK, SOUTH-EASTERN SPUR (locality 21)

'crossopterygian scales (up to 25 mm across) and isolated teeth' Ritchie, 1972: 352.

Material. AMF 54440, 448.

Horizon. Recorded as MS241, the 111 m level in section 3 of Barrett & Webb (1973), although Ritchie (1972) noted that material from two fossiliferous horizons (81 m and 111 m above base) was mixed.

Description. The small collection from this locality includes AMF 54440, a broken tusk from a large crossopterygian, which provisionally may be regarded as an osteolepид on the basis of an associated cosmoid scale (AMF 54448), preserved as an impression of its external surface. Both specimens come from a fish of comparable size to the holotype of *Koharalepis jarviki*.

The absence of rhizodontid scales is consistent biostratigraphically with the identification of *Bothriolepis portalensis* from this locality by Young (1988: fig.41).

SOUTHERN WARREN RANGE, MOUNT RITCHIE
(locality 24)

Fig.19F,G

Material. AMF 54384, 385, 395-397, 55977, 994, 78581-584.

Horizon. Units 54 and/or 62, section A4 of Askin *et al.* (1971), in the upper 30 m of the Aztec Siltstone.

Description. Various cosmoid bones and scales, of which those just listed are well preserved examples, demonstrate the presence of osteolepids from unit 54, associated with probable eusthenopterids (see below). This is the type locality for four species of *Bothriolepis* (*B. alexi*, *B. karawaka*, *B. mawsoni*, and *B. vuwae*; see Young, 1988). Two examples of scales are shown in Figure 19F,G. They are about 24 mm across, with the coarse basal ornament exposed in a peripheral zone, and a central area covered with cosmine. AMF 78582-84 are isolated scales separated from the matrix, showing a similar peripheral zone. AMF 78581 is a large cosmoid bone 78 by 40 mm in maximum dimension, which again shows irregular peripheral zones up to 12 mm across which lack cosmine. This no doubt comes from some part of the skull or cheek of a large osteolepiform.

eusthenopterid gen. et sp. indet.

Remarks. Various isolated or incomplete scales and bone fragments in the collection which cannot be reliably referred to described taxa, but apparently belong to eusthenopterids, are briefly described here according to locality and horizon.

GONDOLA RIDGE, MOUNT SUESS (locality 2)

Material. BMP 40570.

Horizon. Not known.

Description. BMP 40570 from the original 1911 collection shows a round scale about 8 mm across with fine radiating striations. There seems to be a poorly preserved boss on the inner surface, and it may therefore be a eusthenopterid (or small rhizodontid) scale.

MOUNT CREAN (locality 8, MC2)

Figs 18C, 43A

Material. AMF 54332.

Horizon. Unit 8 of section L2 of Askin *et al.* (1971), which may be equivalent to MS 5, the upper horizon of Gunn & Warren (1962), but actual level within the Aztec Siltstone is uncertain (see discussion in Young, 1988).

Description. This specimen comes from the same collecting site as the holotype of *Koharalepis jarviki*. It is the anterior end of a left jaw ramus preserved as bone in a hard matrix. It belonged to a large fish, intermediate in size between AMF 54327 and CPC 26404 referred below to *Notorhizodon*. The marginal teeth (tlj, Fig.18C) and tusk of the dentary (t.De) are broken off, the latter showing the polyplacodont structure of Schultz (1970). The parasymphyseal dental plate is preserved in position (Ps.dp). It is triangular in dorsal view, with its anterior angle elevated as a tubercular prominence, and a short unornamented posterolateral process. The pit for the vomerine tusk is filled with matrix, but its position is clearly delimited laterally by a strong ridge of bone running obliquely forward to support the parasymphyseal dental plate (Mk, Fig.18C). Structures farther back are either embedded in matrix or broken away, but the anterior end of the dentary shows the external ornamented surface, with tubercles and ridges of eusthenopterid type.

Remarks. This specimen differs from *Notorhizodon* in the presence of a strong anterolaterally directed ridge which supports the parasymphyseal dental plate, which results in a smaller pit for the vomerine tusk in a more mesial position than the large rounded pit of *Notorhizodon* (Fig.33). For the present it is provisionally referred to the Eusthenopteridae, but differs from *Eusthenopteron* in possessing a dentary tusk.

SOUTHERN WARREN RANGE, MOUNT RITCHIE
(locality 24)

Fig.42C

Material. CPC 27858, 859, AMF 55592.

Horizon. Unit 54, section A4 of Askin *et al.* (1971), in the upper 30 m of the Aztec Siltstone.

Description. These scales are associated with the indeterminate osteolepid material described above, which occurs with four species of *Bothriolepis* (*B. alexi*, *B. karawaka*, *B. mawsoni* and *B. vuwae*; see Young, 1988).

AMF 55592 is an incomplete external impression, and CPC 27858 and 27859 are preserved in part and counterpart, but the inner surface is not shown, so presence of an internal boss needs confirmation. These resemble the scales of various rhipidistians (including *Eusthenopteron*) which have lost the cosmine cover to their scales, as illustrated by Jarvik (1950a: fig.33). The best specimen (Fig.42C) is about 15 mm across, with a broad anterior overlapped portion, and a narrow posterior segment of radiating rounded ridges and grooves.

Order Rhizodontiformes

Remarks. This grouping is used here in the restricted sense of Andrews & Westoll (1970a,b) and Andrews (1973, 1985), to include the new genus defined below, together with the genus *Sauripterus* (Upper Devonian), and the Carboniferous genera *Rhizodus*, *Strepsodus*, and *Screbinodus* from Europe, *Pycnoctenion* and *Propycnoctenion* from Russia, and *Baremeda* from Australia. Inter-relationships of these taxa are considered in discussion.

Notorhizodon n.gen.

Etymology. From the Greek *notos*, south, *rhiza*, root, and *odon*, tooth.

Diagnosis. A rhizodontiform probably attaining a length of over 3 m, having a dermal skull roof pattern with large extratemporal bones which anteriorly contact the intertemporals, and large frontals relative to dermosphenotics. Coronoid and palatine series bearing large laterally compressed fangs with well-formed vertical laminae bearing smaller teeth and closing around fangs of opposing jaw in occlusion. Anterior margin of lower jaw strongly indented at dentary-infradentary contact. Parasphenoid twice as broad posteriorly as in its middle section, with its ventral face transversely concave throughout its length. Posterior region of ethmosphenoid attached to frontal by a broad posterodorsal process with two lobes. Dermal bones coarsely ornamented with tubercles and ridges, scales round with an ornament of fine tubercles with apical depressions.

Remarks. The new genus is distinguished from *Rhizodus* and *Screbinodus*, the only other rhizodontiforms which bear laterally compressed coronoid and dentary tusks, by the ornament on the scales, and the fact that the lateral line sensory canal does not pass through the parietal. *Notorhizodon* may resemble *Screbinodus* in the shape of the intertemporal, and *Baremeda* (Long, 1989) in the sensory canal pattern, but the latter genus differs in many features, including the ornament of the dermal bones and scales, the cross-sectional shape of the tusks, the size of the dentary tusks, the shape of the anterior margin of the lower jaw, the form of the infradentary overlap, and the absence of curved laminae to receive the tusks of the opposing jaw. In the presence of the deep spiracular notch, and the more anterior position of the ossification centre, the intertemporal of *Notorhizodon* can be readily distinguished from that of *Eusthenopteron*, which also lacks a dentary tusk, and differs in the shape of the parasphenoid, the orientation of the jugular canal, and the absence of an anterolateral bar on the otoccipital. *Notorhizodon* resembles *Eusthenodon* in size, ornament, presence of a dentary tusk, and shape of the intertemporal, but differs in many aspects of jaw

morphology.

Notorhizodon mackelveyi n.sp.

Figs 21-36, 37A, 38B, 39-41, 42A,B

'lower jaw of an ... air-breathing fish', 'pieces of another jaw' Ritchie, 1971a: 16.
 'lower jaw of ... crossopterygian' Ritchie, 1971b: 16 (fig).
 'crossopterygian skull and jaws' McKelvey et al., 1972: fig.4.
 'fossil fish fragments' (pars) Barrett & Webb, 1973: 18.
 'crossopterygian jaw' Young, 1988: 13.
 'large rhizodontiform from ... Antarctica' Long, 1989: 15.
 'large rhizodontiform rhipidistian' Young, 1989b: 48.
 'rhizodontiform' Long, 1990: 161.
 'large rhizodontid-like fish' Young, 1991: 545, fig.15.5(a).

Etymology. After Dr Barry McKelvey, Armidale, who carried out extensive field investigations of the geology of southern Victoria Land.

Holotype. CPC 26404, disarticulated remains preserved as impressions in three large and 19 smaller pieces of hard sandstone (labelled a-v), including the ethmosphenoid, otoccipital and associated dermal bones and an incomplete maxilla (piece a), dermal bones of the left side of the palate (piece b), anterior end of the left and a large posterior section of the right lower jaw (piece c), posterior end of the right lower jaw (piece d), two small anterior and posterior sections of the cast of the meckelian cavity of the right lower jaw (pieces e,f), the posterior part of the left palatoquadrate (piece g), an incomplete parietal bone in external view (piece h), associations of incomplete dermal bones in external (piece i) and one internal view (piece j), incomplete dermal bones in external view showing margins (pieces k,l), or lacking them (pieces m-p), three specimens showing internal surfaces of dermal bones, with bone margins (pieces q-s), and three fragments (pieces t-v). All assumed to come from one individual (see below).

Other material. Isolated scales from the type locality (CPC 27860, 861), an associated skull, shoulder girdle, and right lower jaw from Mount Warren (AMF 54333), isolated lower jaws from Mount Crean (AMF 54327) and Mount Metschel (AMF 55781), and disarticulated teeth, jaw and dermal fragments from Mount Metschel (AMF 55760-76, CPC 27862-864).

Localities. The type locality is Mount Ritchie (locality 24, Fig.2). Other material came from Mount Crean, locality 8 (AMF 54327), Mount Metschel, localities 13 (CPC 27862-864), and 14 (AMF 55781, AMF 55760-76), and Mount Warren, locality 15 (AMF 54333).

Horizon. The holotype came from unit 62 of section A4 of Askin et al. (1971), associated with the holotype of the antiarchs *Bothriolepis macphersoni* and *Pambulaspis antarctica* described by Young (1988).

AMF 54327 came from collecting site MC5, which is near the base of the Aztec Siltstone, but may not have been *in situ*. The Mount Metschel material came from the upper 30 m of the Aztec Siltstone, in units 10 (CPC 27863), 15 (CPC 27864), and horizon unspecified (CPC 27862) in section M1 of Askin *et al.* (1971), the last specimen associated with *Bothriolepis alexi* (CPC 26374) of Young (1988: 84). AMF 54333

came from within several metres of the top of the Aztec Siltstone (MS234, section 8 of Barrett & Webb, 1973).

Diagnosis. As for genus (only species).

Description. The incomplete remains of the holotype were collected over an area of about 10 m²

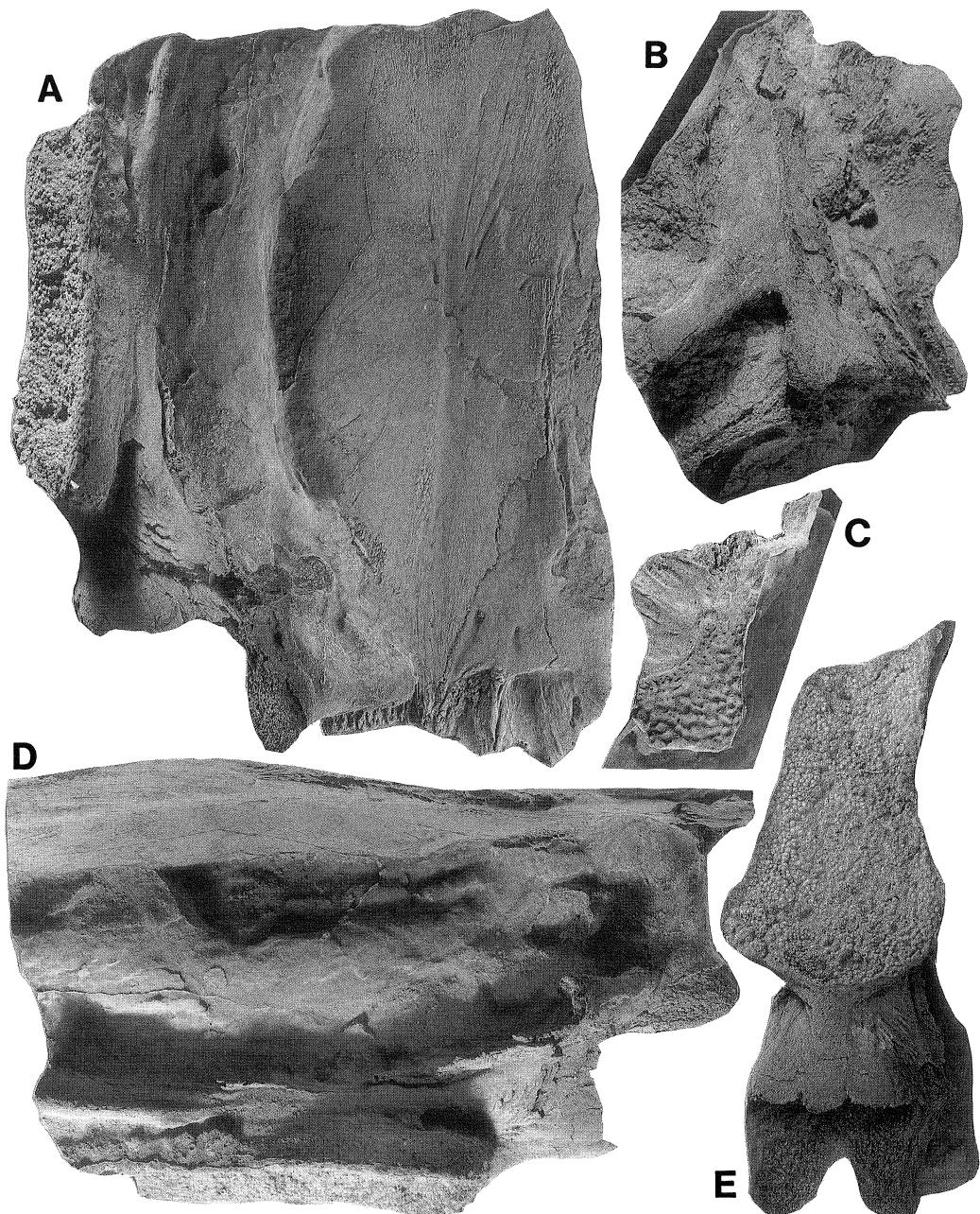


Fig.21. *Notorhizodon mackelveyi* n.gen., n.sp. Holotype (CPC 26404). A, visceral view of left frontal and dermosphenotic with attached ethmosphenoid bone bent to the left side in a ventrolateral view to expose structures more clearly; cf. Figure 24B (x1); B, left side of otoccipital bone attached to the left intertemporal bone, ventral view; C, dorsal view of specimen in B, showing only the preserved part of the external surface of the left intertemporal (both x0.8); D, left lateral, and E, ventral view of ethmosphenoid bone with attached parasphenoid (both x1). All from locality 24 (Mount Ritchie). All specimens latex casts whitened with ammonium chloride.

on a rock ledge; other remains of this fish were presumably lost down the scree slope. The size range of the preserved bones and their lack of duplication suggests that they came from one large individual, with a lower jaw about 400 mm in length. Assuming similar proportions to the small specimen of *?Strepsodus* described by Andrews (1985) a total length of 3.1 m would be indicated for this fish. Comparisons with *Eusthenopteron* as restored by Jarvik (1980a) would give a total length of about 2.6 m. The former is a very small juvenile whose proportions may have elongated with growth, and Jarvik's specimen of *Eusthenopteron* is about half grown, so their proportions would not be strictly comparable with the large individual of *Notorhizodon*. *Eusthenodon* attained a length of about 2.5 m; the largest known fronto-ethmoidal shield (Jarvik, 1952: fig.23C) had a frontal about 10% smaller than that of CPC 26404, but slightly larger specimens of *Eusthenodon* are known (Jarvik, 1952: 58). Assuming that the holotype was not of maximum size, a length of more than 3 m can be suggested for this species. Although it is by far the largest fish known from the Aztec fauna, *Notorhizodon* was still considerably smaller than some Carboniferous

rhizodontids from Europe (6-7 m long, and the largest known osteichthyans; see Andrews & Westoll, 1970b).

The following description is based primarily on the holotype (CPC 26404). Other significant specimens (e.g., AMF 54327, 54333) which supplement the evidence of the holotype are dealt with separately at the end of the description.

Dermal bones of the head. There are many small fragments showing dermal ornament and bone margins, but because of the large original size only four external dermal bones from the skull can be identified with any confidence (frontal, parietal, dermosphenotic, intertemporal). All dermal bone remains are coarsely ornamented with tubercles and short anastomosing ridges, and some (e.g., Fig.23C) resemble in ornament illustrated examples of dermal bones of *Screbinodus ornatus* (e.g., Woodward, 1891: pl.12 fig.5). However, the dermal bone of *Screbinodus* has a dense polished surface on the ridges, in contrast to the more loosely woven surface texture seen in *Eusthenopteron* (S.M. Andrews, personal communication). The ornament of *Notorhizodon* lacks

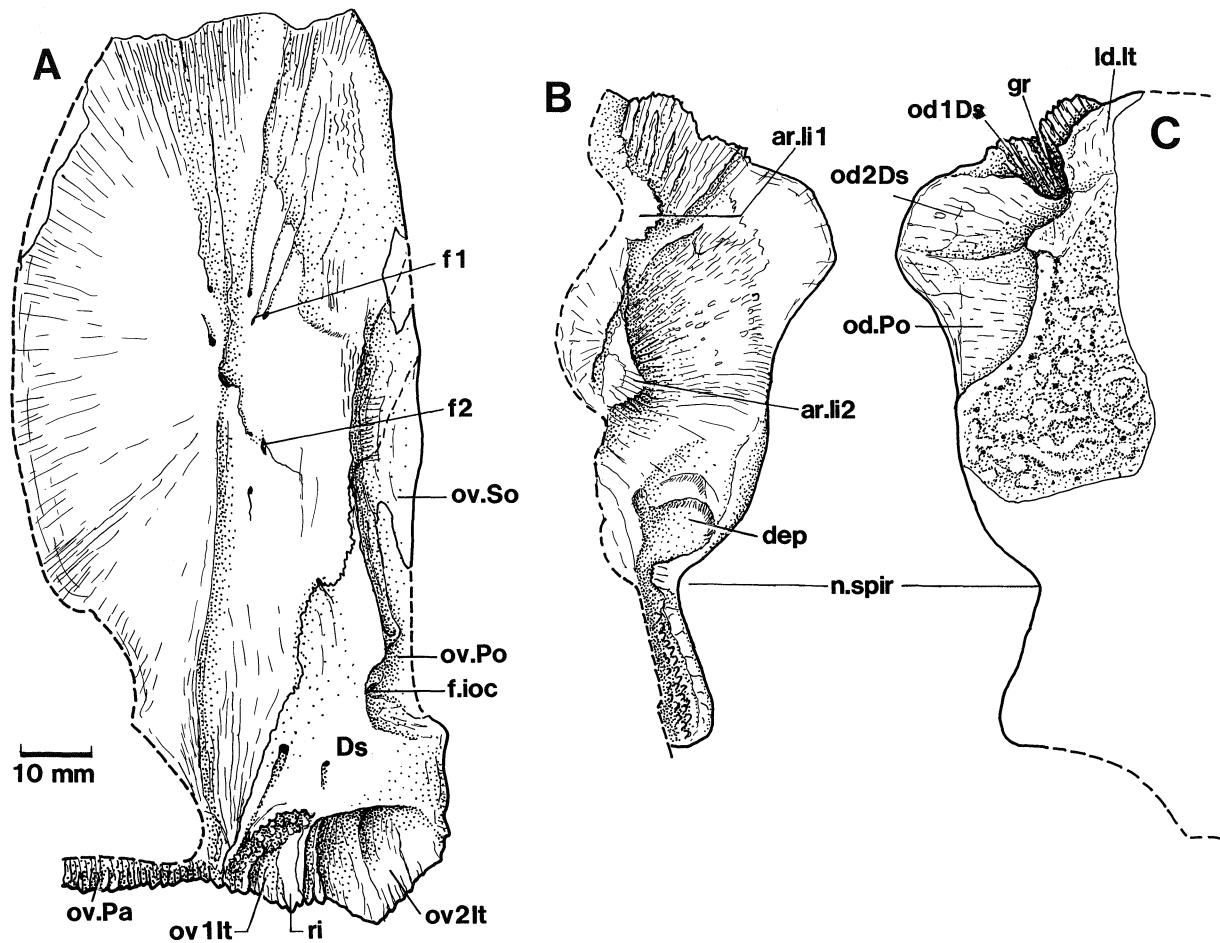


Fig.22. *Notorhizodon mackelveyi* n.gen., n.sp. A, left frontal and dermosphenotic in visceral view; B, left intertemporal bone in visceral view; C, preserved part of the external surface of the left intertemporal. Partly restored after the holotype (CPC 26404).

this dense surface, but since only impressions are available for study it is possible that this may be a preservational difference, or an artefact of preparation.

The left frontal and articulated dermosphenotic are preserved in visceral view attached to the ethmosphenoid section of the braincase (Figs 21A, 24B). There is no indication of distortion in this or the other associated remains of the holotype. Preserved length of the frontal is 134 mm, with a maximum width (estimated from the midline on the parasphenoid) of about 52 mm, to give comparable proportions to *Eusthenodon* (Jarvik, 1952: fig.23). The frontal is unknown in other rhizodontids

except for *Barameda* (Long, 1989), where it is short and broad. As preserved this bone compares well with the corresponding bone in various eusthenopterids, for example *Eusthenopteron* (Jarvik, 1937: figs 4B, 8), *Eusthenodon* (Jarvik, 1952: pl.13), and *Platycephalichthys* Vorobjeva, 1977: fig.44). The mesial margin of the bone is obscured by the ethmosphenoid, where the edge of the braincase attachment is a concave margin as in other forms (e.g., Jarvik, 1937: fig.8). The dorsal part of the braincase at the level of the ossification centre is apparently very narrow as in *Eusthenopteron foordi* (e.g., Jarvik, 1980a: fig.88A). Judging by the position of the

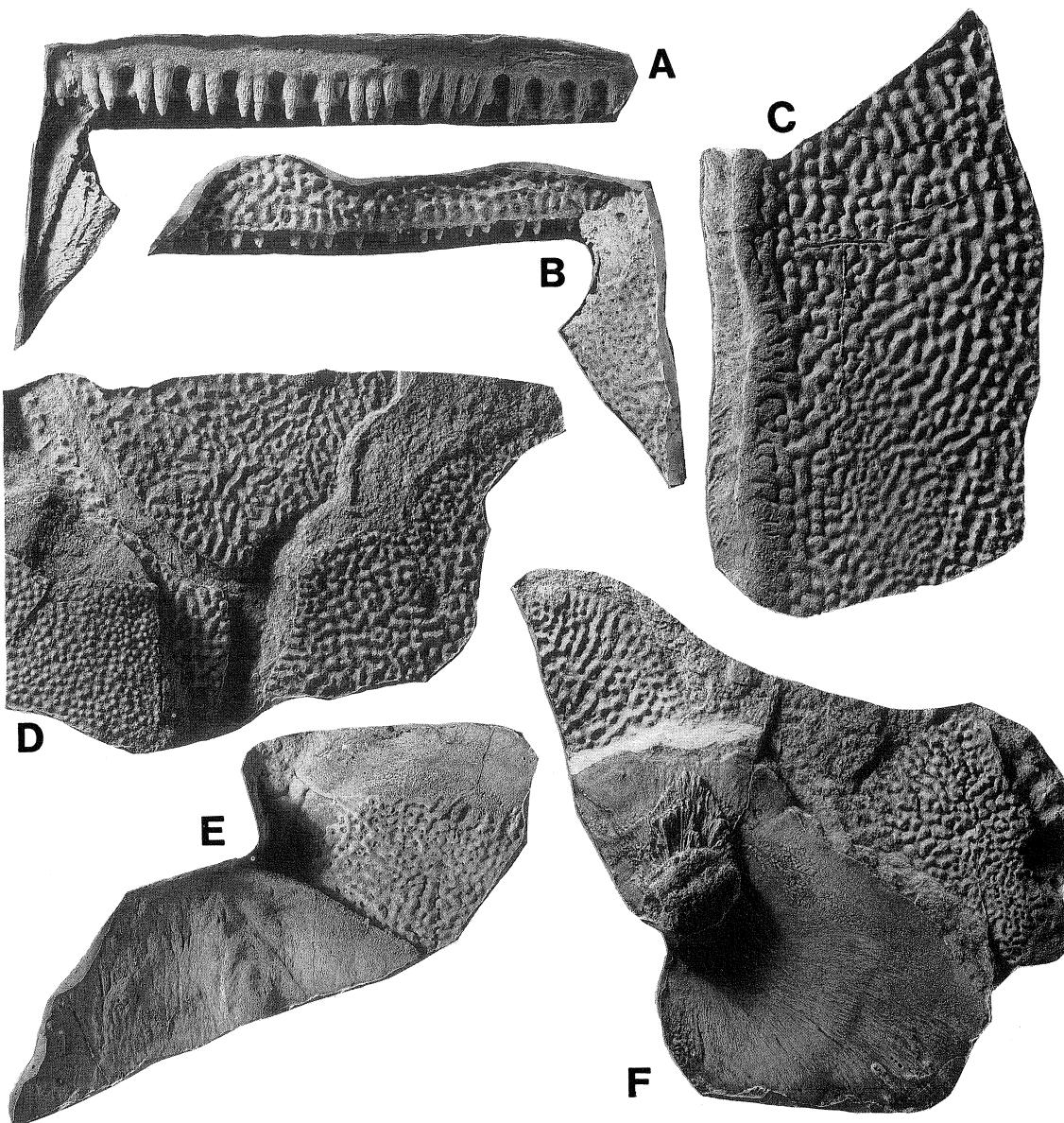


Fig.23. *Notorhizodon mackelveyi* n.gen., n.sp. A,B, maxilla and possible incomplete squamosal in mesial (A) and lateral (B) views; C, incomplete parietal in dorsal view; D, partly dissociated bones from the right side of the skull (cf. Fig.25A,B); E, associated undetermined skull bone; F, median extrascapular in visceral view (central elevation is an impression of a clay gall), with possible left post-temporal (ornamented bone on right side; cf. Fig.26). All specimens are latex casts whitened with ammonium chloride taken from the holotype (CPC 26404), x0.94.

midline on the parasphenoid the edge of the braincase attachment was very close to the midline in *Notorhizodon*.

The inner surface of the frontal is gently concave, with the mesial half fairly smooth and lacking significant features. The lateral margin shows a well-developed contact face where the frontal overlapped an adjacent bone (od.So, Fig.22A), presumably the supraorbital. In *Eusthenopteron* however this bone overlaps the frontal (Jarvik, 1944a: fig.14). Several small foramina at the ossification centre (f1) correspond to those of Jarvik (1937: fig.8). As in other forms (e.g., Jarvik, 1937, 1952; Vorobjeva, 1977) a shallow groove crosses the plate rostrocaudally, from next to the posterodorsal corner of the ethmosphenoid, through the frontal ossification centre, to the anterior margin where it becomes faint. The anterior section follows the course of the supraorbital sensory canal. The posterior course of this sensory canal, passing laterally to the ossification centre of the dermosphenotic, is indicated by a few scattered foramina on a slightly thickened part posterolateral to the ossification centre (f2).

The posterior margin of the frontal is thickened with a roughened texture where it connected with the parietal (ov.Pa, Fig.22A). In contrast to *Megalichthys* (Jarvik,

1966) or *Gogonasus* (Long, 1985b) it projects back slightly over the posterodorsal process of the ethmosphenoid.

The dermosphenotic (Ds, Fig.22A) has a triangular internal shape as in *Eusthenopteron saevesoederberghi* (Jarvik, 1937: fig.4B) rather than the more rectangular shape of *Eusthenopteron foordi* (Jarvik, 1980a: fig.80B). Again this bone is unknown in other rhizodontids (Andrews, 1985) except *Barameda*, where it differs markedly in its shape and much greater size relative to the frontal (Long, 1989). Posteriorly the suture with the frontal is clear, and there is a prominent lateral process on the posterior margin, which would have been overlapped by the postorbital, as in other forms. In front is an elongate depression, broadest posteriorly, where it has a mesial notch, which is the contact face for overlapping the postorbital, continuous with that on the frontal. A lateral foramen probably carried nerve branches to the infraorbital sensory canal (f.ioc, Fig.22A). Another canal and groove runs posteriorly, and presumably connected with the posterior (otic) section of the infraorbital sensory canal (postotic canal of Jarvik), which in other forms passed out of the bone on the external overlap area for the intertemporal (e.g., Jarvik, 1944a: fig.14). There are two distinct contact

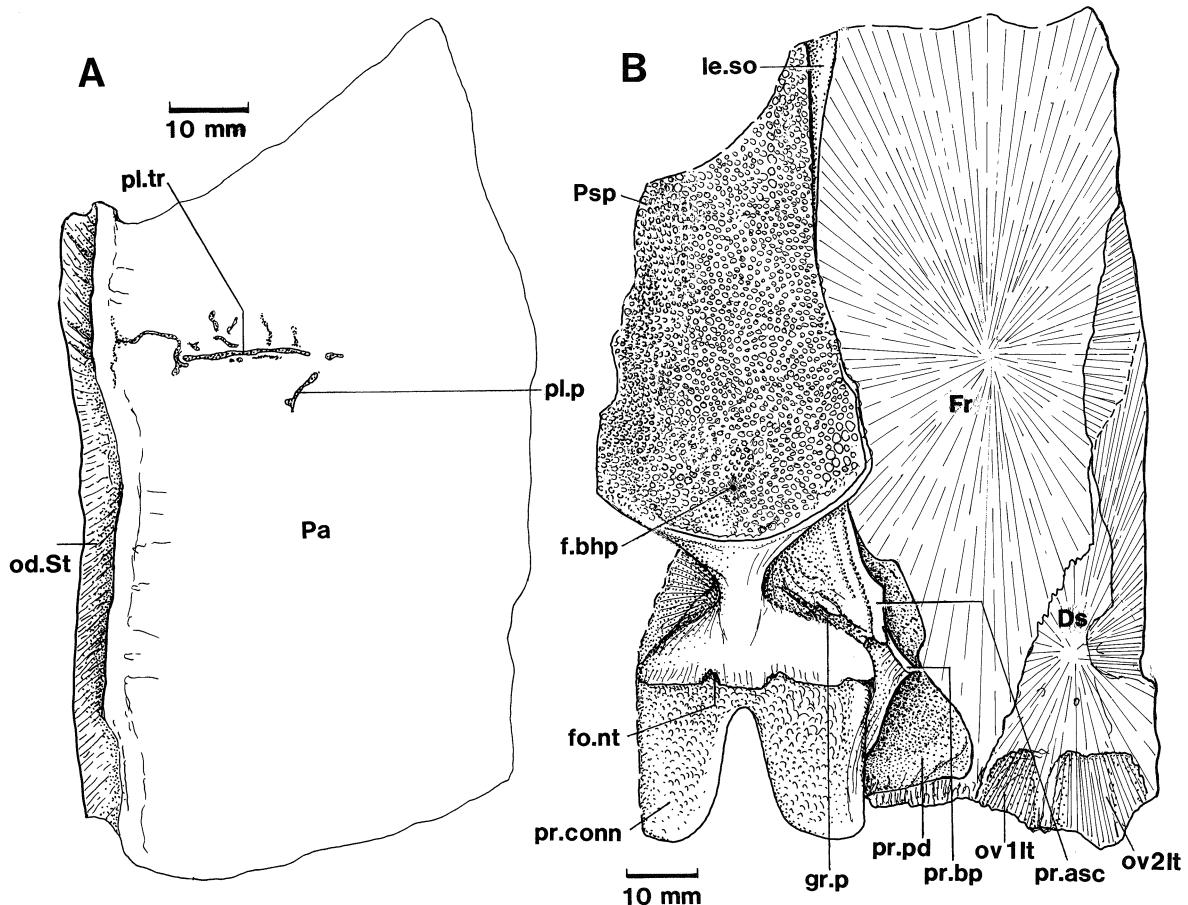


Fig.24. *Notorhizodon mackelveyi* n.gen., n.sp. A, parietal bone in external view (same specimen as in Fig.23C); B, restoration of parasphenoid, ethmosphenoid, and attached dermal bones, ventral view (same specimen as in Fig.21A,D,E). All from the holotype (CPC 26404).

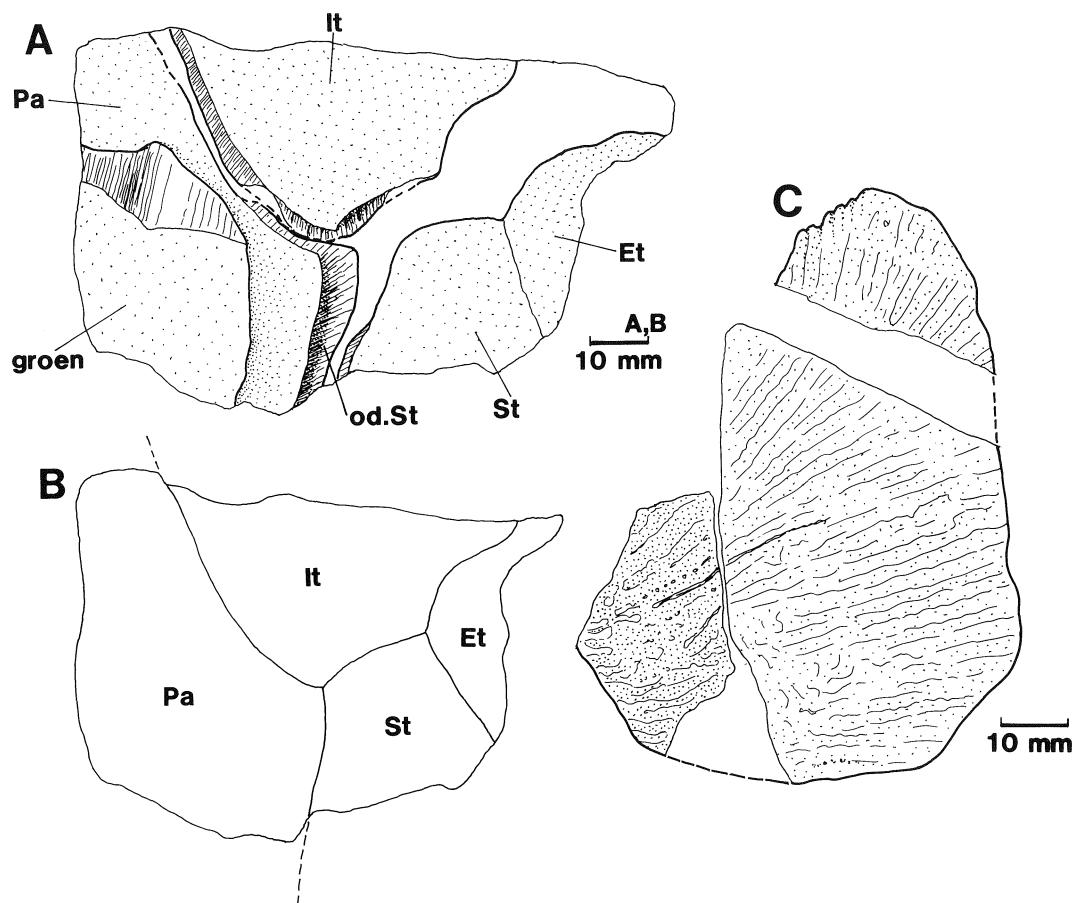


Fig.25. *Notorhizodon mackelveyi* n.gen., n.sp. A-C, various incomplete dermal bones from the head. A is the specimen shown in Figure 23D, with a possible restoration (B); C shows a possible restoration of dermal bone impressions on pieces o (bottom left), k (centre) and p (top), based on radiating ornament. All from the holotype (CPC 26404).

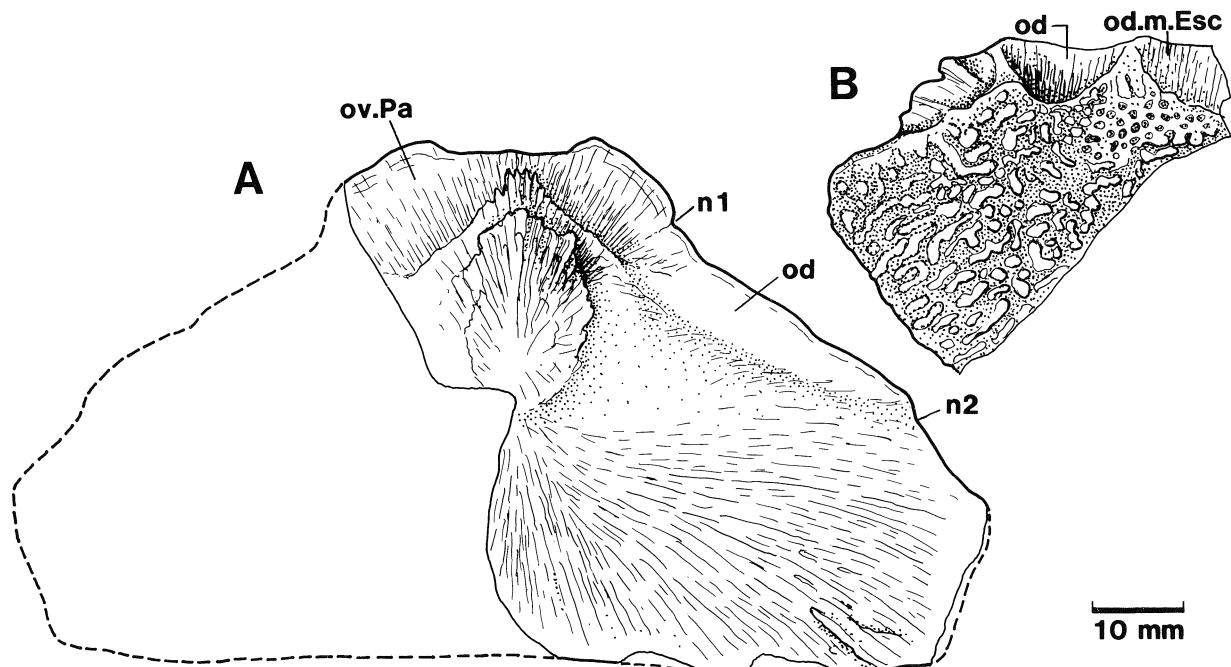


Fig.26. *Notorhizodon mackelveyi* n.gen., n.sp. A, median extrascapular in internal view; B, associated possible left post-temporal (same specimen as in Fig.23F). Restored after the holotype (CPC 26404).

faces on the posterior margin of the dermosphenotic: a mesial one with roughened texture which fitted into the deeper mesial notch and socket on the intertemporal (see below), and a lateral one which overlapped the smooth lateral overlap area of the intertemporal (Fig.22C). Latex casts of the two specimens can be fitted together, with the ridge (ri) of the dermosphenotic fitting into the groove (gr) of the intertemporal (Fig.22C). Such a complex overlap arrangement presumably rendered the intracranial joint immovable (Jarvik, 1944a).

The left intertemporal is preserved in visceral and part external view attached to the otoccipital (Figs

21B,C, 22B,C). A posterior overlap area for the postorbital and an anterior overlap for the dermosphenotic (Fig.22C) are developed exactly as in *Eusthenopteron* (Jarvik, 1980a: figs 115, 116C), with the anterior overlap area subdivided into a smooth lateral and deeply grooved mesial section. The anterior deeply grooved overlap (od1Ds, Fig.22C) continues into the bone as a deep pit which received the process from the dermosphenotic described above in a double overlap.

In visceral view (Fig.22B) the mesial margin is obscured by the otoccipital, so breadth of the plate is not known. Its lateral margin is complete, with a deep

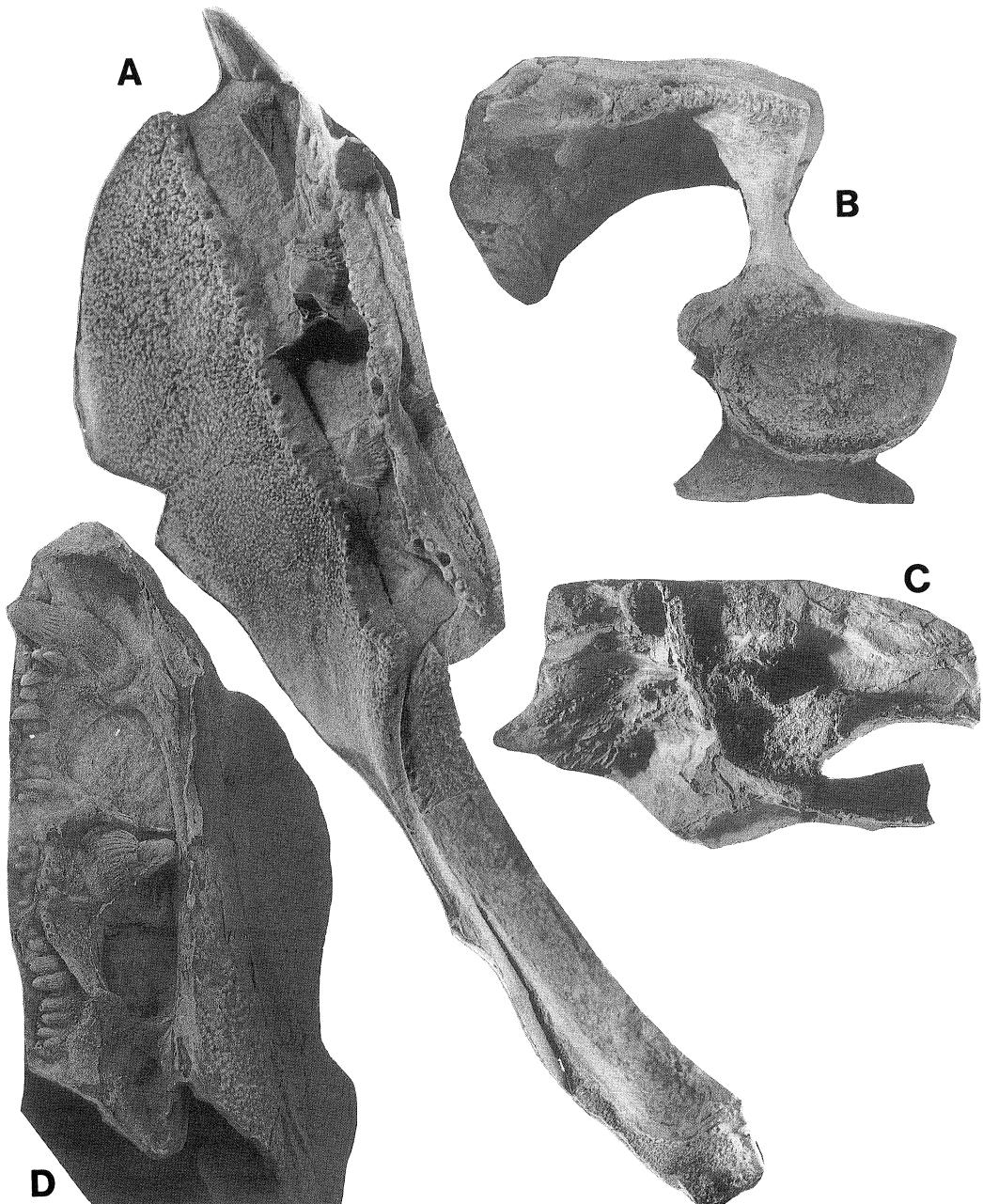


Fig.27. *Notorhizodon mackelveyi* n.gen., n.sp. A, left palate in visceral view; B, ethmosphenoid attached to left frontal, posterior view; C, left otoccipital in posterior view; D, preserved anterior part of left lower jaw in dorsal view. All specimens latex casts whitened with ammonium chloride from the holotype (CPC 26404). (A,B x0.75; C x1; D x0.9)

lateral notch in front of the hyomandibular articular facet and about level with the anterior opening of the jugular canal (see below), behind which the lateral dermal bone margin runs just outside and parallel to the edge of the crista parotica of the otoccipital. In *Eusthenopteron* (Jarvik, 1980a: figs 120, 123), this part of the otoccipital was covered by the supratemporal bone, with its lateral margin just lateral to the crista parotica. In contrast, the indented margin of *Notorhizodon* resembles the spiracular notch on the lateral margin of the intertemporal in *Eusthenodon* (Jarvik, 1952) or *Screbinodus* (Andrews, 1985). The rhizodontid intertemporal is otherwise only known in *?Strepsodus aculonamensis* and *Barameda*, in both of which it narrows anteriorly and lacks the lateral notch (Andrews, 1985; Long, 1989).

The preserved part of the internal surface of the

intertemporal is gently concave, with a shallow depression of unknown function in front of the spiracular notch (dep, Fig.22B). Two roughened areas are seen, one posteriorly where a shallow ridge curves mesially around the edge of the otoccipital, and another anteriorly where the roughened surface which contacted the process of the dermosphenotic extends back to a slight elevated boss of roughened bone above the ossification centre. These correspond respectively to the ligament attachment areas for the ascending and paratemporalis processes of the palatoquadrate in *Eusthenopteron* (Jarvik, 1980a: fig.118).

On the same block is an impression of the ventral toothed margin of a maxilla (Fig.23A,B), but with no other margins preserved. Associated is a dermal bone fragment displaying a distinct corner, with an overlap

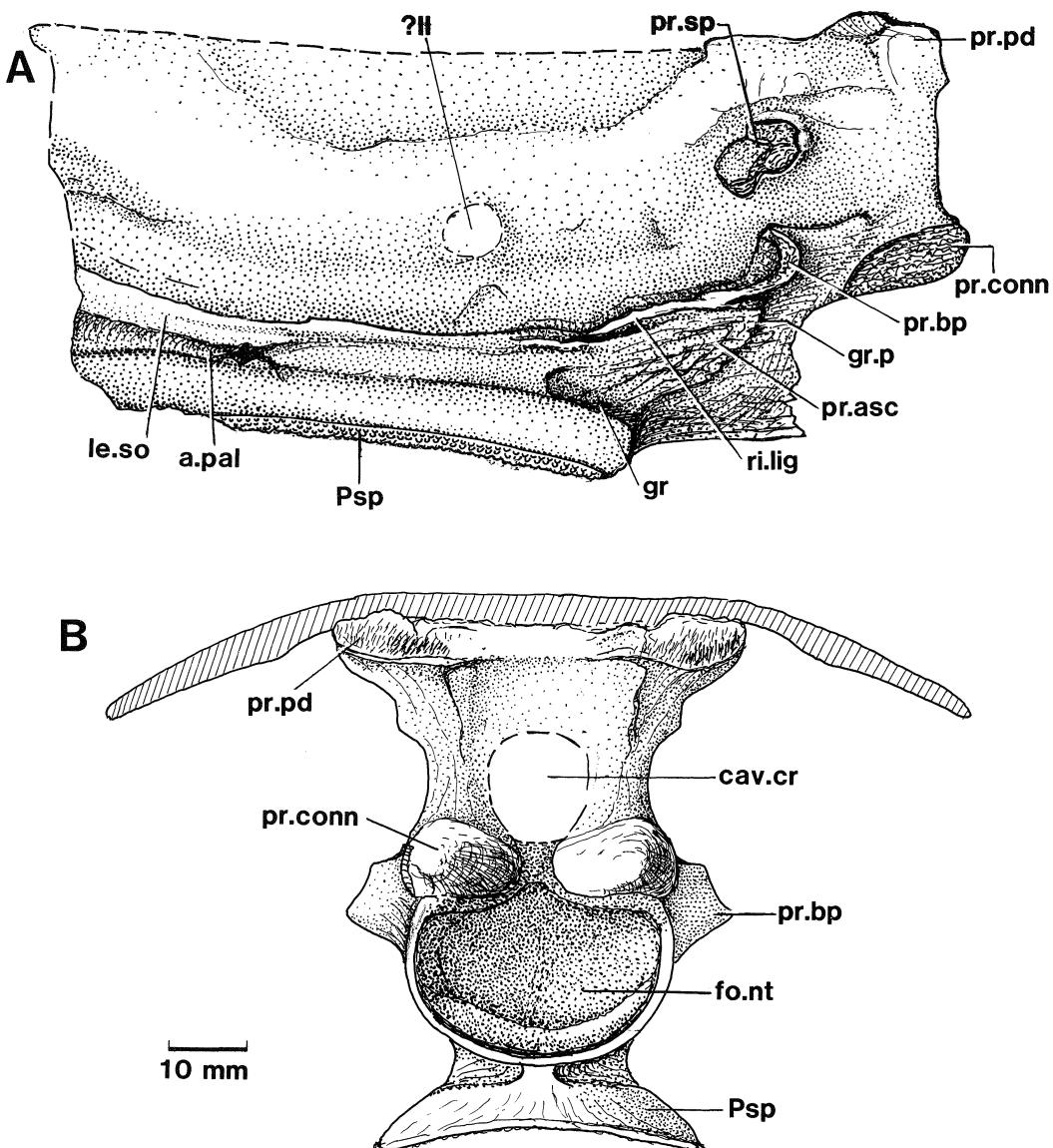


Fig.28. *Notorhizodon mackelveyi* n.gen., n.sp. Ethmosphenoid in left lateral (A), and restored in posterior (B) views (cf. Figs 21D, 27B). In B dermal bones of the skull roof are cross-hatched. After the holotype (CPC 26404).

area on its upper margin, and a contact face inside its lower margin. This fragment may be a displaced left squamosal, the overlap area being for the posterodorsal margin of the maxilla (not preserved), and the contact face for overlapping the anterodorsal margin of the quadratojugal, as in *Eusthenopteron* (Jarvik, 1944a: fig.9A). If correct then the associated maxilla is also likely to be from the left side, while the possible squamosal has a more pronounced ventral angle than in *Eusthenopteron* or *Eusthenodon* (Jarvik, 1944a, 1952), or other related forms where known (Vorobjeva, 1962, 1977). This detail is poorly known in other rhizodontids (Andrews, 1985; Long, 1989).

An incomplete parietal (specimen h) is preserved in external view, its only complete margin showing an overlap area for adjacent bones (Fig.23C). It was at least 52 mm wide and 106 mm long. The short irregular sections of pitlines (Fig.24A) can be clearly distinguished from grooves in the ornament by microscopic study of whitened latex casts. This specimen is assumed to be a left plate, based on the arrangement of sensory pitline grooves (pl.tr, pl.p, Fig.24A) which were evidently some distance from the posterior end of the bone, but still at its lateral side as is normal in rhipidistians. On the

evidence of an interpreted incomplete right parietal of the holotype (Figs 23D, 25A; see below), the overlap on the left parietal (od.St, Fig.24A) must have been for the supratemporal, in contrast to *Eusthenopteron* where the parietal is overlapped by the intertemporal anteriorly, but overlaps the supratemporal posteriorly (Jarvik, 1944a: fig.14). The alternative hypothesis, that this is a right plate with the margin bearing the overlap area forming the median suture with the left parietal, is discounted because the midline position of the pitlines is not known in other rhizodontids. Furthermore, a second much smaller specimen, described below (AMF 54333), also shows a corresponding lateral overlap area (Fig.39B).

There is no sign on this overlap area of a foramen indicating passage of a sensory canal, suggesting a difference to the rhizodontids figured by Andrews (1985), where the otic section of the infraorbital canal looped through the ossification centre of the parietal.

The interpreted portion of the right parietal of *Notorhizodon* (specimen i of the holotype), is one of four associated but incomplete bone impressions, two still connected by a suture, and the others separated to partly show overlap relations (Fig.23D). This specimen apparently represents part of the associated parietal,

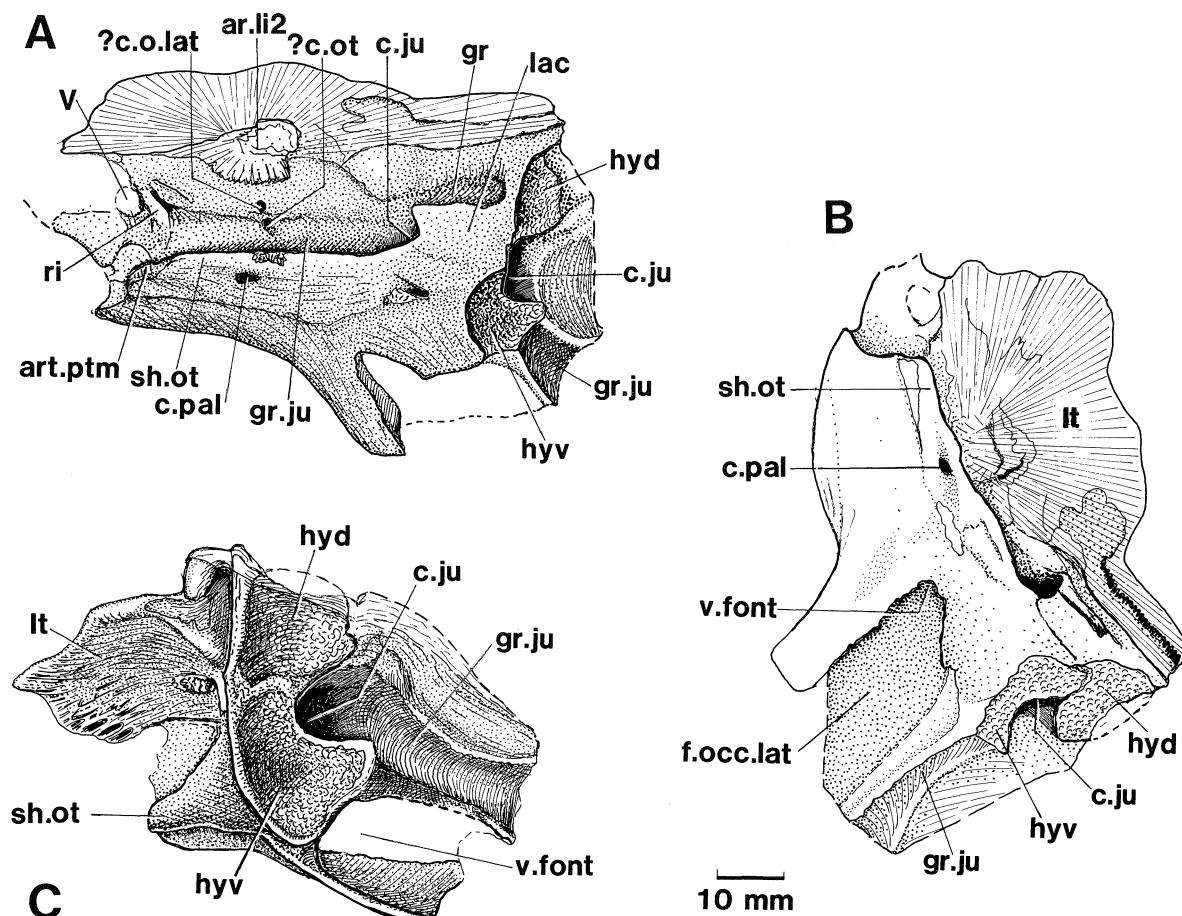


Fig.29. *Notorhizodon mackelveyi* n.gen., n.sp. Right half of otoccipital bone in ventrolateral (A), ventral (B) and posterior (C) views (cf. Figs 21B, 27C). A and B include the attached intertemporal bone. After the holotype (CPC 26404).

intertemporal, supratemporal, and extratemporal of the right side (Fig.25A,B), based on the close resemblance to the arrangement of these bones in *Barameda* (Long, 1989). The overlap area just behind the lateral corner of the parietal (od.St, Fig.25A) is presumably the anterior end of the lateral overlap seen on the previous specimen. Based on the two specimens it seems that the parietal of *Notorhizodon* was not dissimilar in shape to that of *Screbinodus*, with a lateral indentation for the intertemporal, and the pitlines (and ossification centre) some distance in front of the posterior margin. In

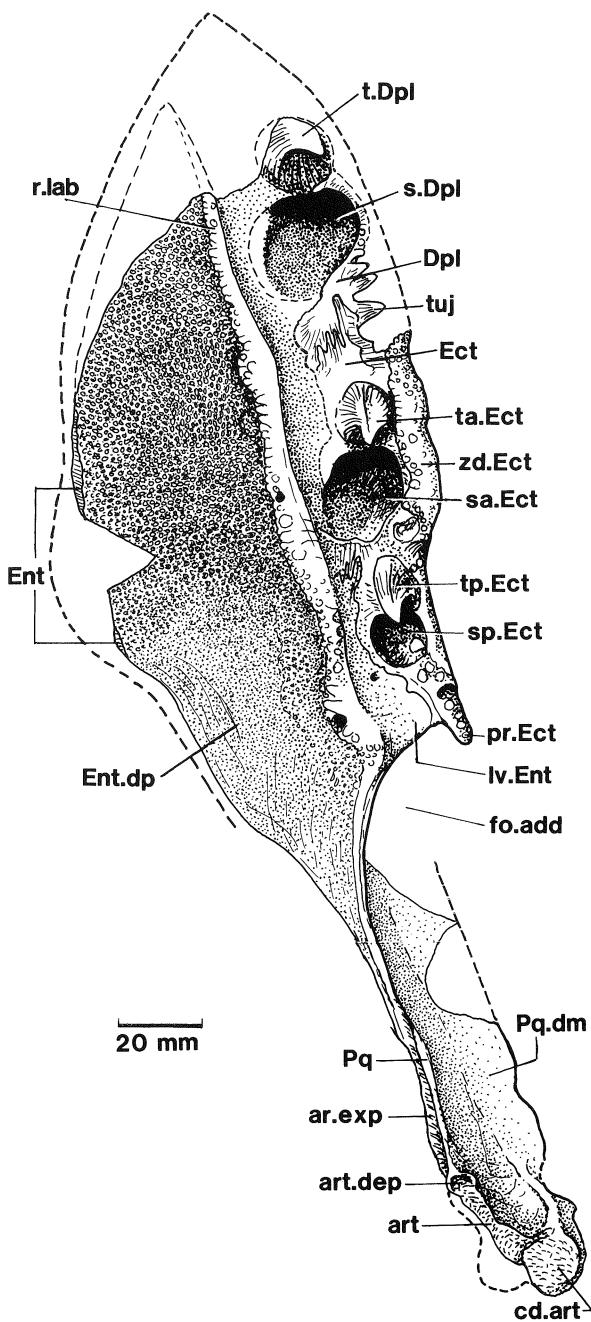


Fig.30. *Notorhizodon mackelveyi* n.gen., n.sp. Left palatoquadrate and attached dermal bones in visceral view. Partly restored after the holotype (CPC 26404).

contrast, *Barameda* resembles *Eusthenopteron* in having the ossification centre in a posterior position (Long, 1989; Jarvik, 1980a). AMF 54333 also includes an incomplete parietal shield (Figs 39, 40), which indicates a similar overlap arrangement in a much smaller individual than the holotype (see below). However *Notorhizodon* resembles *Barameda* (Long, 1989: fig.2), and differs from *Eusthenopteron*, in that anteriorly the parietal overlaps the intertemporal.

The median extrascapular is preserved in specimen j (Fig.23F) as a short broad apparently symmetrical bone in visceral view. Most of the left half and the anterolateral margin are well preserved. The impression of the posterior preserved margin is at the edge of the sample, but a short lateral section seems complete, and it is considered to approximate the natural margin. As restored (Fig.26A) it is about 110 mm wide with a midline length of about 60 mm. Anteriorly there is a broad shallow median embayment with symmetrically placed contact faces (ov.Pa) delimited posteriorly by a thickened region of radiating ridges forming a low boss over and in front of the ossification centre. The contact face fades laterally on the visceral surface, and probably stopped at or just lateral to a notch (n1) in the anterolateral margin. Further laterally the visceral surface is slightly elevated (od) inside the margin as far as a second notch (n2). The contact faces on the visceral surface presumably received posterior projections of the parietal shield, as seen in *Eusthenopteron* and *Eusthenodon* (e.g., Jarvik, 1952: fig.24; 1980a: fig.115), and the bone was overlapped laterally by the lateral extrascapulars, as in osteolepiforms and other rhizodontiforms where known. In *Notorhizodon* the posterior projections from the parietal bones met in the midline. Noteworthy is the similarity in shape of this bone as restored to the median extrascapular of *Canowindra* as described by Long (1985a). In both *Screbinodus* and *Barameda* the median extrascapular was evidently much less broad. In *Barameda* the lateral extrascapulars met at a point, but the extent of the overlap on the external surface in *Notorhizodon* is unknown, so a similar arrangement cannot be excluded. The convex posterior margin of the median extrascapular in *Barameda* would appear to be an obvious difference to the straight (but incompletely preserved) margin indicated for *Notorhizodon* (Fig.26A). An associated incomplete bone preserved in external view shows several small overlap areas (Fig.26B), and may be a left post-temporal, by comparison with this bone in *Eusthenopteron* (Jarvik, 1944b: fig.2D).

The remaining dermal bone fragments from the head are too small for reliable identification, the best preserved showing no features other than ornament and one natural margin. The impression on piece k has a convex natural margin to a flat portion of bone notable for its ornament, with a strong linear arrangement of tubercles coalesced into radiating ridges separated by grooves sometimes developed as rows of pores. These indicate the approximate position of the ossification centre. Two much smaller pieces (o, p) show similar

radiating ridges, in contrast to all the other dermal fragments in the collection. Piece o could represent the other side of the bone as restored in Figure 25C, although fit of specimens is only approximate. If these two do go together approximately as shown the bone has a gentle transverse curvature, and its long axis must have been oriented rostrocaudally. Piece p might fit on the anterior end where approximately parallel broken edges give a reasonable alignment of ornament, although if it does belong here the margins indicate that a portion of unknown size is missing. Piece q shows a gently convex plate with a curved margin preserved mainly as an impression of the visceral surface (Fig. 23E). Possibly it represents the missing portion of the plate tentatively restored from the previous three specimens. There is no conclusive evidence from association of samples, but they do show that specimen 1 is not its counterpart. The

latter also has a curved margin but much more irregular ornament than the previous specimens, and slight transverse convexity indicating a bone longer than broad oriented rostrocaudally in the head, perhaps one of the lateral gulars which are elongate bones in *Screbinodus* (Andrews, 1985). These fragments cannot be identified without further material, but their curved margins, gentle curvature and absence of other distinguishing features suggests that they belong to some of the subcircular bones of the lateral side of the head lacking sensory canals or pitlines, such as the opercular or subopercular, which were probably quite large in CPC 26404. The circular form and lack of overlaps for these bones in other rhizodontids suggest that they were held in flaps of skin in the operculum (Andrews, 1985).

Braincase. Impressions of the braincase are

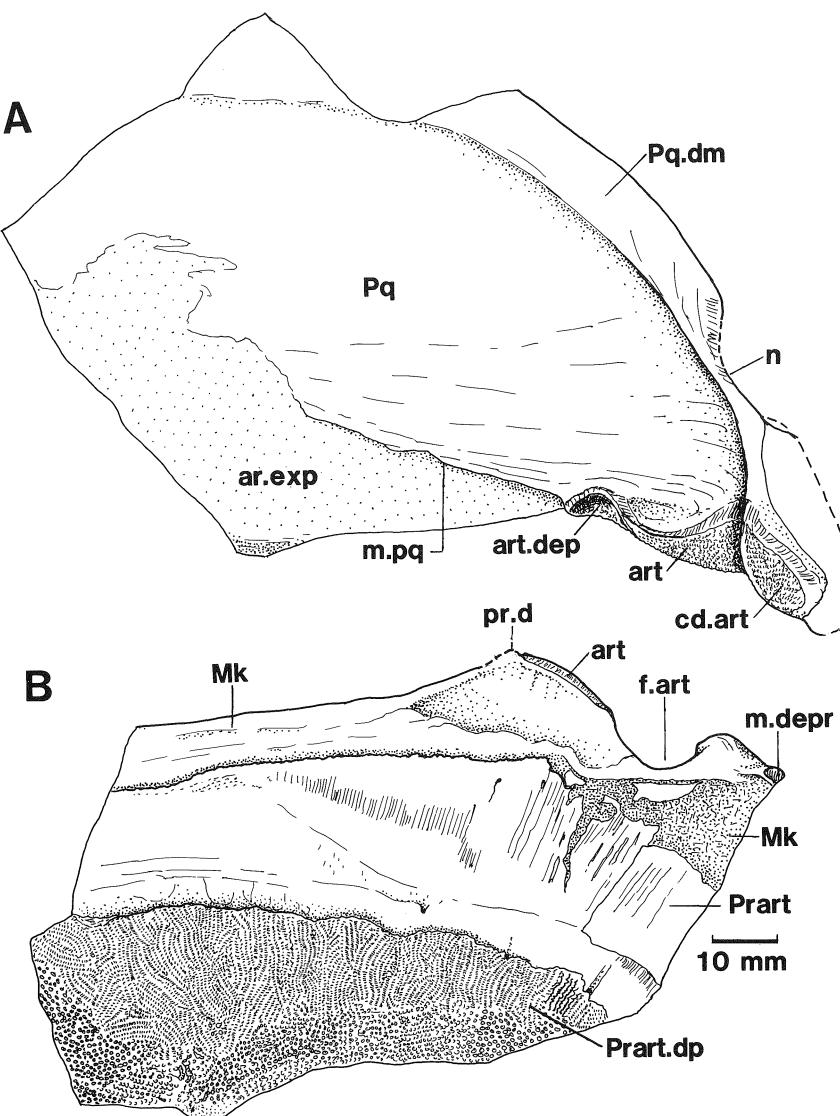


Fig.31. *Notorhizodon mackelveyi* n.gen., n.sp. A, preserved posterior part of left palatoquadrate and entopterygoid in lateral view (for position of this specimen relative to the anterior part of the palatoquadrate see Figs 30, 35A); B, preserved posterior part of right lower jaw in mesial view (for position relative to anterior part of jaw see Fig.35B). After the holotype (CPC 26404).

preserved attached to the frontal and intertemporal dermal bones (Figs 21A,B, 27B,C). These provide information on the structure of the neurocranium in *Notorhizodon*. The braincase is unknown in other rhizodontids, but comparisons can be made with *Eusthenopteron*, in which it has been described in detail (e.g., Jarvik, 1942, 1954, 1959, 1980a). Attached to the frontal of CPC 26404 is an impression of the left posterior region of the ethmosphenoid, with the posterior part of the parasphenoid attached, and beneath the intertemporal is an impression of the middle lateral division of the otoccipital from the left side. They are readily identified from their general resemblance to the

detailed restorations of the neurocranium of *Eusthenopteron* published by Jarvik.

The posterior region of the ethmosphenoid is attached to the frontal by a broad posterodorsal process with two lobes (Fig.21A; pr.pd, Fig.24B). The anterior lobe of the process, immediately above the suprapterygoid process (pr.sp, Fig.28A) is apparently absent in *Eusthenopteron* (Jarvik, 1954: fig.1B). Anteriorly the attachment decreases in width to a narrow median attachment in the interorbital region, as in *Eusthenopteron*. Posteroventrally the basipterygoid process (pr.bp) is strongly developed as a lateral process with the concave articular area facing anteriorly, and extending forward

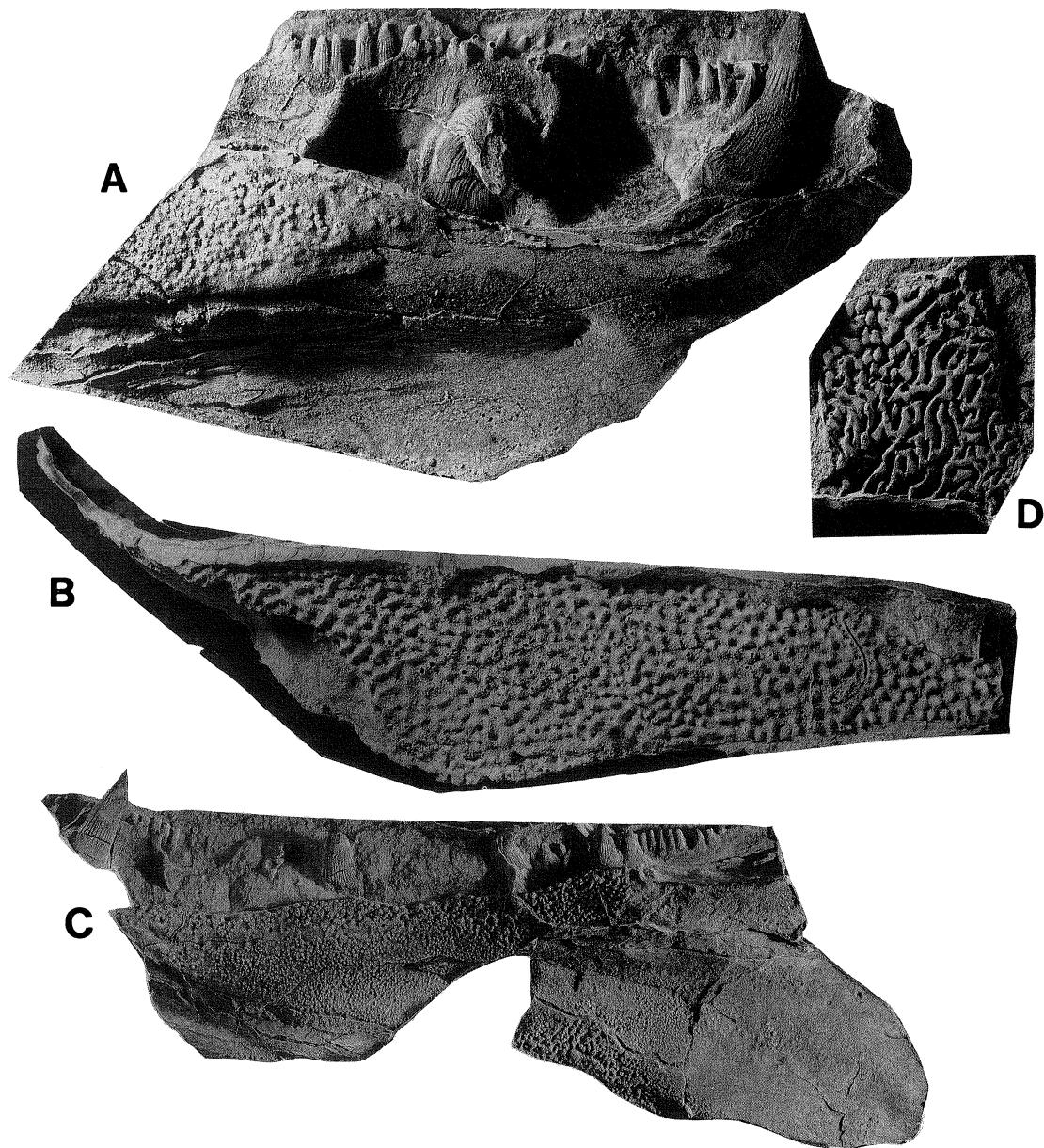


Fig.32. *Notorhizodon mackelveyi* n.gen., n.sp. A,B; preserved anterior part of left lower jaw in mesial (A) and lateral (B) views (for dorsal view see Fig.27D); C, preserved part of right lower jaw, mesial view; D, possible anterior branchiostegal, external view (A-C, holotype, CPC 26404; D, CPC 27862). All specimens latex casts whitened with ammonium chloride. (A,B,D x1; C x0.5)

as a horizontal shelf (ri.lig, Fig.28A). A similar arrangement is seen in other osteolepiforms (Long, 1985b: fig.7). The corresponding ligamentous ridge in *Eusthenopteron* has a different orientation, running obliquely downwards (Jarvik, 1954: fig.1) rather than horizontally. A depression in the wall of the braincase just in front of the basipterygoid process may have been an insertion area for some of the external eye muscles (as suggested for *Gogonasus* by Long, 1985b), and probably contained the foramen for the pituitary vein (not clearly seen from the cast). Nor is there any sign of foramina for the internal carotid artery, ophthalmica magna, or oculomotor nerve, nor the major foramen for the optic nerve, all of which must have opened in this region (see Jarvik, 1980a: fig.85). The assumed position of the optic nerve foramen is indicated by a dashed line (II, Fig.28A). There is a well-defined shelf running anteriorly from the basipterygoid process (le.so), which presumably received the mesial thickened edge of the autopalatine, as in *Gogonasus* (Long, 1988: fig.10). Compared to transverse sections and restorations of *Eusthenopteron* showing the parasphenoid (e.g., Jarvik,

1954: figs 6A, 25), the parasphenoid and the suborbital ledge which carried it are much more pronounced in *Notorhizodon*. Dorsal to the basipterygoid process is the well-defined suprapterygoid process (pr.sp), which comprises posterodorsal and posteroventral articular surfaces elevated from the surrounding bone, and a somewhat rectangular anteroventrally oriented opening through the periosteal lining, the whole structure surrounded by a rim of bone. Ventral to and supporting the basipterygoid process is a strong posterodorsal projection of the parasphenoid (pr.asc), clearly the anterior ascending process identified in *Eusthenopteron* (Jarvik, 1954: fig.18). However there is no clearly defined ‘prespiracular groove’ as recorded for *Eusthenopteron*, and his ‘posterior groove’ (gr.p) in this specimen is clearly just the posterior border of the dermal ascending process. This groove is continued forward as a short deep horizontal groove (gr, Fig.28A), but whether it pierced the parasphenoid as Jarvik observed in *Eusthenopteron* cannot be seen on the specimen.

The posterior face of the ethmosphenoid is similar to

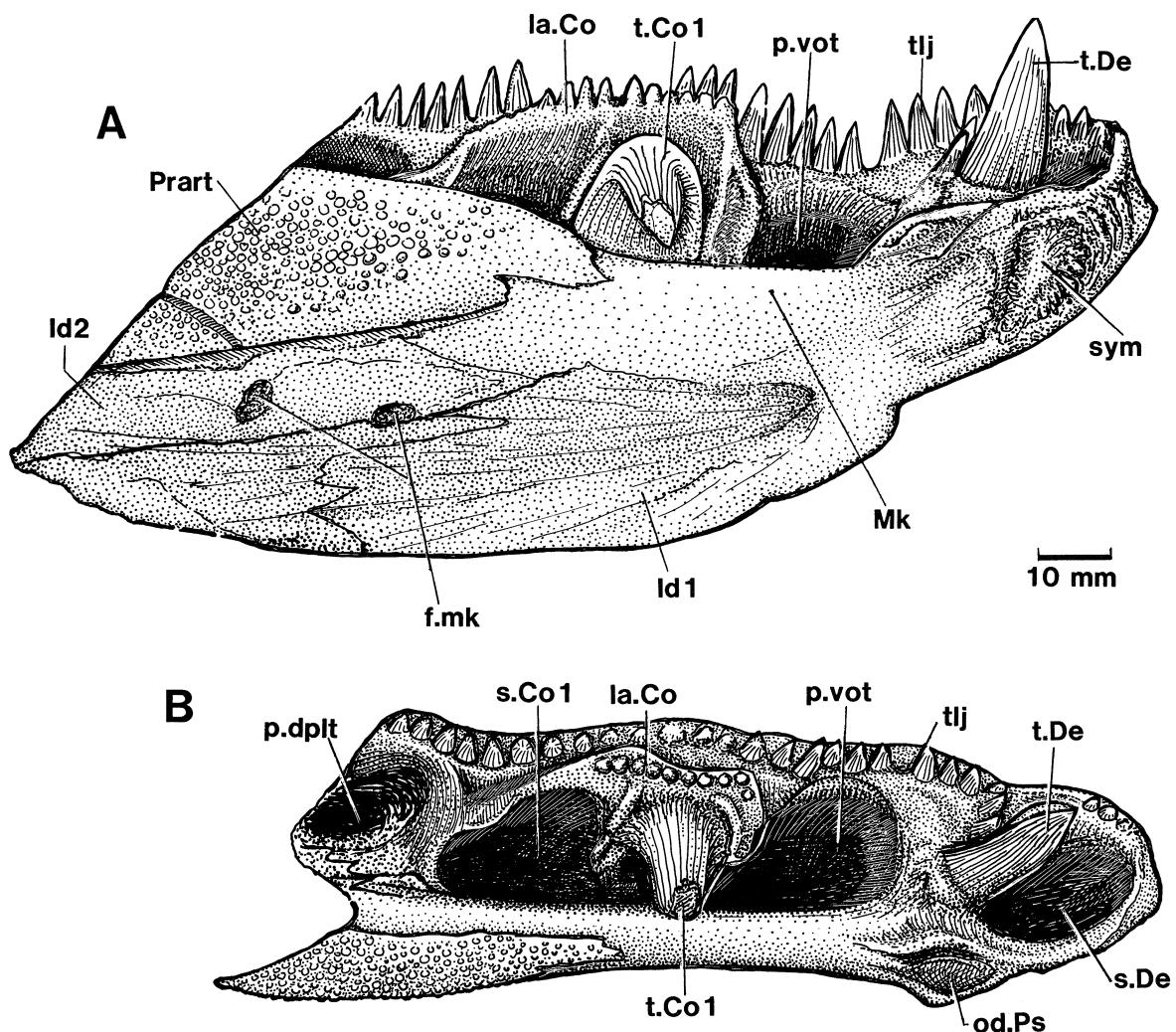


Fig.33. *Notorhizodon mackelveyi* n.gen., n.sp. Preserved anterior part of left lower jaw in mesial (A) and dorsal (B) views. Partly restored after the holotype (CPC 26404).

that of *Eusthenopteron*, with a strong paired processus connectens (pr.conn) projecting back over the notochordal pit (fo.nt, Fig.28B). However, the constriction of the ventral surface immediately posterior to the denticulate surface of the parasphenoid (possibly for attachment of the basicranial muscles; see Bjerring, 1968) is much more pronounced than in other described forms. The posterior preserved part of the parasphenoid (Fig.21A,D,E) is relatively broad, with a concave ventral surface in its posterior division, and in this respect differs considerably from the parasphenoids in eusthenopterid osteolepiforms (Jarvik, 1954; Vorobjeva, 1977). Thus the parasphenoid has a narrow rounded posterior margin in *Eusthenopteron*, *Eusthenodon*, and apparently *Glyptopomus* (Jarvik, 1950b: fig.6; 1952: fig.29). In CPC 26404 the tooth-bearing surface is irregular, with crowded tubercles sometimes elevated in small patches, or separated by spaces lacking tubercles. The buccohypophysial foramen (f.bhp, Fig.24B) is a small opening about 8 mm from the posterior margin of the ornamented region. At its anterior preserved end the parasphenoid is just over half the maximum width at the level of the buccohypophysial foramen. The lateral surface adjacent to the anterior part of the parasphenoid shows an irregular ridge, and a distinct groove for a nerve or vessel (a.pal, Fig.28A). The ridge may have carried a ligamentous attachment between the parasphenoid and the palatoquadrate complex, and the groove may have contained the palatine artery, as

Bjerring (1972: fig.5) has restored these structures in *Nesides*.

The middle region of the left side of the otoccipital (Fig.29) is preserved as an impression showing the two articular areas for the hyomandibula (hyd, hyv), the canal for the jugular vein (c.ju), the otic shelf (sh.ot), and adjacent structures. In ventral view the mesial margin of the bone is completely preserved (Fig.29B). This formed the border of the ventral fenestra of the neurocranium (fe.v, Fig.37A). This margin is convex anteriorly and concave posteriorly where it curves inwards as a projection enclosing the lateral occipital fissure anteromesially (f.occ.lat). The latter structure is represented by its dorsal boundary, which forms a deep notch with broken margins, and was presumably completed in cartilage around the vestibular fontanelle (v.font), as Jarvik has restored it in *Eusthenopteron* (Fig.37B). Posterodorsal to this is the anterior end of the groove for the jugular vein (gr.ju, Fig.29), which curves posteromesially to the posterior opening of the jugular canal, again as in *Eusthenopteron*. More dorsal parts of the otoccipital are not preserved in this region. The two articular facets for the head of the hyomandibula straddle the posterior opening of the jugular canal, and are similarly developed to *Eusthenopteron* or *Youngolepis* (Chang, 1982). The ventral articulation in posterior view (hyv, Fig.29C) is a roughly L-shaped depression devoid of smooth periosteal lining, which is notched for the jugular canal just as in *Eusthenopteron*.

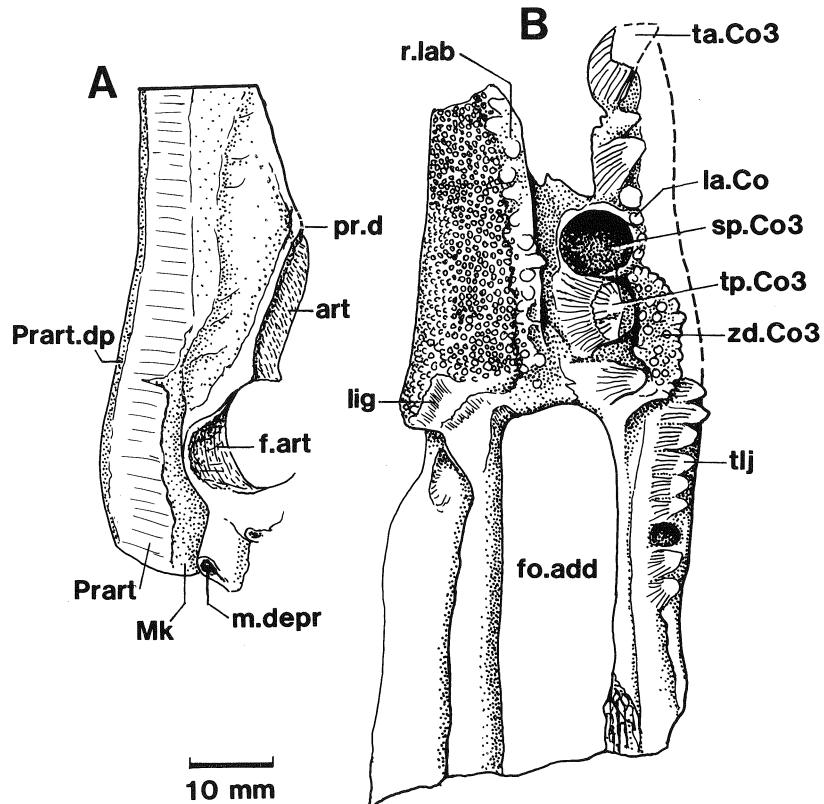


Fig.34. *Notorhizodon mackelveyi* n.gen., n.sp. A, preserved part of right mandibular joint of lower jaw in dorsal view (same specimen as in Fig.31B); B, detail of posterior part of dentition of right lower jaw in dorsal view. After the holotype (CPC 26404).

The dorsal articulation (hyd) lacks its dorsal margin, but was clearly a subcircular depression with a thickened lateral margin, as in *Eusthenopteron* and *Youngolepis*.

On the lateral surface (Fig.29A) the groove for the jugular vein (gr.ju) runs forward above the otic shelf (sh.ot), but without the jugular bridge of Jarvik's restoration. An irregular area at the anterior end of the shelf presumably corresponds to the articulation for the paratemporal process of the palatoquadrate in *Eusthenopteron* (art.ptm). The canal for the palatine branch of the facial nerve has a similar position to that of *Eusthenopteron* (c.pal). The anterior margin of the lateral wall curves forward and upward, but its dorsal part is incomplete, although there is no indication of an anterolateral bar as restored for *Eusthenopteron*. An oblique ridge behind a curved edge to the preserved periosteal lining (ri) is possibly the posterior border of the trigeminal nerve foramen (V). Two smaller openings farther back beneath the ossification centre of the intertemporal (ar.li2) may be openings for the r. ophthalmicus lateralis or r. oticus (?c.o.lat, ?c.ot), and posteriorly a groove (gr) on the lateral surface of the lateral commissure (lac), not recorded in *Eusthenopteron*, could have contained a posterior branch of the oticus lateralis, which has been restored in a similar position

in *Nesides* (Bjerring, 1972: fig.5).

The two parts of the neurocranium have been restored together in lateral and ventral views for comparison with *Eusthenopteron* in Figures 37 and 38. The position of the otoccipital in relation to the ethmosphenoid is fairly well constrained by the dermal overlap areas and contact faces between the intertemporal, frontal and dermosphenotic. These indicate that the anterior end of the otic shelf was approximately level with and lateral to the processus connectens of the ethmosphenoid. However, an articular surface for connection with the process is not evident, the preserved margin on the otoccipital being a complete discrete edge to the periosteal layer. The actual connection may therefore have been cartilaginous, and thus a somewhat different arrangement to that described for *Eusthenopteron*. Alignment of the anterior edge of the intertemporal against the edge of the contact face on the frontal gives a position for the preserved part of the otoccipital, with its mesial process reaching approximately to the midline, and a posterolateral orientation for the hyomandibular articular facet, much as in *Eusthenopteron* (Fig.37). An obvious difference however is the more transverse orientation of the jugular groove, perhaps indicating a narrower occipital region than in *Eusthenopteron*. The position of the

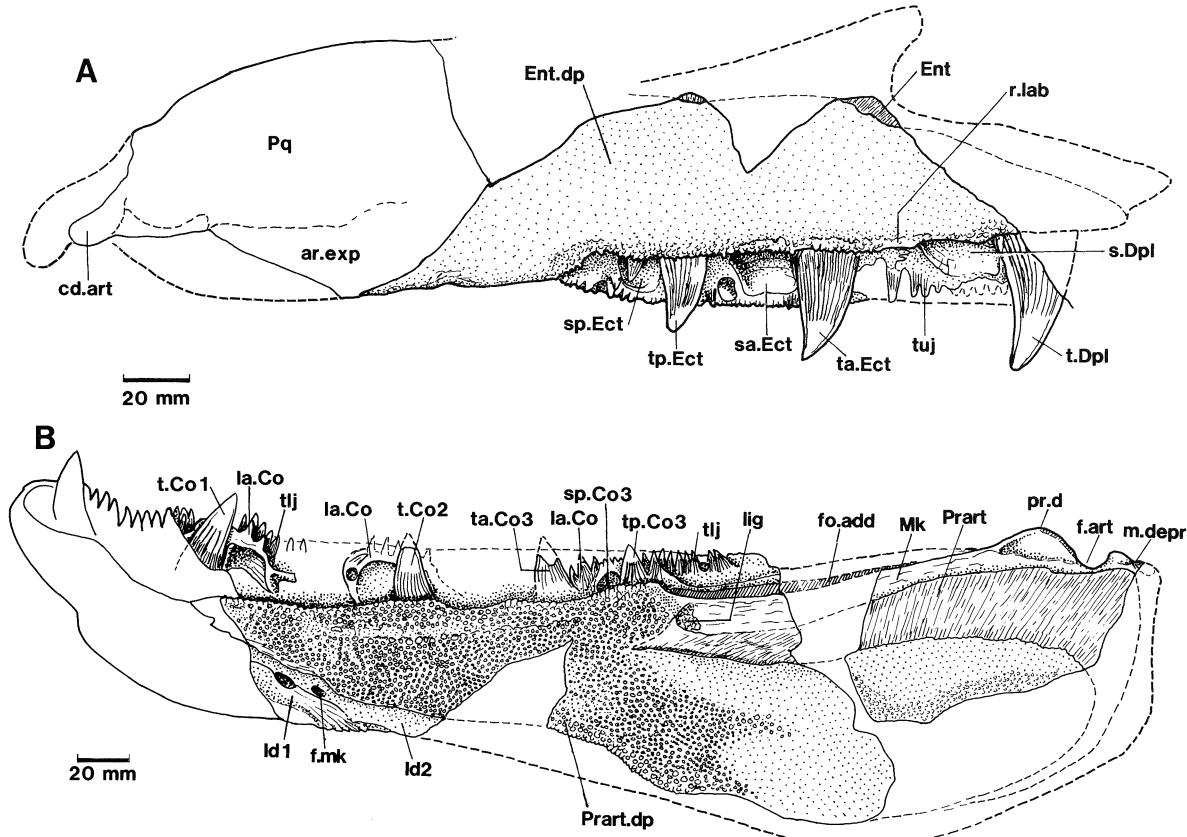


Fig.35. *Notorhizodon mackelveyi* n.gen., n.sp. A, mesial view of left palatoquadrate and attached dermal bones, with structures on lateral surface of posterior part restored after Figure 31A. B, restoration of right lower jaw in mesial view. After the holotype (CPC 26404).

hyomandibula (Fig.37A) in relation to the palatoquadrate (see below) has been restored after Jarvik's (1954: fig.25) restoration of *Eusthenopteron*.

In summary, the braincase of *Notorhizodon* as far as preserved agrees essentially with that of Osteoleipiformes as represented by *Eusthenopteron* (Figures 37B, 38A), for example in the shape and development of the hyomandibular articular areas, the large vestibular fontanelle, the position of the palatine nerve foramen, the jugular canal and lateral commissure, and on the ethmosphenoid the development of the connecting processes and notochordal pit (Fig.28B; cf. Jarvik, 1980a: fig.86B), and basipterygoid and suprapterygoid processes. Main differences are the shape of the parasphenoid, the strong development of the suborbital ledge, the horizontal orientation of the ridge leading

from the basipterygoid process, the configuration of the posterodorsal process of the ethmosphenoid, and its near vertical posterior face in lateral view, the absence of an anterolateral bar and jugular bridge, the orientation of the posterior jugular groove, and possibly the nature of the connection between the otoccipital and the processus connectens of the ethmosphenoid.

Palate and lower jaw. In comparison to the dermal bones of the skull, those of the palate and the remains of the lower jaw are much more informative. The palate (Fig.27A) is represented by impressions of the entopterygoid, ectopterygoid and dermopalatine from the left side, partly preserved in external view, with part of the inner surface of the entopterygoid attached to the lateral surface of the posterior part of the palatoquadrate,

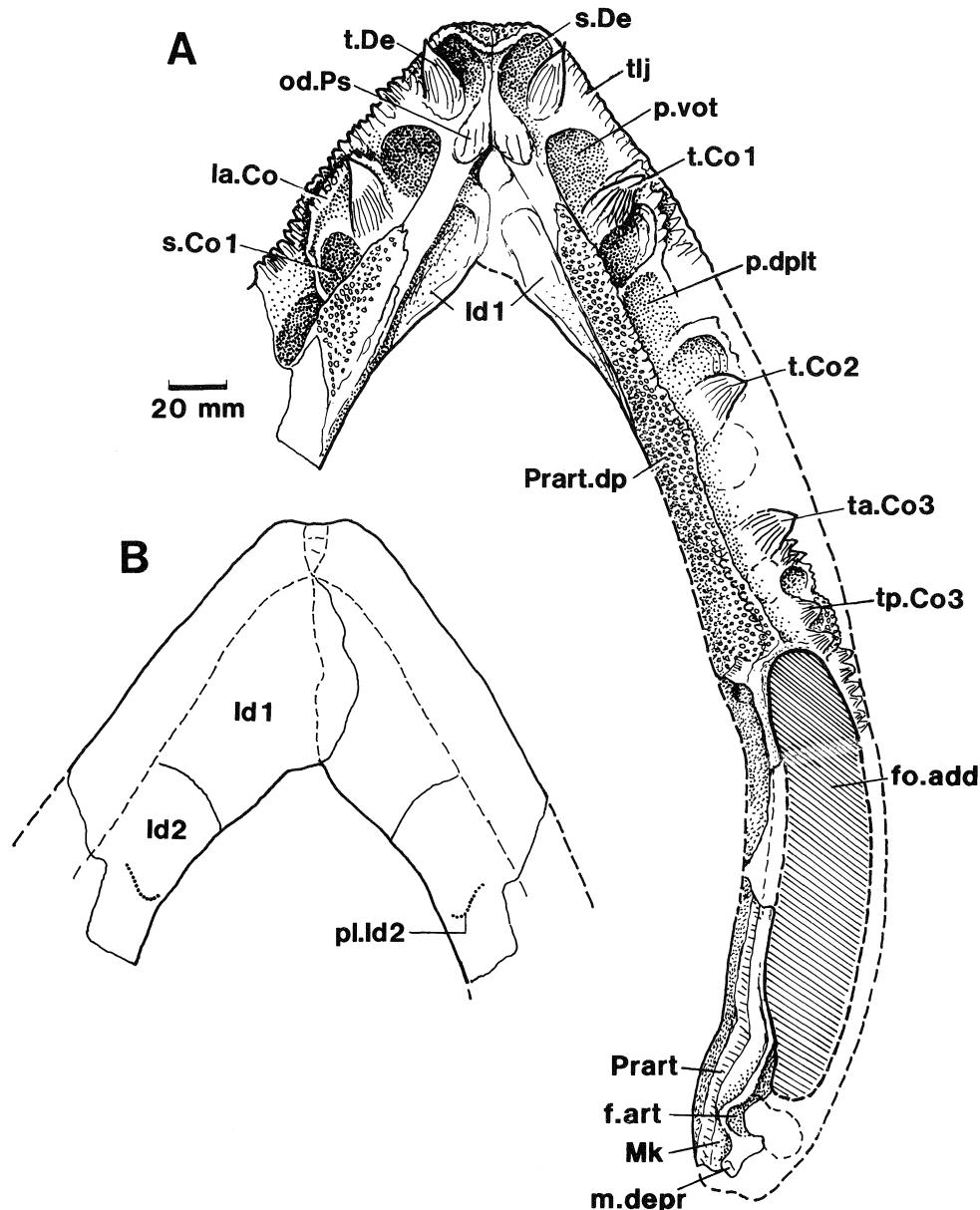


Fig.36. *Notorhizodon mackelveyi* n.gen., n.sp. Restoration of lower jaws. A, dorsal view; B, ventral view of preserved dermal bones. After the holotype (CPC 26404).

including an incomplete mandibular joint. The main impression passes off the edge of piece b anteriorly (Fig.30). Posteriorly the anterior margin of the adductor fossa formed by the entopterygoid is preserved on piece b (fo.add), with the inner surface of the entopterygoid and mandibular joint (cd.art) on piece g giving the length of the fossa (about 140 mm to the centre of the articular condyle).

The preserved dentition comprises three large tusks decreasing in height to the posterior, each with a large 'socket' immediately behind for the replacement tusk. The term 'pit' is used here to distinguish depressions between the tusks which received the tip of an opposing tusk with the jaws closed, from the replacement 'sockets' adjacent to each tusk. The arrangement of the tusks in

pairs in *Notorhizodon*, with one tusk of each pair generally missing, is the same as was fully described for *Eusthenopteron* by Jarvik (1944a: 37). The tusks were conical with anteroposterior 'cutting' edges, and thus the same type of tooth as occurs in *Rhizodus* and *Screbinodus* (Andrews, 1985: table 1). However, variation in tooth shape and section within species or within individuals is well known for rhipidistians (e.g., Jarvik, 1937, 1944; Andrews, 1985).

The anterior dermopalatine tusk was about 45 mm long (t.Dpl, Figs 30, 35A), and thus comparable in size to the largest tusks reported for *Eusthenodon* (Jarvik, 1952: 67). As in *Eusthenopteron* (Jarvik, 1944a: figs 12, 13) there were two tusks on the ectopterygoid (ta.Ect, tp.Ect), in contrast to porolepiforms (e.g., Jarvik, 1972:

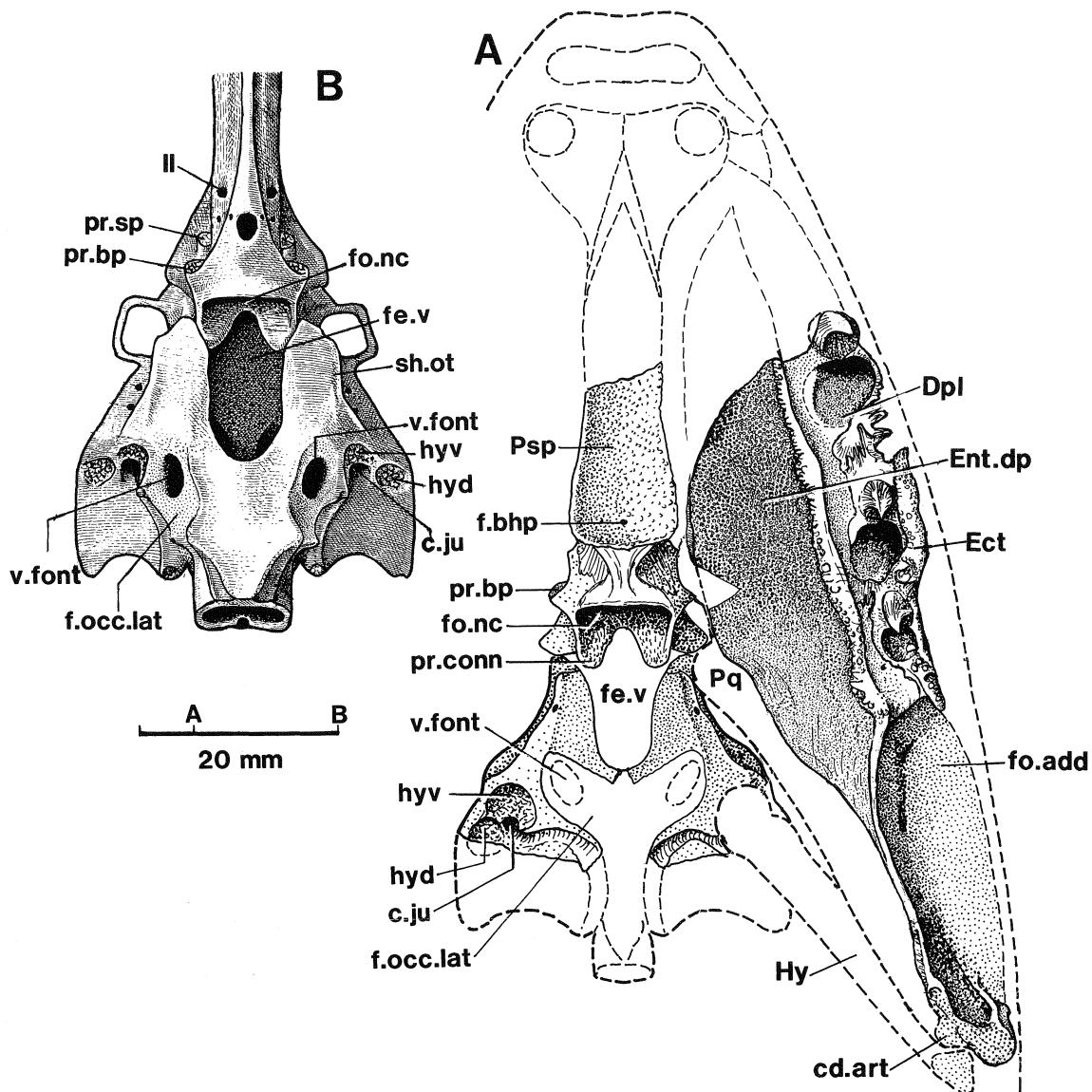


Fig.37. A, *Notorhizodon mackelveyi* n.gen., n.sp. Attempted restoration of the palate and braincase in ventral view. Anterior part of snout and palatoquadrate, and hyomandibula, restored after *Eusthenopteron* (Jarvik, 1954: fig.25); B, posterior part of braincase of *Eusthenopteron* in ventral view (modified after Jarvik, 1954: fig.1C).

fig.30), which have only one. The points on all tusks were smooth, but the basal two-thirds show primary and secondary grooves about 1 mm apart, corresponding to the infolding of the dentine (see below). The basal third of the tooth was covered with many fine longitudinal striations.

Three large teeth (up to 15 mm high and striated) and several smaller teeth are arranged on a curved ridge running laterally around the dermopalatine tusk and associated socket. The junction of the dermopalatine (Dpl, Fig.30) with the ectopterygoid (Ect) is clearly seen laterally, as an interdigitating suture adjacent to the largest tooth of the tooth row behind the dermopalatine socket (tuj). The mesial part of this suture has been lost. Lateral to the anterior tusk of the ectopterygoid an irregular broad tuberculate surface is seen (zd.Ect), with a more ordered tooth row along its mesial edge. Some of these are striated, and apparently formed a series with the much larger teeth on the dermopalatine (tuj, Figs 30, 35A). These irregular tubercles may correspond to the external and internal palatal rows of the marginal teeth described for *Eusthenopteron* (Jarvik, 1944a). This irregular arrangement may be primitive since it is also seen in upper and lower jaws of *Youngolepis* (Chang, 1991). A similar zone of irregular fine tubercles has been described on the coronoids of the lower jaw of a primitive megalichthyid from the Devonian of Turkey (Janvier, 1983: fig.9). Posterior to the second main socket of the ectopterygoid (in which the tip of an emerging tusk can be seen) is the impression of a larger tooth of the internal tooth row, which has a more lingual position than the other teeth. Behind this level the marginal series of teeth was reduced to a thin edge carrying a few scattered teeth. The lateral surface is preserved as a smooth overlapped area, presumably for

the maxilla. The posterior margin of the ectopterygoid is completely preserved, and projects posteriorly (pr.Ect) to form the anterior part of the lateral border of the adductor fossa, a condition suggested in Jarvik's restoration of *Glyptolepis* (1972: fig.30), and different from *Eusthenopteron*, where the maxilla forms the whole of the lateral border (Jarvik, 1944a).

The entopterygoid (Ent.dp, Fig.27A) was covered with irregular crowded blunt denticles. They were largest anteriorly and along a prominent labial ridge (r.lab, Fig.30), where they form short pointed teeth. The denticles become much finer mesially and posteromesially, and posteriorly grade into a smooth bone surface near the adductor fossa, essentially as in *Eusthenopteron*. Posteriorly the smooth lateral lamina of the entopterygoid (lv.Ent) forms the anterior border of the adductor fossa, in contrast to *Eusthenopteron* where a prominent mesial edge of the entopterygoid dental plate apparently curved around this margin. In *Notorhizodon* there is a mesial inflection in the denticulate lateral ridge of the entopterygoid dental plate just in front of the adductor fossa. The mesial margins of the entopterygoid dental plate are largely incomplete, but two small sections lacking ornament are presumed to be the peripheral parts of the entopterygoid itself, which were not covered by the dental plate (Ent, Fig.30), as in *Eusthenopteron* and other rhipidistians. These give some indication of the shape of the mesial edge of the bone. The suture between the entopterygoid and ectopterygoid is well preserved posteriorly, where it runs forward around the entopterygoid lateral lamina (lv.Ent), and the mesial edge of the posterior socket (sp.Ect), and forms an interdigitating suture behind the anterior socket of the ectopterygoid. Here it turns mesially to disappear beneath the entopterygoid dental plate. The anterior end

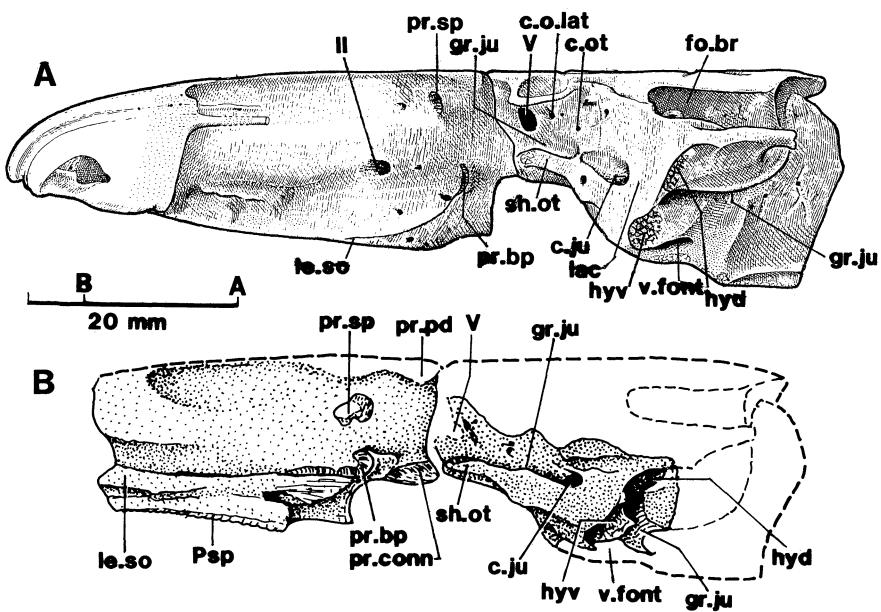


Fig.38. A, braincase of *Eusthenopteron* in left lateral view (modified after Jarvik, 1954: fig.1A); B, *Notorhizodon mackelveyi* n.gen., n.sp. Restoration of preserved parts of braincase in the holotype in left lateral view.

of the suture is missing, but it is clear that the lateral lamina of the entopterygoid was more deeply situated in the roof of a trough between the prominent lateral ridge of the entopterygoid dental plate (*r.lab*), and the tusks and tooth rows of the dermopalatine and

ectopterygoid. The form of the suture suggests that the lateral lamina of the entopterygoid (*lv.Ent*) actually overlapped the ectopterygoid, in contrast to other forms where the ectopterygoid had an external position (e.g., Jarvik, 1954: fig.6A). The surface of the entopterygoid

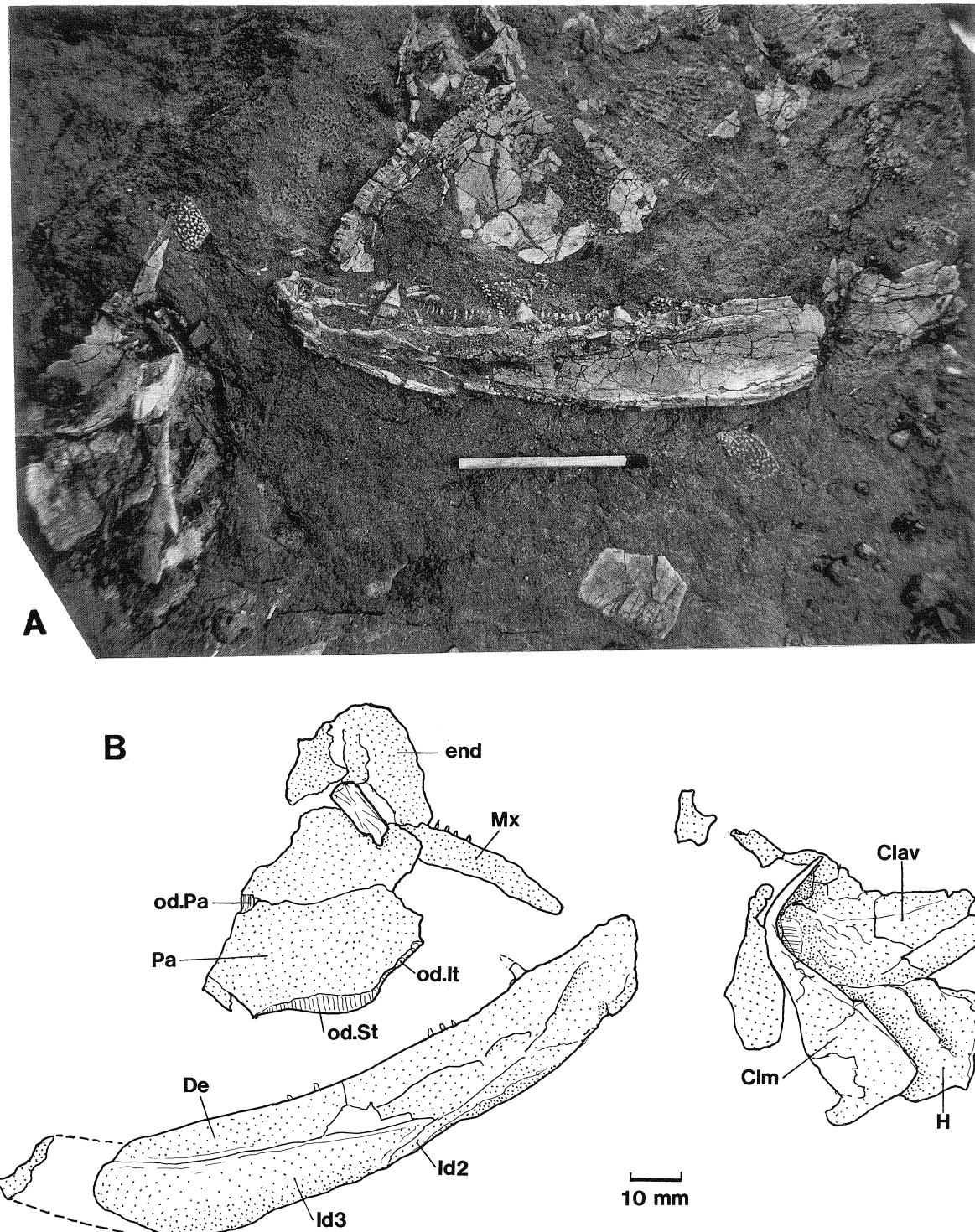


Fig.39. *Notorhizodon mackelveyi* n.gen., n.sp. Associated skull, shoulder girdle and right lower jaw from Mount Warren (AMF 54333). A, specimen before collection, mainly in visceral view; B, outline of associated elements in external view as collected (embedded in wax to preserve association).

dental plate is slightly concave laterally and transversely convex mesially. Just behind the broadest preserved part is a slight convexity followed by a shallow groove, also seen in *Eusthenopteron* (Jarvik, 1954: fig.16C), and interpreted in *Glyptolepis* as a groove which probably received the lateral side of the hypobranchial apparatus (Jarvik, 1972: fig.31).

The outer surface of the posterior part of the palatoquadrate is preserved with a clear ventral border, where it is overlapped ventrally by the smooth inner (lateral) surface of the entopterygoid (ar.exp, Fig.31A),

as in *Eusthenopteron* (Jarvik, 1980a: fig.107). As displayed by the latex cast, the posterodorsal margin is sharply inflected laterally (Pq.dm); although somewhat crushed it shows a notch in its lateral border (n). There is no indication of lateral rugosities as figured by Lelievre & Janvier (1986) on the quadrate of an indeterminate eusthenopterid from Morocco. Ventrally the articular area for the mandibular joint is well exposed, but incomplete mesially (Fig.30); the incomplete mesial side of the articular cotylus can be restored as a bilobed structure, broader than long, after its shape in other forms

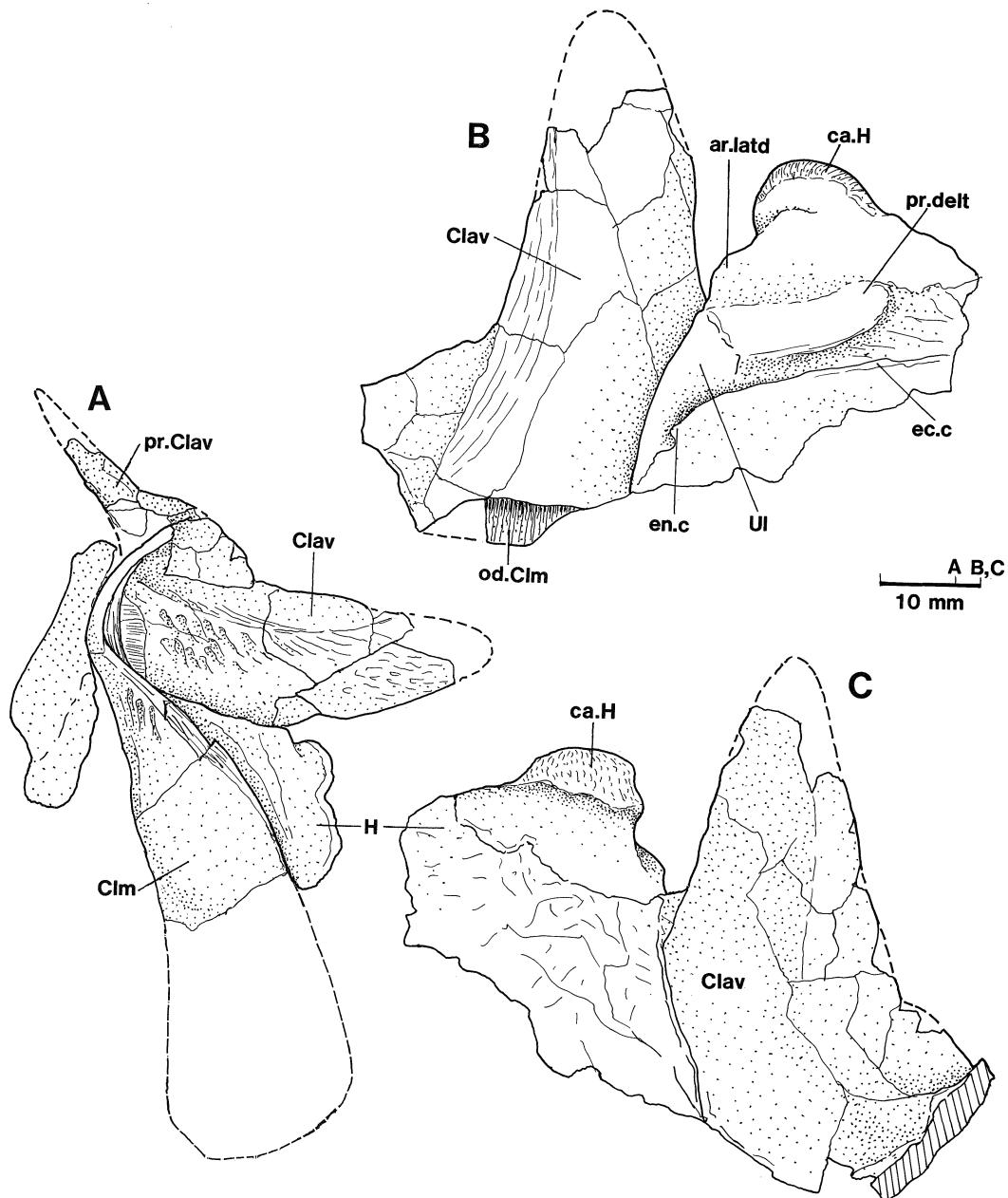


Fig.40. *Notorhizodon mackelveyi* n.gen., n.sp. AMF 54333. Remains of the shoulder girdle. A, association of elements, after removal from wax (cf. Fig.39B; restored dorsal lamina based on its shape in *Sauripterus* as figured by Andrews & Westoll, 1970b: fig.15); B, cleithrum removed to show right clavicle in external view and humerus in dorsal view; C, right clavicle in internal view and humerus in ventral view.

(e.g., Jarvik, 1954: fig.25; Lelievre & Janvier, 1986). The restored second condyle positioned anteromesial to the preserved one gives a corresponding shape to that of the articular fossa on the mandible preserved in other forms (e.g., Jarvik, 1980b: fig.97C; Lelievre & Janvier, 1986: fig.4A). There is in addition an anterior articular pit (art.dep), and a posterior rounded cotylus (cd.art), connected by a broadly convex strip (art), all showing the fine roughened to pustulose texture of an articular surface. The cotylus is about 15 mm across in an anteroposterior direction, which approximates in size to the articular fossa of the meckelian cartilage preserved for the opposite side (f.art, Fig.31B, about 14 mm across). The correspondence is only approximate because

only the lateral side of the assumed bilobed cotylus is preserved on the palatoquadrate, and only the mesial side of the assumed bilobed fossa is preserved on the meckelian cartilage. However, the mesial and lateral lobes of the cotylus were approximately the same size in *Eusthenopteron* (Jarvik, 1944a: fig.12). The convexity in front of the cotylus on the palatoquadrate (art, Fig.31A) presumably articulated against the articular pad (art, Figs 31B, 34A) on the lateral side of the process in front of the articular fossa of the meckelian cartilage.

In *Eusthenopteron* the mandibular joint was a simple bilobed articulation (Jarvik, 1944a: fig.12), but in *Notorhizodon* it was evidently more complex. The knob-like lateral articulation (cd.art) clearly corresponds to the

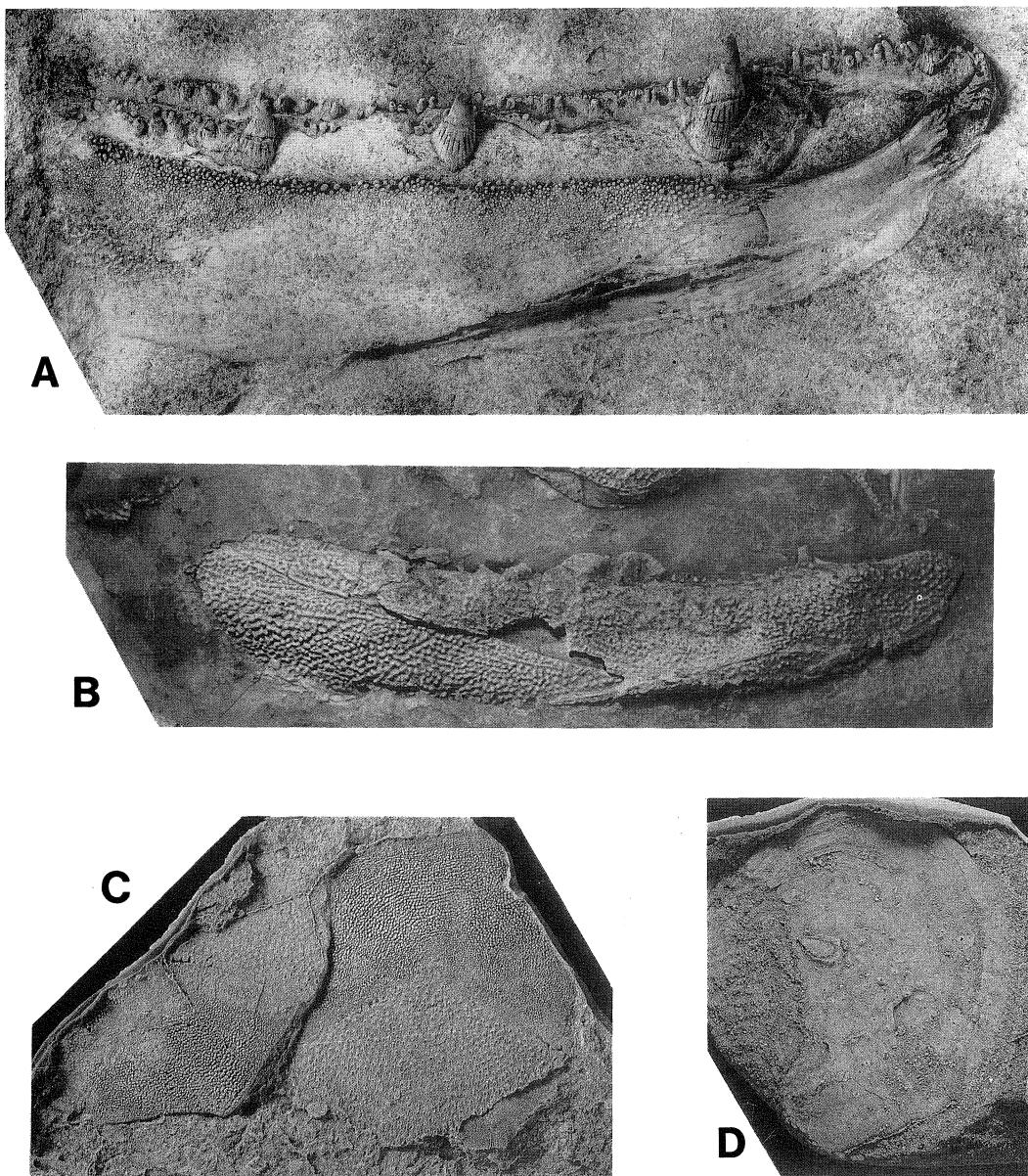


Fig.41. *Notorhizodon mackelveyi* n.gen., n.sp. A, left lower jaw from Mount Crean in mesial view (AMF 54327); B, right lower jaw from Mount Warren in external view (AMF 54333); C, two isolated scales in external view (CPC 27860); D, incomplete isolated scale (CPC 27861) in internal view (both from Mount Ritchie). A,C,D are latex casts whitened with ammonium chloride. (A x1; B x1; C,D x1.5)

same structure projecting from the thickened dorsal margin of the palatoquadrate in *Platycephalichthys* (Vorobjeva, 1962: pl.13), behind which the back end of the quadrate projects ventrally. The anterior pit (art.dep, Fig.30) is an additional articulation not previously described in rhipidistians, although the shape of the ventral edge of the quadrate in *Platycephalichthys* (Vorobjeva, 1962: pl.13) suggests that it may have been present also in that form.

The posterior part of the ventral margin of the entopterygoid is incomplete, and its externally exposed part has been restored after the shape in *Eusthenopteron* (ar.exp, Fig.35A). The articular condyle is positioned somewhat above the level of the ventral edge of the entopterygoid, as in *Platycephalichthys* (Vorobjeva, 1962),

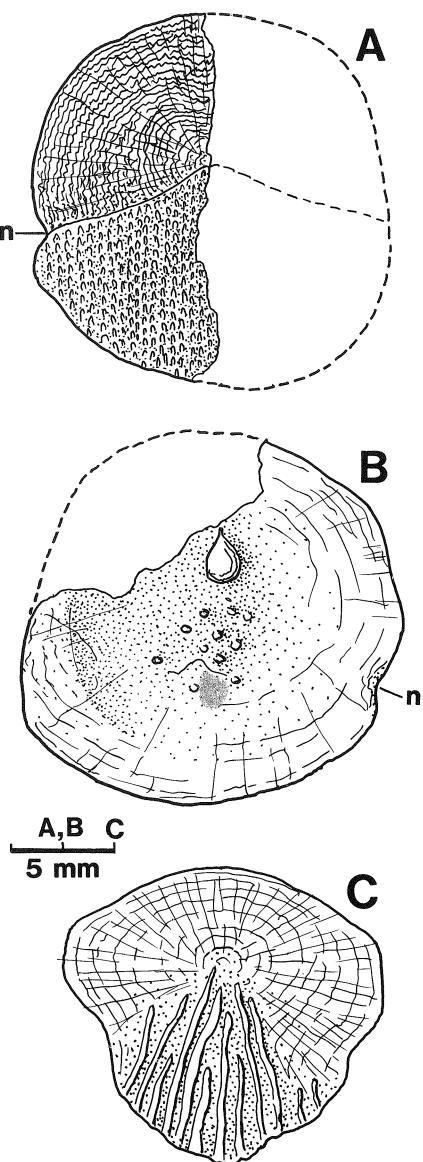


Fig.42. A,B. *Notorhizodon mackelveyi* n.gen., n.sp. Restoration of isolated scale in external (A) and internal (B) views (CPC 27861); C, eusthenopterid gen. et sp. indet. Isolated scale restored in external view (CPC 27858). All scales oriented with anterior to the top.

and in contrast to *Eusthenopteron*.

Significant portions of both rami of the lower jaw are preserved. The anterior region of the left jaw (Figs 27D, 32A) comprises parts of the first two infradentary plates in external view (Figs 32B), the anterior bone showing an extensive overlap area, presumably for the opposite bone (Fig.36B), and the posterior with a well-developed pitline (pl.Id₂). Their inner surfaces are shown in mesial view (Fig.33A) together with the anterior end of the prearticular, the dentary, the symphysial area of the meckelian bone, and the first coronoid. Two tusks are preserved, a dentary tusk (t.De), and that of the first coronoid (t.Co₁), the latter deformed in this individual with the point bent over towards the base of the tooth (Fig.32A). The large size of the dentary tusk is noteworthy. In *Platycephalichthys* it is also large (Vorobjeva, 1977: pl.14), but in *Litoptychus* it is much smaller than the coronoid tusks (Denison, 1951). In dorsal view four deep depressions are seen between the tusks (Fig.33B); that anterior to the dentary tusk must be the socket for its replacement tusk (s.De). The pit immediately behind (p.vot) received the vomerine tusk according to Jarvik's (1972: fig.49A) interpretation of *Eusthenodon*. Behind the first coronoid tusk is a deep socket for its replacement tusk. A special feature is the strongly developed crescentic tooth-bearing ridge which curves mesially around and in front of the tusk and behind the replacement socket (la.Co). This corresponds to the 'tooth-bearing coronoid lamina' of Jarvik (1972: figs 49, 50), but as illustrated there it is much less pronounced and lacks the strong mesial inflection. Similar ridges are possibly present in *Litoptychus* (Denison, 1951), but are much less prominent. A strong row of striated marginal dentary teeth up to 12 mm long forms the lateral preserved edge of this specimen (tlj). At the posterior preserved end is another pit which must have received the dermopalatine tusk (p.dpIt). Also evident in dorsal view is a roughened area mesial to the dentary tusk (od.Ps), which was clearly an attachment for a parasymphysial dental plate, just as in *Eusthenodon* (Jarvik, 1972: fig.49A; the 'predentary' of Vorobjeva, 1962), although the plate itself has been lost.

The right ramus of the lower jaw is exposed in mesial view from the level of the first coronoid tusk back to the anterior end of the adductor fossa (Fig.32C). The coronoid lamina is well exposed for the first coronoid, and partly preserved for the second, where the posterior socket contains the erupted tusk (Fig.35B). There is a considerable gap between the first and third coronoid tusks, where the dentary tooth row is not preserved. On the third coronoid only the base of the anterior tusk is preserved (ta.Co₃), but it was evidently of similar size to that of the second. The posterior tusk (tp.Co₃) is smaller (basal diameter about 12 mm). Behind this tusk is a smaller tusk right on the margin of the adductor fossa, and in front is a deep replacement socket (sp.Co₃), bounded by a lateral tooth-bearing lamina (la.Co), anterior to which is another large striated tooth sitting just behind the anterior tusk of the third coronoid. Posteriorly the tooth-bearing lamina is expanded laterally

to the posterior tusk as a broad ridge carrying irregular tubercles in at least four longitudinal rows (zd.Co3, Fig.34B), which closely resembles the irregular zone of denticles on the ectopterygoid. Lateral to this again is the dentary tooth row, well preserved beside the adductor fossa, where eight striated teeth and one socket form a closely spaced row (tlj).

On the mesial surface the prearticular dental plate is fractured (Fig.32C), but its boundaries are clear, as is the suture between the first and second infradentaries, which is somewhat behind the level of the first coronoid tusk, the same position as seen on the left jaw. Two large foramina (f.mk, Fig.35B), also seen on the left jaw (Fig.33A), open within and just above the suture between the first two infradentaries, as in other forms (e.g., Jarvik, 1972: figs 47A, 49E; 1980a: fig.125B). In some other forms (e.g., *Panderichthys*; Vorobjeva, 1962: pl.18 fig.3b) these foramina are much more pronounced. Vorobjeva (1977: fig.16B) interprets them as having contained veins. Farther back the infradentaries are not preserved, the preserved ventral margin being the ventral border of the prearticular dental plate (Prart.dp, Fig.35B). This margin is irregular, with coarse denticles ventrally, where it is of maximum depth. Posteriorly the preserved surface is largely devoid of ornament near the ventral and dorsal margins, but with a few scattered large denticles extending back in the middle of the bone, which are replaced by a shagreen of very fine denticles near the posterior preserved margin. A similar pattern of denticulation is seen in the lower jaw described by Lelievre & Janvier (1986). The dorsal margin of the prearticular is also irregular, forming a ridge of crowded coarse denticles (r.lab, Fig.34B), which presumably engaged with the corresponding ridge on the entopterygoid (Fig.30) when the mouth closed. This ridge terminates at the anterior end of the adductor fossa. On the mesial surface is a roughened area, possibly for ligamentous attachment (lig), although a corresponding structure has not been reported in other rhipidistians. Beneath is a distinct bone margin which must be the dorsal margin of the prearticular dental plate (Prart.dp, Fig.35B). The anterior course of the suture is not certain because of fracturing, but it appears to turn back and upward at a sharp angle to pass around the anterior rim of the ligamentous attachment area. Above it another margin, delineated by a low ridge running back beneath the ligamentous attachment, must be the upper edge of the prearticular itself (Prart). In both *Eusthenopteron* and *Holoptychius* the denticulate part of the prearticular apparently extended dorsally right to the adductor fossa (Jarvik, 1972: fig.47; 1980a: fig.125), although the corresponding part is smooth in the jaw described by Lelievre & Janvier (1986). In *Eusthenopteron* the meckelian cartilage is exposed only posteriorly, in the region of the mandibular joint.

An impression of the posterior part of the right lower jaw is preserved on a separate specimen (piece d), which shows a dorsal articular fossa (f.art, Figs 31B, 34A) behind an elevated margin, clearly part of the mandibular joint, with a posterior process bearing an attachment

surface for muscles or ligaments (m.depr). That the preserved surface faced into the buccal cavity is shown by the very fine ornament, similar to that on the posteromesial region of the entopterygoid, and the posterior preserved part of the prearticular on the previous specimen. This specimen is presumed to represent the missing posterior end of the previous specimen (Fig.35B), but this raises several problems in attempting to restore the lower jaw. The ornament on the posterior preserved part of the prearticular dental plate in the previous specimen is very faint, although more pronounced toward the posterior margin. But on the second specimen (Fig.31B) the ornament is strongly developed. However, the features which confirm its identification include the well-developed articular fossa (f.art, Fig.31B), the small posteromesial process (m.depr) identified in *Eusthenopteron* as an insertion for the depressor mandibulae muscle (Jarvik, 1980a: fig.125B), and distinct margins for two bone layers overlapping the meckelian cartilage. The unornamented flange with radiating striations is the prearticular (Prart). It is exposed only along the posteroventral margin in *Eusthenopteron*, but extends up to the edge of the adductor fossa in some other eusthenopterids, and *Holoptychius* (Jarvik, 1972: fig.47A; Lelievre & Janvier, 1986: fig.3B). As in other forms it is covered by a dental plate with a surface of fine denticles and tubercles (Prart.dp). The strong dorsal elevation in front of the articular fossa (pr.d), not recorded in other rhipidistians, presumably fitted against the anterior articular depression on the palatoquadrate (art.dep, Fig.31A), since the process carries a roughened articular surface on its dorsal and lateral faces. The whole articulation is more dorsally placed than in the lower jaw figured by Lelievre & Janvier (1986).

The blocks containing the two right lower jaw impressions do not fit together, but assuming they do come from the same jaw, the size of the missing portion must have been small (Fig.35B), estimating from the known length of the adductor fossa for the upper jaw. Experimentation with latex casts shows that the orientation of the ornamented surface of piece d only approaches that of the main jaw impression if the dorsal edge of the adductor fossa is aligned with a strong mesial curvature. This has been assumed in the restoration in dorsal view (Fig.36).

In the restoration (Fig.35B) the anterior part of the left and the main part of the right jaw ramus have been combined using the common position of the suture between infradentaries and associated foramina. As restored the length from the anterior end of the adductor fossa to the articular fossa for the jaw joint is about 160 mm. This exceeds the corresponding measurement for the upper jaw (140 mm), but the distance cannot be reduced without overlapping the specimens. Either the adductor fossa was slightly larger in the lower than the upper jaw, or else the two portions of the right lower jaw come from different individuals, a possibility which cannot be excluded, but for which there is no strong supporting evidence in the associated material. Using the

provisional restoration of Fig.35B therefore, the total length of the lower jaw is estimated to have been about 430 mm, of which adductor fossa length comprised about 37%. In *Eusthenopteron* the adductor fossa was about 30% of lower jaw length (Jarvik, 1944a: fig.11). In *Notorhizodon* the maximum depth of the prearticular (about 95 mm) is at the posterior preserved end of the anterior part of the right ramus, and well behind the anterior edge of the adductor fossa. In contrast, *Eusthenopteron* has the maximum depth of the prearticular about level with the anterior edge of the adductor fossa. This difference in proportion is consistent with the adductor fossa being proportionately longer in *Notorhizodon*. In proportion (between 5 and 6 times as long as deep) the restored jaw of *Notorhizodon* is comparable to *Eusthenodon* (Jarvik, 1952: fig.27B), whereas in *Eusthenopteron* (Jarvik, 1944a: fig.11) the lower jaw was more slender (6.3 times as long as deep).

Although they come from opposite sides, the latex casts of upper and lower jaws could be approximately overlapped to gain an idea of jaw engagement. Of the three preserved tusks in the upper jaw, the dermopalatine tusk fits closely behind the replacement socket for the first coronoid, and the two ectopterygoid tusks fitted behind the two main tusks of the second coronoid, the normal arrangement as seen in *Eusthenopteron* (Jarvik, 1980a). The pit on the left lower jaw between the first coronoid tusk and the dentary tusk must have received the vomerine tusk, as noted above.

With the symphyseal area of the preserved anterior part of the left jaw ramus aligned vertically the two jaws can be restored together (Fig.36), to indicate a similar rather elongate snout to that of *Eusthenopteron* (e.g., Jarvik, 1954), compared to such forms as *Megalichthys* (Jarvik, 1966: fig.17), or various porolepiforms such as *Glyptolepis* (Jarvik, 1972), which have a much broader snout. In external view the large overlap area on the first infradentary is positioned close to the midline, which implies either median symphyseal bones (but in *Eusthenopteron* these separate the dentaries of each side, not the infradentary; Jarvik, 1944a), or an extensive overlap of the right first infradentary onto the left, as shown in Figure 36B. This is the reverse of the condition illustrated for *Eusthenopteron* (Jarvik, 1944a: fig.10C), where the left infradentary overlaps the right.

This restoration of the two jaw rami has been combined with the restoration of the preserved portion of the left palate against the parasphenoid to give an idea of outline of the snout region (Fig.37B). The position of the vomerine tusks on the palate can be approximated from the corresponding pits on the lower jaw, and other details of the anterior region indicated by dashed lines (outlines of premaxilla and anterior palatal recess) are modelled on restorations of *Eusthenopteron* by Jarvik (1954: fig.25). The length of the lower jaw as restored fixes the position of the mandibular joint relative to the vomerine tusks, and requires that the anterior margin of the upper adductor fossa lies at the level of the middle of the length of the basicranial fenestra (fe.v). This is slightly farther

back than in *Eusthenopteron*, and places the first ectopterygoid tusk just anterior to the level of the buccohypophysial foramen, whereas in *Eusthenopteron* the posterior tusk is in this position. The unornamented margins of the entopterygoid can be assumed to approximate the mesial edge of the palatoquadrate. Casts of the two specimens of *Notorhizodon* can be placed together such that the denticulate surfaces of the parasphenoid and entopterygoid form a transversely concave palatal surface, with the unornamented mesial border of the entopterygoid in a deeper position, presumably embedded in soft tissue as previously restored (see Jarvik, 1954: fig.27C). By combining the restoration of the otoccipital against the ethmosphenoid as discussed above, an approximate position for the hyomandibula is given which agrees well with the relative positions of this element against the palatoquadrate in *Eusthenopteron* (Jarvik, 1954: figs 22, 25).

The bone of the holotype was not well preserved, and the teeth too deeply embedded in the matrix to be studied histologically, although a displaced tusk in the replacement socket of the dermopalatine (Fig.27A) shows an impression of the broken base of a tooth showing the remains of the polyplacodont pattern.

Other material. Of the other specimens referred to *Notorhizodon*, AMF 54333 includes a portion of the parietal shield, some fragmentary endocranial remains, part of the maxilla, the right lower jaw, and remains of the cleithrum, clavicle, and pectoral fin skeleton (Fig.39B). This specimen was first identified from photographs by Ritchie (see McKelvey *et al.*, 1972: fig.4) where the dentary and three coronoid tusks are clearly seen (Fig.39A). It is considerably smaller than the holotype (preserved length of jaw 132 mm).

The parietal shield (Fig.39B) is incomplete on all margins except the right lateral, which shows an overlap area for the supratemporal posteriorly (od.St), and an oblique somewhat broken anterior edge with remains of an overlap for the intertemporal (od.It). The median re-entrant overlap between parietals is clear posteriorly (od.Pa), but the pitlines are obscured by the coarse ornament. In front of the parietal shield is a short section of the left maxilla 36 mm long with a row of marginal teeth visible on the inner surface, which apart from its smaller size closely resembles that of the holotype (Fig.23A,B).

The lower jaw is crushed, but provides some information not available from the holotype. The inner surface shows a small dentary tusk, about half the size of the coronoid tusks. There are two tusks on the first and one on the second coronoid. The tusks have about 16 grooves, and are laterally compressed with cutting edges. The teeth of the marginal tooth row are also grooved, and the prearticular dental plate has a labial ridge of coarser tubercles, all features observed in the holotype. The coronoid laminae are obscured by crushing, and the symphyseal area is poorly preserved, but in view of the other similarities they also were probably developed as in the holotype. In external view the

dentary (De, Fig.39B) and an overlap on the anterior infradentaries can be seen, but any pitlines are obscured by the surface coating, and the ventral margin of the infradentaries is now broken, although it was evidently more complete in the specimen before collection (Fig.39A).

The remains of the dermal shoulder girdle are somewhat crushed, but the following structures can be made out (Fig.40). The ventral lamina of the right clavicle is gently curved both rostrocaudally and transversely. The anterior margin is missing, and the length of the ascending process could only be determined from some incomplete fragments preserved in association (pr.Clav, Fig.40A). As far as preserved this process appears to resemble that of osteolepiforms, and lacks the inrolled form characteristic of rhizodontids as described by Andrews & Westoll (1970b). The ventral lamina of the clavicle narrows anteriorly as in other forms. Its posteromesial margin is broken, but approximates the edge of the bone, which is gently convex. There is no sign of an overlap for the interclavicle. The exposed mesial part of the posterior margin is convex. There is ridged ornament ventrally, and on the ventral part of the postbranchial lamina, but the dorsal part and ascending process are smooth. The most significant feature is a posterior overlap area on the clavicle which received the cleithrum (od.Clm, Fig.40B), this being part of the special overlap arrangement characteristic of rhizodontids as described by Andrews & Westoll (1970b) and Andrews (1985). However, the overlap area has a more transverse orientation compared to *Rhizodus hibberti* (Andrews & Westoll, 1970b: fig.9), and the strong posteromesial process on the clavicle of that form appears to be missing. Again, in this respect *Notorhizodon* seems to more closely resemble *Eusthenopteron*, this being perhaps the primitive condition for this character.

The right cleithrum (Clm, Fig.40A) has a broken dorsal margin, but the complete posterior and anterior margins of the dorsal lamina indicate that it was broader dorsally (at least 20 mm across) than ventrally, where it is inflected into the ventral surface. A comparison can be made with the shoulder girdle and fin of *Sauripterus* illustrated by Andrews & Westoll (1970b: fig.15), in which the humerus has much the same shape and size (at the scale of their figure) as in AMF 54333, and the preserved part of the cleithrum has the same width. This indicates that if the cleithrum was of proportionate size, up to half of its dorsal lamina may be missing. Compared to *Eusthenopteron* (e.g., Andrews & Westoll, 1970a: fig.1) the preserved part of the dorsal lamina has a more narrow waisted form, and we infer that it was probably expanded dorsally as in other rhizodontids, although this needs to be confirmed with new material. The ventral surface is sharply twisted around the clavicle and at least 25 mm long, but it seems, insofar as preserved, that the ventral lamina lacked the broad expansion described for other rhizodontids, including *Barameda* (Andrews & Westoll, 1970b; Long, 1989). The external surface is sculptured with ridged ornament similar to that on the clavicle.

The humerus is incompletely preserved stuck on the clavicle (H, Fig.40). The head of the humerus (ca.H) forms a large rounded articular surface of unfinished bone with a slightly constricted neck, as in other rhizodontids (Andrews & Westoll, 1970b; Long, 1989), and in contrast to *Eusthenopteron* (Andrews & Westoll, 1970a). It compares fairly well with the humerus of *Sauripterus* rather than the more elongate element of *Strepsodus* (Andrews & Westoll, 1970b: fig.15, pl.12). The dorsal surface is slightly convex, with prominent protuberances corresponding to the deltoid and supinator processes of other forms (pr.delt). These run diagonally onto the entepicondyle (en.c). A curved ridge may represent the ectepicondyle (ec.c). Comparison with *Sauripterus* suggests that the ulna may be included (Ul), but this region is fractured and poorly preserved, and may be part of a large entepicondyle as in other forms, including *Barameda* (Long, 1989).

In ventral view (Fig.40C) the proximal part including the articular head of the humerus is well preserved, but distally it is badly fractured. Overall the surface is concave, and it differs clearly from *Barameda* and the restoration of *Sauripterus* in the expanded mesial margin, although in *Barameda* this is probably incomplete. Andrews & Westoll (1970b) noted the short broad form of the humerus in *Sauripterus*, with its strong preaxial expansion, as strikingly different to the humerus of *Strepsodus* and *Rhizodus*. Like *Sauripterus* (Andrews & Westoll, 1970b: fig.16), the humerus as preserved in *Notorhizodon* is incomplete distally, but its similar preserved shape suggests that it was also short and broad. This might have been its primitive form in rhizodontids.

AMF 54327 from Mount Crean (Fig.41A) is the impression of a left lower jaw in mesial view, previously figured by Ritchie (1971a,b). It shows the dentary and three coronoid tusks. The first coronoid tusk is the largest. The small dentary tusk may not be fully erupted, as it is much larger on the holotype. Estimated total length is about 210 mm. Apart from its smaller size, and the proportionately greater space between the first and second coronoid tusks, this jaw agrees with that of the holotype in such characteristic features as the crescentic coronoid laminae, and the anterior notch and expanded ventral lamina of the first infradentary. AMF 55781 from Mount Metschel is an incomplete external impression some 165 mm long which came from a lower jaw probably at least twice the length of the previous specimen. The suture between the dentary and infradentaries is clearly seen, and the ornament is very similar to that on the lower jaw of the holotype.

Various impressions with straight margins, thought originally to be large scales, have a coarse ornament as on the dermal bones of the holotype (Fig.32D). These are now interpreted as small bones from the head, the example illustrated from Mount Metschel being possibly from the branchiostegal series, as suggested by its rhomboid shape.

Impressions of large isolated scales from the type locality (but not necessarily belonging to the holotype)

are attributed to *Notorhizodon* because of their size, and resemblance to the scales of *?Strepsodus* (Andrews, 1985) and other rhizodontids. An example is CPC 27861, a large round scale with extensive overlap areas about 38 mm across, which is preserved in part and counterpart. The inner surface (Fig.42B) shows a teardrop-shaped boss with a rounded posterior end over the ossification centre, and scattered tubercles just as described by Andrews (1985: fig.5H) for the large Foulden rhizodontid, and figured from Turkey (erroneously as an external view) by Janvier *et al.* (1984: fig.9C). The margin is notched (n) between the exposed and overlapped portions of the scale. The external ornament of scattered tubercles is not well preserved, but good detail is shown by another specimen (CPC 27860). The tubercles are evenly spaced (Fig.41C), but not clearly aligned in rows, in contrast to '*Strepsodus*' *portlocki* figured by Andrews (1985). A special feature is the central depression on each tubercle, with the elevated part forming a u-shaped ridge open posteriorly (Fig.42A).

rhizodontiform gen. et sp. indet.

ALLIGATOR PEAK (locality 17)

Fig.43B

'large scales and teeth of crossopterygians ...similar to ...
Holopychius' Ritchie, 1972: 352.

Material. AMF 55502, 544, CPC 27865, 866.

Horizon. Unit 32, section A1 of Askin *et al.* (1971), about 8 m below the top of the formation, corresponding to MS236 in section 6 of Barrett & Webb (1973).

Description. AMF 55502 is a large scale or bone with coarse anastomosing ridged ornament and an overlap area. An associated large tusk (AMF 55544) is comparable in size and all preserved features to those on the holotype of *Notorhizodon*. This scale is much more coarsely ornamented than those referred above to *Notorhizodon*, and it is not clear whether all such large scale-like elements can be attributed to small skull bones of this genus, or whether a second form is present with a body squamation of coarsely sculptured scales. At present there is insufficient evidence to demonstrate that *Notorhizodon* occurs in the phyllolepid zone, for which this is the type locality, so these remains are treated as indeterminate.

CPC 27866 is an incomplete and poorly preserved jaw fragment which shows a small area of coarse ornament, and in view of associated remains is tentatively regarded as rhizodontid. CPC 27865 (Fig.43B) is an incomplete cleithrum, probably from the left side, with an ornament of coarse anastomosing flat-topped ridges separated by deep grooves, often undercut on the anterior side. The ornament is much coarser than on the cleithrum referred

above to *Notorhizodon* (AMF 54333), but is reminiscent of the specimen from Alligator Peak figured by White (1968) as a right gular (see below), and of the ornament on the shoulder girdle of *Beelarongia* (Long, 1987a). In the former the ornament is less strongly developed, and in the latter it is restricted to the central part of the bone. The affinities of this specimen are very uncertain, but in view of the more common rhizodont remains from

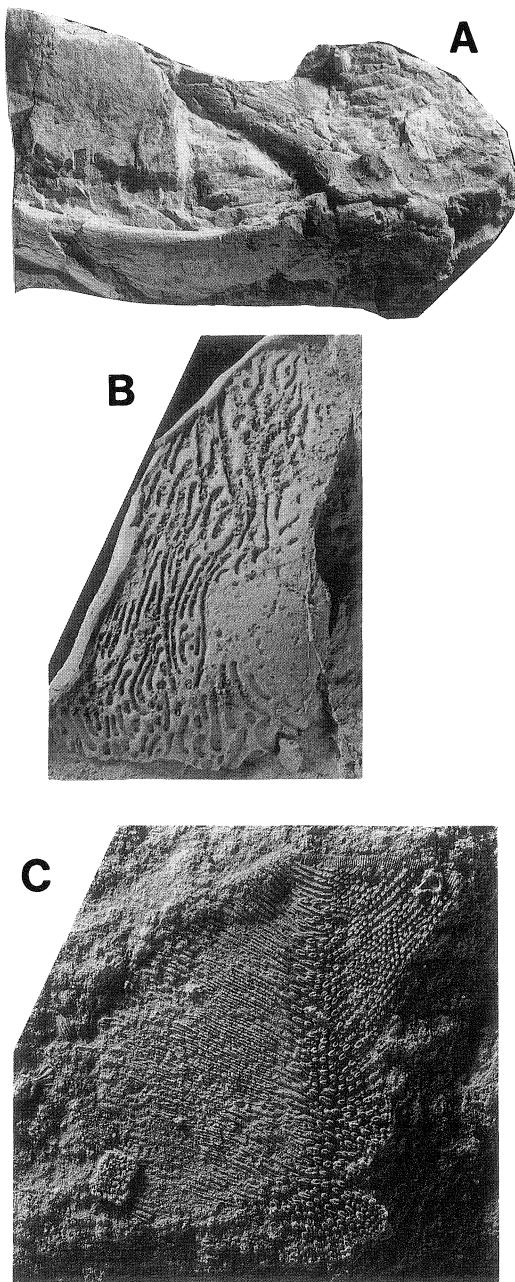


Fig.43. A. eusthenopterid gen. et sp. indet. Anterior part of left lower jaw from Mount Crean in mesial view (AMF 54332); B, rhizodontid gen. et sp. indet. Incomplete left cleithrum from Alligator Peak in ventrolateral view (CPC 27865); C, porolepiform gen. et sp. indet. Incomplete scale from Mount Fleming; external view, assumed posterior to the left (AF 166B). B,C, latex casts whitened with ammonium chloride. (A,B x1.5; C x6)

the upper parts of the sequence, it is provisionally included here.

ALLIGATOR PEAK, EASTERN SPUR (locality 20)

Gyroptychius ? antarcticus (A.S.W.) (pars), ?rhizodont tooth
White, 1968: 8, 23.

Material. BMP 49168, GS 7395/10.

Horizon. The upper horizon (MS2, at least 60 m above the base of the Aztec Siltstone) collected by Gunn & Warren (1962), probably equivalent to the fossiliferous horizon 70 m above the base in section 4 of Barrett & Webb (1973).

Description. BMP 49168 figured by White (1968: pl.1 fig.7) as a right gular plate is preserved as an elongate impression about 36 mm long by 19 mm wide. The irregular ornament of vermicular ridges and grooves is reminiscent of that on the cleithrum of *Strepsodus* (e.g., BMP 57805, 59743), but differs in the flattened tops of the ridges. The preserved portion has longitudinal curvature and is unlikely to be a gular plate. It could be a eusthenopterid left subopercular, but is too incomplete for positive determination. The specimen of a possible rhizodont tooth (GS 7395/10) was not located in the collection of the NZGS.

Order Porolepiformes

porolepiform gen. et sp. indet.

Fig.43C

'glyptolepid-like' scale' Young, 1991: 545.

Material. AF 168B, an impression of an isolated scale.

Locality. The north-facing slope near the end of the east ridge of Mount Fleming (locality 4, Fig.2).

Horizon. According to M.A. Bradshaw (personal communication) this specimen came from unit 17, section H6 of Barrett & Webb (1973), some 62 m above the base of the Aztec Siltstone.

Description. AF 168B is an impression of a broken scale some 11 mm across in maximum dimension, preserved immediately adjacent to the thelodont scales and *Bothriolepis* plates illustrated by Young (1988: pl.1 figs 4,5). Orientation is uncertain, but it seems that less than half the scale is preserved. As oriented in Figure 43C it shows three zones of different surface ornamentation. Posteriorly is a zone of closely spaced subparallel ridges representing the exposed part of the scale. In front is a zone of radiating rows of small denticles, each pointed backwards with an peripherally-facing depressed surface, corresponding exactly to the

early generation dentine tubercles described by Orvig (1957) in the central part of the overlapped portion in various porolepiform and onychodontid scales. At the dorsal edge is a narrow zone devoid of denticles but showing fine radiating striations of the outer overlapped zone.

Remarks. This is clearly a porolepiform scale belonging to a fish presumably closely related to the Euramerican form *Glyptolepis*, which has similar scales (e.g., Jarvik, 1950a: figs 32F,G, 33C), but with coarser ridges. Coarser still are the ridges on scales of *Holoptychius* and *Litoptychus*, while the scales of *Laccognathus* differ in having tubercles rather than ridges on the exposed part. Glyptolepid scales have also been reported from the Bunga Beds on the south coast of New South Wales (Fergusson *et al.*, 1979), and from the Frasnian Mount Howitt fauna of eastern Victoria (JAL, personal observation). The latter are rather similar to the scale described here. A small sample of the Bunga Beds scales differs from the Antarctic scale by their less regular and more widely spaced ornamental ridges, and much less extensive zone of early generation denticles.

Discussion

Phylogenetic Relationships

Two (e.g., Jarvik, 1980a, 1985) or three (e.g., Andrews & Westoll, 1970a,b; Andrews, 1973, 1985) major groups have been considered to constitute the rhipidistian fishes (porolepiforms, osteolepiforms, and rhizodontiforms). However, their inter-relationships in the context of osteichthyan inter-relationships generally (Fig.47A) have been subject to many different opinions, particularly over the last decade (e.g., Rosen *et al.*, 1981; Gardiner, 1984; Long, 1985a,b, 1989, in press; Holmes, 1985; Maisey, 1986; Forey, 1987; Schultze, 1987; Panchen & Smithson, 1987; Ahlberg, 1989). The difficulties in placing a fossil group like the rhipidistians in a phylogenetic scheme is exacerbated by the fact that there is little agreement about how the major living groups of fishes (actinistians, actinopterygians, chondrichthyans, dipnoans) are inter-related to each other, and to tetrapods (see Young, in press: fig.7). These uncertainties mean that the evidence on which a phylogeny must be based (observed character distributions) is difficult to assess in the absence of a clear outgroup to establish character polarity. In addition there is disagreement about the interpretation or homology of morphological features used as synapomorphies, while for many poorly known rhipidistian taxa, including some described above, the state of such characters is completely unknown.

Given these problems, we are not in the position to propose here a well-supported new scheme of osteichthyan and/or rhipidistian inter-relationships. Nor does our new evidence provide strong support for some existing scheme. Rather, we have incorporated some of

the new taxa described above in a scheme modified from earlier proposals (Fig.47B), on which new characters or character combinations as expressed in our new taxa may be organised in a parsimonious way. We have indicated homoplasies in these characters on the tree, but a rigorous parsimony analysis has not been attempted, because for many taxa a large number of characters is unknown. A data matrix of characters used (Table 2) summarises these gaps in knowledge, as a guide for future investigation. Our new scheme (Fig.47B) is put forward as a phylogenetic framework to make explicit the character distributions and morphological interpretations on which provisional placement of new taxa in the preceding systematic account is based. The characters used are mostly taken from the literature, where they have previously been accepted as synapomorphies defining major groups, even though in many cases character polarity was not considered in detail. We therefore preface our phylogenetic discussion with comments on character polarity for each of the 38 synapomorphies used in Figure 47B, based primarily on outgroup comparison with the groups incorporated in the phylogenetic scheme of Figure 47A.

A1 (lateral extrascapulars overlap median extrascapular). Primitive actinopterygians lack a median extrascapular. There is uncertainty about the number of extrascapulars in dipnoans (e.g., Gardiner, 1984; Schultze, 1987), but they have a median bone, which overlaps the lateral bones adjacent to it (Miles, 1977), as is also the case in the actinian *Rhabdoderma* (Forey, 1981), and in porolepiforms. This is therefore regarded as the primitive state. Tetrapods have lost extrascapulars so this character is inapplicable (X, Table 2).

A2 (polyplodont teeth). The histology of the teeth is not known for canowindrids. The assumption that the polyplodont condition is derived is based on increasing complexity in a transformation series from the simple folded plicidentine of *Youngolepis* and *Powichthys*, to the more complexly folded dendrodont condition in porolepiforms, to the still more extensive folding in osteolepiforms and tetrapods.

A3 (seven bones in cheek, with large squamosal). This has been regarded as the derived state, but supporting evidence is weak. *Ichthyostega* also has seven bones, while porolepiforms and dipnoans have more, and actinopterygians less, so outgroup comparison provides no clear indication of character polarity.

A4 (deltoid and supinator processes on humerus). Ahlberg (1989) noted that the ectepicondyle and entepicondyle on the humerus are probable synapomorphies of sarcopterygian fishes generally, rather than shared derived characters of osteolepiforms and tetrapods as proposed by Panchen & Smithson (1987). However, the elaboration of the dorsal process into foraminated deltoid and supinator processes is a similarity seen only in rhizodontids, osteolepiforms, and tetrapods, but outgroup comparison does not clearly indicate whether this is a synapomorphy or symplesiomorphy

(Ahlberg, 1989: 153). For the purposes of this analysis we have provisionally assumed the former.

A5 (humerus with rounded caput humeri). The fact that the convex part of the shoulder articulation is on the proximal pectoral fin element (humerus) has been put forward as a synapomorphy of osteolepiforms and tetrapods (e.g., Schultze, 1987). In various outgroups the reverse articulation is seen (convex condyle on the scapulocoracoid), which can be assumed to be primitive. This condition is known in porolepiforms (e.g., *Glyptolepis*; Ahlberg, 1989: fig.3), actinians and dipnoans (e.g., Schultze, 1987: fig.8; the condition illustrated for the modern lungfish *Neoceratodus* is also seen in the Devonian *Chirodipterus*, as evidenced by WAM 90.12.135 from Gogo). There is no single proximal element equivalent to the humerus in actinopterygians. Because rhizodontiforms also share the specialised condition (e.g., Andrews & Westoll, 1970b) this character emerges as a synapomorphy of all the groups included on the scheme of Figure 47B.

A6 (caput humeri fits into groove on scapulocoracoid). This character is clearly functionally related to A5 just discussed, and has the same distribution. By comparison with the outgroups on Figure 47A where this aspect is known (porolepiforms, actinians, dipnoans), character A6 can be assumed to represent the derived condition. Again, new evidence from a Gogo specimen of *Chirodipterus* (WAM 90.12.135) confirms that the condition in the modern *Neoceratodus* is primitive for the group as a whole, as is also the case with the articulation between the pelvic fin and girdle (Young *et al.*, 1989).

B1 (large basal scutes at origins of fins). This feature was first noted by Andrews (1973: 161) as a specialisation of osteolepiforms, and was proposed by Long (1985c) as an osteolepiform synapomorphy. It is not known outside this group, and is assumed to be derived on the grounds of parsimony.

B2 (one pair of external nares). Two pairs of external nares can be assumed primitive, since this is the condition in non-rhipidistian fishes (e.g., actinopterygians, actinians, chondrichthyans, placoderms).

B3 (large dermal anocleithrum separating post-temporal from cleithrum). The 'large externally exposed anocleithrum' previously proposed as a synapomorphy (Long, 1987a: 850) may be symplesiomorphic for osteichthyans (Rosen *et al.*, 1981; Forey, 1987). In other sarcopterygian groups, such as porolepiforms, the anocleithrum may be a small bone, not subdermal, but covered completely by body scales (Ahlberg, 1989: 124). The condition for onychodontiforms is not known, and in primitive dipnoans the anocleithrum is subdermal, and articulates dorsally with a process projecting from the I bone (e.g., *Chirodipterus* from Gogo, Western Australia). However, an anocleithrum enlarged to form a dermal bone firmly sutured to and

externally separating the post-temporal from the cleithrum is a condition unique to osteolepiforms. As expressed here, this synapomorphy implies that the subdermal anocleithrum arose more than once in other groups, by independent loss of its small dermal component. We suggest that the primitive condition is shown by the postcleithrum of actinopterygians, which is situated behind, not between, the post-temporal and cleithrum (see Jarvik, 1944b).

C1 (similar size of the lachrymal, jugal, and postorbital bones in the cheek). The jugal is elongate in porolepiforms and ichthyostegids, whereas in actinistians, onychodontids and actinopterygians it has quite a different configuration to that of rhipidistians, with a very extensive orbital margin (e.g., Rosen *et al.*, 1981: figs 43, 44). In dipnoans, the short and broad bone 5 carries the corresponding sensory canal junction (e.g., Campbell & Barwick, 1987: fig.13). The restoration of the rhizodontid cheek by Long (1989: fig.5) shows an elongate jugal, but it is apparently short and broad in *?Strepsodus* (Andrews, 1985: fig.8). Thus evidence from outgroup comparison regarding the polarity of this character is at best equivocal. It seems that elongation of the jugal in early tetrapods (and panderichthyids; Schultze, 1987) may be related to the changes in skull roof proportions. We have provisionally retained character C1 as a synapomorphy on Figure 47B, even though we also propose that the elongate jugal is a synapomorphy of canowindrids (character E3). Demonstrating osteolepiform monophyly with convincing synapomorphies at this node remains a problem.

C2 (equilateral shape of extrascapulars). This is difficult to assess by an outgroup criterion, since *Porolepis* also has an equilateral median extrascapular, whereas rhizodontids and canowindrids have a similar triangular shape. The arrangement in *Megalichthys* is poorly known, but in the single specimen illustrated by Andrews & Westoll (1970b: fig.2) the median bone seems to have a narrow anterior margin, as is apparently also the case in a specimen of *Ectosteorhachis nitidus* figured by Thomson (1975: fig.7). A triangular median extrascapular was also described for *Thysanolepis* by Vorobjeva (1977). In other osteichthyan groups the median bone has a broad anterior margin in *Diplocercides*, lungfish (the A bone), and *Rhabdoderma*. In onychodontids the median extrascapular may be absent (*Strunius*, Jessen, 1966), or be of equal width anteriorly to the lateral extrascapulars (*Onychodus* sp., Andrews, 1973). Within the sarcopterygians this character is highly variable, but within familial or subfamilial groups the included taxa have either broad anterior margins on the median extrascapular (Osteolepidinae, Gyroptychinae, Glyptopominae, Eusthenopteridae) or an anteriorly narrow median extrascapular (Canowindridae, Megalichthyidae, Thysanolepididae, Lamprotolepididae). For the present it is assumed that the former condition is derived, but because of uncertainties about the distribution of the character the evidence is not considered sufficient to break up the polytomy at this

node (Fig.47B).

C3 (loss of extratemporal). The presence of an extratemporal in the skull table has been regarded as primitive for osteolepiforms because it tends to occur in older, and be absent in younger taxa (palaeontological argument), and it is also present in porolepiforms as an outgroup. However, among other osteichthyan groups the bone is only known in onychodontids (Fig.46) so the outgroup argument is not strongly supported. In any case its distribution among rhipidistian taxa involves homoplasy in the scheme of Figure 47B (see below).

D1 (vomers broader than long, with short median suture). In the rhizodontiform *Barameda* the vomer is a small ovoid bone with a median suture, and may be relatively broad, but its morphology as far as known is clearly different from that of *Megalichthys*. Although the evidence is not strong, we judge this ‘intermediate’ condition of the vomer, between that of *Eusthenopteron* (with a long posterior process) and that of *Megalichthys* (with a pronounced mesial process), to be the primitive condition, since it resembles that seen in such outgroups as actinopterygians (e.g., Gardiner, 1984), and *Diabolepis* (e.g., Chang & Yu, 1984).

D2 (posterior tectal bone enclosing posterior half of naris). Amongst those groups with one external naris, the simpler osteolepid condition exemplified by *Eusthenopteron* (e.g., Jarvik, 1966: fig.14) is assumed to be primitive, and the U-shaped posterior tectal of *Megalichthys* advanced.

D3 (posterior nasals notched into frontals). The more simple outline of the frontals seen in osteolepids (e.g., Jarvik, 1948), rhizodontids (e.g., Long, 1989) and other osteichthyan groups (see Fig.46) is assumed to be the primitive condition.

D4 (loss of pineal foramen). The pineal foramen is primitively present in all osteichthyan groups, and some others with dermal roofing bones, such as placoderms, so this widespread condition is assumed to be primitive.

D5 (short broad parasphenoid). This character depends to some extent on the overall breadth of the snout, but the parasphenoid is much more elongate in *Eusthenopteron* than in some other forms regarded as outgroups (e.g., *Diabolepis*, Chang & Yu, 1984; actinopterygians, Gardiner, 1984), and this ‘intermediate’ condition is provisionally interpreted as primitive.

D6 (slit-like nares). This feature in *Megalichthys* and *Ectosteorhachis* (Jarvik, 1966: fig.14) distinguishes these taxa from other groups, in which a circular or subcircular naris is typical.

D7 (interpremaxillary bone or process on premaxilla). This feature is not known in other groups, and may be assumed to be a specialisation of *Megalichthys* and *Ectosteorhachis*.

D8 (broad, flat snout). Many other groups have broad-snouted taxa (e.g., porolepiforms, *Koharalepis*),

but in the narrow phylogenetic context applicable here this character distinguishes *Megalichthys* and *Ectosteorhachis* from other osteolepiform genera within the Eusthenopteridae and Osteolepididae.

D9 (enlarged sigmoid dentary tusk). This resemblance between two poorly known taxa (*Vorobjevaia* and *Thysanolepis*) is assumed advanced within the phylogenetic context of Fig.47B. Other characters exclude *Vorobjevaia* n.gen. from the rhizodontids, in which a large sigmoid dentary tusk may also be developed (see above), while the strong sigmoid tusks of onychodontids are carried on a separate tooth-whorl at the front of the dentary (e.g., Jessen, 1966).

E1 (skull very broad across the extratemporals). There is an obvious similarity in the shape of the parietal shield of the three canowindrid genera, which is not seen in other osteichthyan groups (Figs 45, 46),

and cannot therefore be readily interpreted as a symplesiomorphy.

E2 (parietal, intertemporal and supratemporal probably fused). Since sutures between these bones are not evident in *Canowindra*, which lacks cosmine, we assume this to be the case also in the two cosmoid genera included in the canowindrids. No other osteichthyan group shows this fusion, so the absence of these bones cannot be parsimoniously interpreted as primitive.

E3 (jugal at least twice as long as high). This similarity in the canowindrid cheek (Fig.44) may be related to the presence of additional bones separating the postorbital from the orbital margin (character E4). As noted above the jugal is also elongate in porolepiforms and ichthyostegids. For porolepiforms a similar explanation may apply (there is an extra 'postspiracular' bone in the cheek), and elongation of the jugal in early tetrapods may be correlated with skull roof proportions. Outgroup analysis does not clearly indicate the polarity of this character, which for the present we regard as independently derived, at least in canowindrids and tetrapods, which are widely separated phylogenetically on the evidence of many other characters.

E4 (postorbital bone excluded from orbital margin). The postorbital bone reaches the orbital margin in other osteichthyan groups, including porolepiforms, dipnoans, actinopterygians, actinistians, and tetrapods (e.g., Rosen *et al.*, 1981: figs 43, 44; Long 1985c: fig.8). By outgroup comparison therefore this is regarded as the primitive osteichthyan condition. Rosen *et al.* (1981: 226) have suggested that the additional bones of the cheek in porolepiforms and dipnoans are autapomorphies. However in *Koharalepis* it is the extra dermosphenotic behind the orbit which excludes the postorbital from the orbital margin. Together with the smaller anteriorly placed orbits, the arrangement is suggestive of *Youngolepis* or *Powichthys* (Fig.45C), which are interpreted as stem group rhipidistians by Chang (1991). This suggests an alternative hypothesis, that these additional bones are primitive, implying therefore that the canowindrid cheek pattern is also primitive. However, this has other unparsimonious consequences on our preferred scheme of relationships (Fig.47B), so we retain the interpretation indicated by outgroup analysis.

F1 (round scales lacking cosmine). It is widely accepted that within the phylogeny of both the osteolepiforms and the porolepiforms cosmine cover to the dermal bones has been independently lost, together with the change from rhomboid to round scales (e.g., Orvig, 1957; Schultze, 1977). That cosmoid scales in rhipidistians are primitive is based both on stratigraphic grounds (they occur in Upper Silurian-Lower Devonian strata, whereas round scales first appear in the Middle Devonian; e.g., the eusthenopterid *Tritychopterus*), and by outgroup comparison with dipnoans (round scales first occur in the Late Devonian, and scales of the earliest known lungfish are very similar to rhipidistian cosmoid

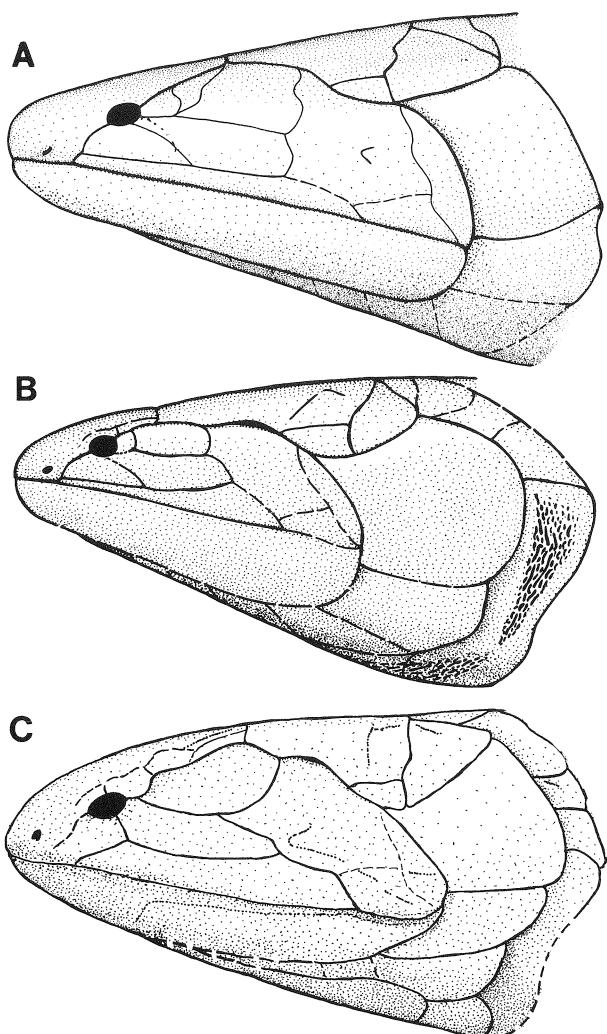


Fig.44. Restoration of the head of three canowindrids in left lateral view. A, *Canowindra grossi* Thomson (after Long, 1985a); B, *Beelarongia patriciae* Long (modified after Long, 1987a); C, *Koharalepis jarviki* n.gen., n.sp.

scales; Denison, 1968). Within lungfishes cosmine is also lost independently several times according to the phylogeny of Miles (1977). However, cosmine is not known in actinistians, onychodontids or actinopterygians, so in the context of the scheme of osteichthyan inter-relationships given in Figure 47A the outgroup argument is not strong.

F2 (reverse overlap of cleithrum onto clavicle). This condition of the ventral laminae of these bones is not seen in other osteichthyan groups, which generally exhibit a simple overlap of the anterior onto the posterior element (e.g., porolepiforms, Jarvik, 1972; actinistians, Forey, 1981; actinopterygians, Gardiner, 1984). The clavicle also overlaps the cleithrum ventrally in most

Palaeozoic dipnoans where known (e.g., Campbell & Barwick, 1987: fig.11), and the more complex interlocking connection seen in *Uranolophus* (Campbell & Barwick, 1989: fig.25) is regarded as a specialisation.

F3 (parietal ossification centre in anterior position). The polarity of this character is potentially resolvable using ontogenetic data, but the analysis by Schultz (1984) of juvenile *Eusthenopteron* does not give a clear answer on this point. The posterior elongation of the parietal in rhizodontids illustrated by Andrews (1985: fig.7) resembles the condition in some other groups (e.g., actinistians, onychodontids; Fig.46A,D), and could therefore be primitive, but in the context of the scheme of osteichthyan inter-relationships

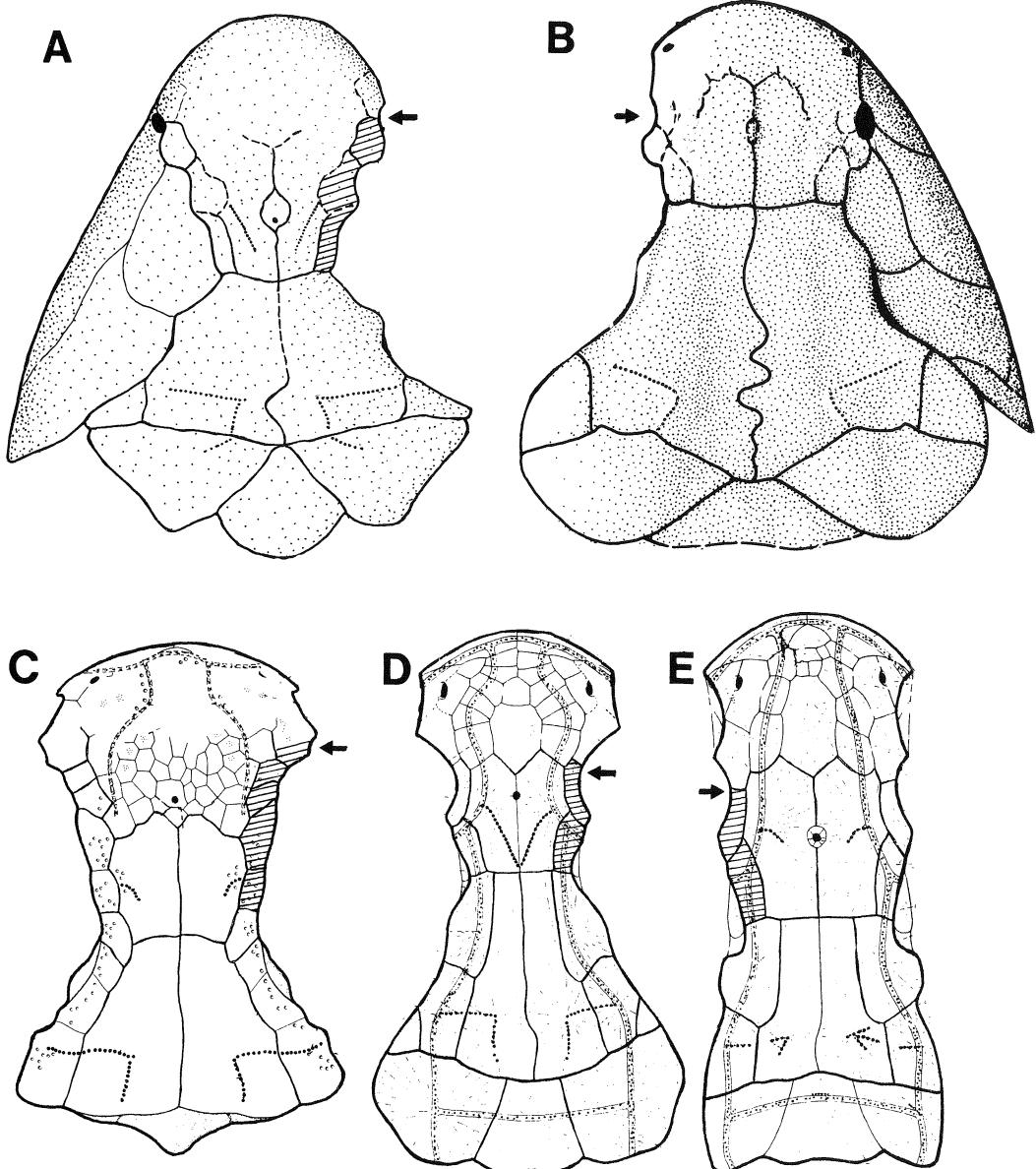


Fig.45. A,B, restoration of the kanowindrid head and cheek in dorsal view; A, *Koharalepis jarviki* n.gen., n.sp; B, *Beelarongia patrichae* Long (modified after Long, 1987a). C-E. Skull roof in dorsal view; C, *Powichthys*; D, *Osteolepis*; E, *Eusthenopteron* (C after Jessen, 1980; D,E, after Jarvik, 1980a). Marginal paired bones behind the orbit of the fronto-ethmoidal shield cross-hatched.

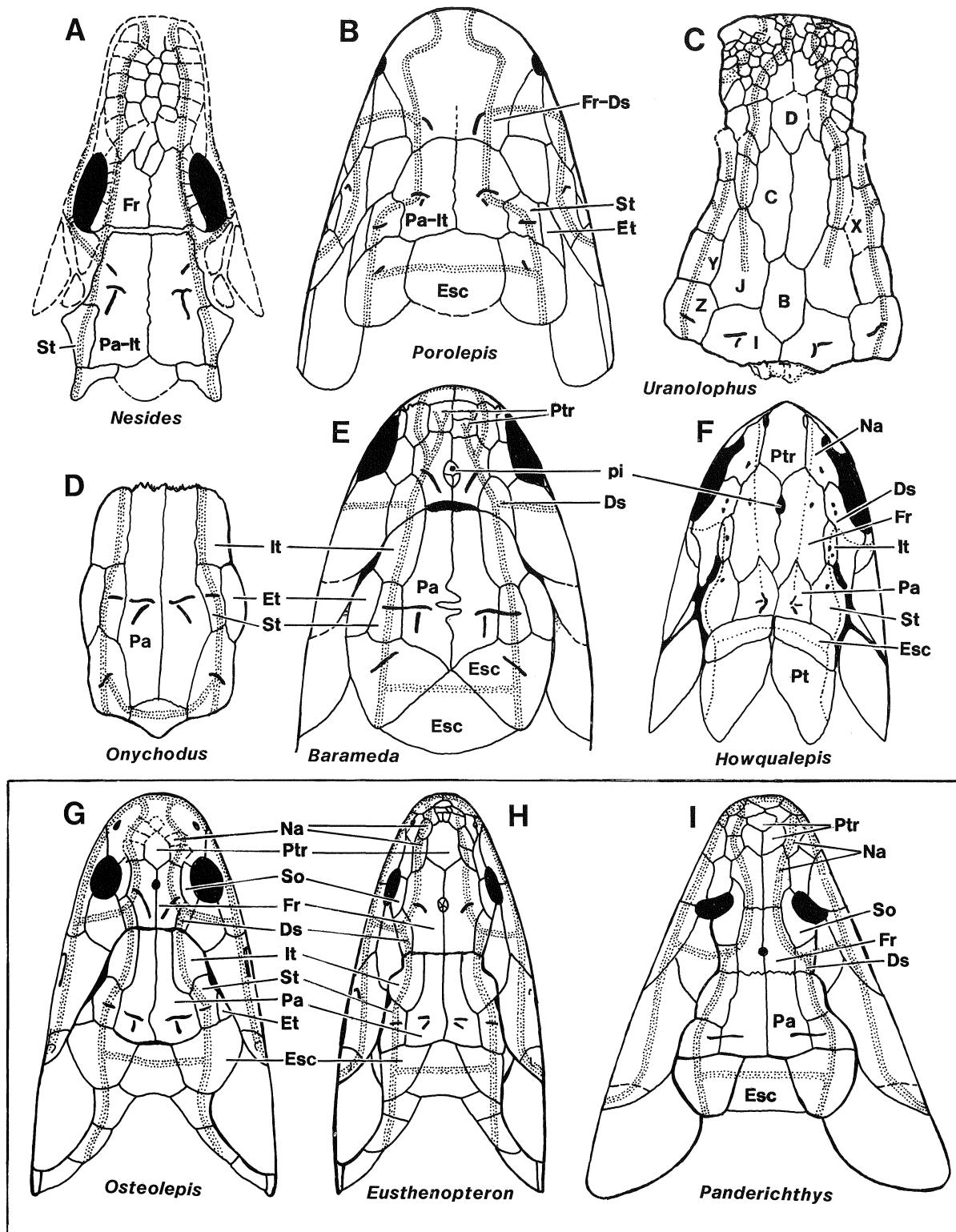


Fig.46. Skull-roof patterns in various osteichthyan groups. A, actinistian (after Stensio, 1937); B, porolepiform (after Jarvik, 1972); C, diplopoan (after Schultze & Campbell, 1987); D, onychodontid (after Andrews, 1973); E, rhizodontid (after Long, 1989); F, actinopterygian (after Long, 1988); G,H, osteolepiforms (after Jarvik, 1980a); I, panderichthyid (after Vorobjeva, 1977).

followed here (Fig.47A) we suggest that youngolepids and porolepiforms show the primitive rhizodontid condition.

F4 (fins with long unjointed lepidotrichia over most of their length, fringed with short branching lepidotrichia). This condition has been inferred for *Notorhizodon*, since it occurs in other rhizodontids. In contrast to rhizodontids, jointed lepidotrichia occur widely in other osteichthans (e.g., actinopterygians, Gardiner, 1984; actinistians, Forey, 1981; dipnoans, Campbell & Barwick, 1989, etc.), and their probable derivation from scales supports this being the primitive condition.

F5 (humerus elongate and lacking preaxial expansion). This feature of advanced rhizodontids may be assumed derived, because a short broad proximal pectoral fin element occurs in most other osteichthyan groups possessing a humerus or its presumed homologue. An exception is *Panderichthys*, but the elongate humerus in this form is probably an autapomorphy (Ahlberg, 1989). Andrews & Westoll (1970b) regarded the short, broad humerus of *Sauripterus* as specialised on functional grounds, but a palaeontological argument that the two Devonian rhizodontids show a more primitive arrangement than Carboniferous forms is consistent with the evidence from outgroup comparison.

F6 (depressed posterior lamina on dorsal part of cleithrum). This feature is unique to typical rhizodontids amongst osteichthyans, as first noted by Andrews & Westoll (1970b), a distribution which can only be interpreted parsimoniously by assuming it is derived.

F7 (cleithrum with expanded ventral blade). As with the previous character, this unique condition of higher rhizodontids can be assumed to be a specialisation.

F8 (spirally inrolled clavicular spine). Like characters F6 and F7, this special feature of higher rhizodontids is assumed to be derived.

F9 (parietal ossification centre traversed by postotic sensory canal). This condition described by Andrews (1985) is specialised on the evidence of outgroup comparison, since other osteichthyans with a typical primitive osteichthyan bone pattern (e.g., actinopterygians, onychodontids, osteolepids) have the main sensory canal passing through the series of bones lateral to the frontal-parietal complex (e.g., Andrews, 1973; Jarvik, 1944a; Gardiner, 1984). Although porolepiforms and actinistians do not conform to this pattern, the course of the sensory canal across the parietal can be attributed to the fact that the intertemporal is secondarily lost (Fig.46A,B), which is not the case in rhizodontids.

F10 (very large size). Although the rhizodontids as a group all tended to be large fishes, species of *Strepsodus* and *Rhizodus* were probably the largest osteichthyans ever to have lived, with a length in the

5 to 7 m range. This is assumed to be a specialised condition.

F11 (reduced thickness of round scales). The thin scales of advanced rhizodontids (Andrews, 1985, table 1) represent a derived character state, thick rhomboid scales being the primitive osteichthyan condition (see comments for character F1 above).

G1 (lateral rostral not in contact with supraorbito-tectal). The assumed polarity of this character is difficult to establish by outgroup comparison, since snout bones are unclear in the many cosmine-covered forms within the group characterised by a single pair of external nares (i.e., above character B2, Fig.47B). We provisionally follow Jarvik's (1966) interpretation of snout bones.

G2 (vomers with long posterior processes). As noted above under character D1, the evidence from outgroup comparison regarding shape of the vomer is not strong, but its development in such groups as actinopterygians (e.g., Gardiner, 1984), and *Diabolepis* (e.g., Chang & Yu, 1984) suggests that the long posterior process of *Eusthenopteron* is a specialised condition.

The most significant systematic result of the above descriptions is the erection of the new family Canowindridae, a grouping first proposed by Long (1985a, 1987a), to which we have now referred three genera (*Canowindra* Thomson 1973, *Beelarongia* Long 1987a, and *Koharalepis* n.gen.). The evidence supporting inclusion of our new genus in this group, and the status and phylogenetic position of the group itself, can be discussed with reference to the cladogram of Figure 47B. The canowindrid group was initially indicated (Long, 1987a: 850) by the similar pattern of cheek bones (Fig.44), the broad and short extrascapulars, and the broad posterior part of the parietal shield with apparent fusion of component bones except for the large extratemporals (Fig.45A,B). Except for the short and broad extrascapulars, we now propose these as synapomorphies of the group (characters E1, E3, E4, Fig.47B). Fusion of bones in the parietal shield (character E2) is another possible synapomorphy. As previously noted (Long, 1985a, 1987a), accepting some or all of these as valid synapomorphies of the group implies that the loss of cosmine and appearance of round scales occurred independently in the canowindrids (character F1). However, it is widely accepted that within the phylogeny of both the osteolepiforms and the porolepiforms cosmine cover to the dermal bones has been independently lost, together with the change from rhomboid to round scales (e.g., Orvig, 1957; Schultze, 1977).

By outgroup comparison (see discussion under F1 above) the presence of cosmine may be regarded as primitive, implying that *Koharalepis* n.gen. and *Beelarongia* are the more primitive representatives of the Canowindridae. There may also be differences in the arrangement of cheek bones within the group, but the

evidence is equivocal. The presence of 'accessory postorbital bones' in the cheek was proposed as a defining character of canowindrids by Long (1985a, 1987a), but it is now clear that in *Koharalepis* the additional bone is part of the fronto-ethmoidal shield, and not a cheek bone. A similar interpretation is possible for *Beelarongia* (Fig.45B), where the corresponding area is fractured (Long, 1987a: fig.1). The precise arrangement in *Canowindra* (Fig.44A) cannot be clarified without new specimens - it may also have had a similar pattern to *Koharalepis*, but the only known specimen

suggests that the extra bones form part of the cheek unit (Long, 1985a). If confirmed in new specimens, this difference would be interpretable as a derived condition for *Canowindra*. This uncertainty exemplifies the difficulty of dealing with fossil taxa represented by single specimens. The preservation of *Koharalepis* provides only circumstantial evidence supporting a reinterpretation of the other two forms. Because this is provisional, to be checked when new specimens become available, we have not used these characters as synapomorphies, and the three canowindrid taxa are left

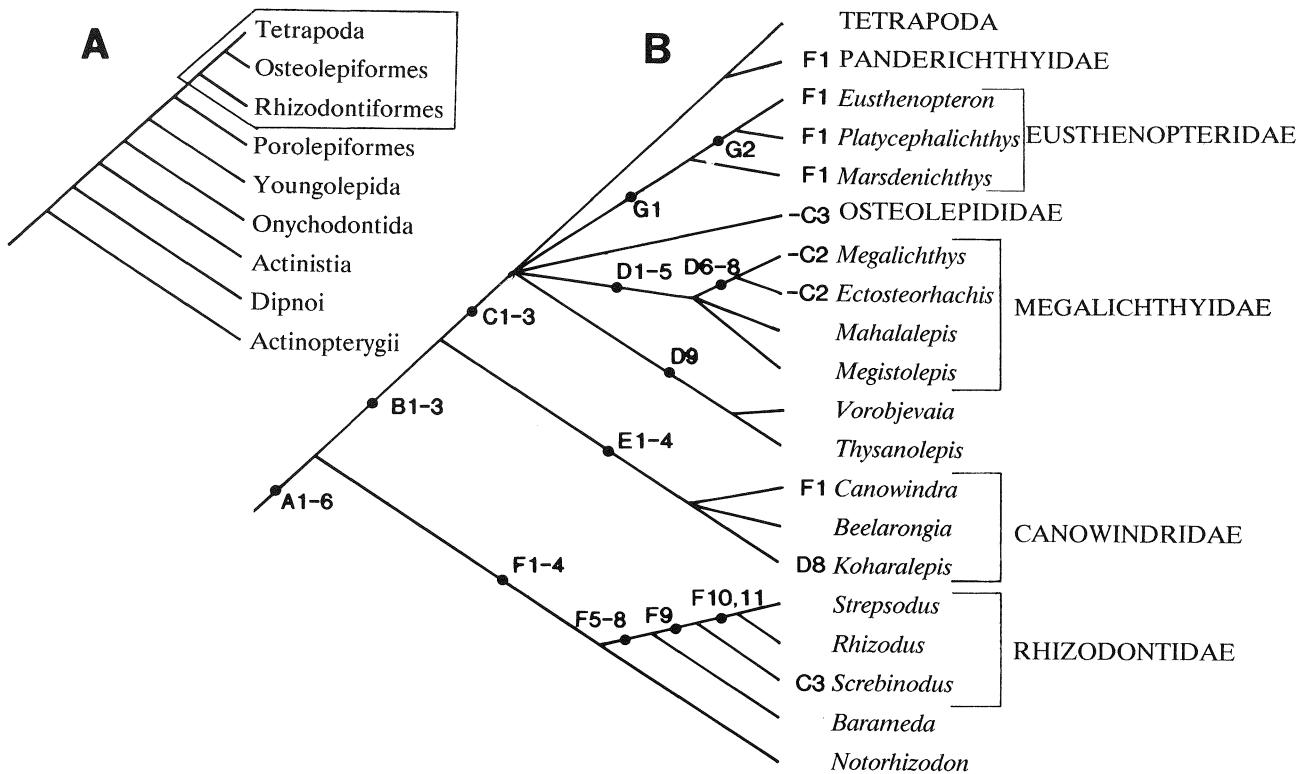


Fig.47. A, one scheme of inter-relationships for major osteichthyan groups (after Schultze, 1987; Long, 1989). Boxed part of cladogram represented in B; B, cladogram of possible inter-relationships for certain taxa in the families Canowindriidae n.fam., Osteolepididae, Megalichthyidae, Eusthenopteridae and Rhizodontidae, and various stem rhizodontiforms. Synapomorphies are: A1, lateral extrascapulars overlap median extrascapulars; A2, polyplodont teeth (not known for canowindrids); A3, seven bones in cheek, with large squamosal; A4, deltoid and supinator processes on humerus (see Ahlberg, 1989); A5, humerus with rounded caput humeri; A6, caput humeri fits into groove on scapulocoracoid; B1, large basal scutes at origins of fins; B2, one pair of external nares; B3, large dermal anocleithrum separating post-temporal from cleithrum; C1, similar size of the lachrymal, jugal and postorbital bones in the cheek; C2, equilateral shape of extrascapulars; C3, loss of the extratemporal; D1, vomers broader than long, with short median suture; D2, posterior tectal bone enclosing posterior half of naris; D3, posterior nasals notched into frontals; D4, loss of pineal foramen; D5, short broad parasphenoid; D6, slit-like nares; D7, interpremaxillary bone or process on premaxilla; D8, broad, flat snout; D9, enlarged sigmoid dentary tusk; E1, skull very broad across the extratemporals; E2, parietal, intertemporal and supratemporal probably fused; E3, jugal at least twice as long as high; E4, postorbital bone excluded from orbital margin; F1, round scales lacking cosmine; F2, reverse overlap of cleithrum onto clavicle; F3, parietal ossification centre in anterior position; F4, fins with long unjointed lepidotrichia over most of their length, fringed with short branching lepidotrichia (inferred for *Notorhizodon*); F5, humerus elongate and lacking preaxial expansion; F6, depressed posterior lamina on dorsal part of cleithrum; F7, cleithrum with expanded ventral blade; F8, spirally inrolled clavicular spine; F9, parietal ossification centre traversed by postotic sensory canal; F10, very large size; F11, reduced thickness of round scales; G1, lateral rostral not in contact with supraorbital-tectal; G2, vomers with long posterior processes. Character distributions are summarised in Table 2. Homoplasies are indicated to the left of each terminal taxon (- = reversal). For a discussion of panderichthid-tetrapod synapomorphies see Schultze (1987).

in an unresolved trichotomy in Figure 47B.

The relationships of canowindrids as a group to other rhipidistians are not obviously constrained by any well-supported scheme of relationships for rhipidistians generally. The small anteriorly placed orbits, and the extra dermosphenotic behind the orbit in *Koharalepis*, are suggestive of *Youngolepis* or *Powichthys* (Fig.45C), variously regarded by other authors as most closely related to porolepiforms, or osteolepiforms, or as stem group rhipidistians (see Chang, 1991). The additional cheek bones of *Canowindra* and *Beelarongia* (Long, 1985a, 1987a), if their presence is confirmed, invite comparison with the additional (postspiracular) bone in the cheek of porolepiforms, while the arrangement and shape of the extrascapulars is similar to that of rhizodontids as described by Andrews (1985).

We have approached the problem of canowindrid relationships in the context of a recent summary of the defining features of major rhipidistian groups presented by Chang (1991). She listed various characters previously used in the literature, of which five were considered to constitute synapomorphies of osteolepiforms, and eight as synapomorphies of porolepiforms. Two of the osteolepiform synapomorphies are possessed by *Koharalepis* (cheek plate of seven bones with broad sutural contact between squamosal and maxillary; large basal scutes at origins of fins), to which can be added three characters put forward by Long (1987a) as supporting osteolepiform affinity for *Beelarongia* and *Canowindra* (overlap relationship of extrascapulars, one pair of external nares, shoulder girdle structure). This gives five characters which might be considered to support a sister-group relationship between canowindrids and osteolepiforms, but two of these (A1, A3 in the list above) are now known to occur also in rhizodontids (Long, 1989). The remaining three characters are placed in our scheme as synapomorphies uniting the canowindrids with other osteolepiforms (characters B1-3, Fig.47B).

As just mentioned, two characters previously proposed as osteolepiform synapomorphies are now known to occur also in rhizodontids. These can be added to four other characters to define a larger clade (rhizodontiforms plus osteolepiforms plus tetrapods; A1-6, Fig.47B). Characters used at the next node in our cladogram are also found in panderichthyids and tetrapods, in accordance with the view that these groups must be regarded cladistically as a subgroup of the Osteolepiformes (e.g., Schultze, 1987). The question of tetrapod relationships has attracted much comment and analysis in recent years since the publication by Rosen *et al.* (1981), but is outside the scope of this paper. See Schultze (1987) for a recent discussion of synapomorphies which support a panderichthyid-tetrapod relationship.

Three characters (C1-3) are used at this node to define the remaining osteolepiforms. By comparison with canowindrids, the similar size of the lachrymal, jugal and postorbital, and the similar shape of the extrascapulars, are possible synapomorphies of osteolepids, megalichthyids, and eusthenopterids. This assumes that

the similar size of the circum-orbital cheek plates (C1) is the derived state, which is problematic in that the elongate jugal is also proposed as a synapomorphy of canowindrids (character E3). As noted above this bone is also elongate in porolepiforms and ichthyostegids, on which grounds its status as a synapomorphy might be questioned. Alternatively the canowindrid cheek could be interpreted as a symplesiomorphic pattern of stem osteolepiforms, with canowindrids as a paraphyletic group. We cannot exclude this possibility, but consider that the loss of cosmine and development of round scales in *Canowindra* is consistent with the group being monophyletic.

It is also assumed that the similar arrangement of extrascapulars in canowindrids and rhizodontids is symplesiomorphic, and the resemblance seen in eusthenopterids and osteolepids in this feature is derived (character C2). Although poorly known, it seems that at least some megalichthyids, as well as *Thysanolepis*, may also have had a triangular median extrascapular, the assumed primitive state of this character. This would be interpretable either as a retention of the primitive condition or as an evolutionary reversal. The former could be accommodated in our scheme by considering megalichthyids, *Vorobjevaia* and *Thysanolepis* as a paraphyletic stem group within the clade defined by this node, but this is contradicted by the evidence of the extratemporal bone in the skull (character C3). Many taxa within this clade lack an extratemporal, a feature provisionally interpreted as a secondary loss using outgroup comparisons (see above). The presence of an extratemporal in osteolepids and *Marsdenichthys* could be interpreted as a reversal, or more likely as evidence for independent loss of this bone. This could be partly accommodated within our scheme by placing osteolepids as a sister group to megalichthyids plus eusthenopterids, panderichthyids and tetrapods, the latter united by the loss of the extratemporal. However, this contradicts the evidence of character C2, as just discussed, in the placement of megalichthyids. In addition, *Marsdenichthys* would still require independent loss or reversal of this character within the eusthenopterids. It is also noted that the extratemporal is apparently absent in some rhizodontids (*Screbinodus*). Because of uncertainty regarding the polarity of both these characters (see above), we do not consider the evidence currently available to be strong enough to resolve the polytomy at this node.

Four genera are included as megalichthyids, but the status of several synapomorphies in *Megistolepis* from the Upper Devonian of Tuva, USSR, is uncertain (e.g., characters D2,3), and it is placed as a trichotomy in the cladogram. However, the short, broad vomers with a short median suture, and the short parasphenoid (Vorobjeva, 1977: fig.35) suggest megalichthyid affinities (characters D1,5). *Panderichthys* also has a short parasphenoid, but the overall configuration of the anterior end of the palate is quite different to that of *Megalichthys* (see Vorobjeva, 1977: fig.3). Other megalichthyid characters are taken from descriptions by Jarvik (1966)

and Schultze (1974). The shape of the vomers in *Megalichthys hibberti*, with a strong mesial process and short midline contact as illustrated by Jarvik (1980a: fig.146A) may be variable in this species, as some specimens show no mesial process (S.M. Andrews, personal communication). In addition Jarvik (1985: 8) has cast doubt on Schultze's (1974) interpretations regarding a separate paired 'interpremaxillary' bone in *Megalichthys*, and supposed differences in the shape of the nares between *Megalichthys* and *Ectosteorhachis*. These issues can only be resolved with the study of new material. Jarvik (1985) also corrected the erroneous view (e.g., Thomson, 1964; Young & Gorter, 1981) that *Megalichthys* lacked a median extrascapular. Bjerring (1972) described some other apparently characteristic features of *Megalichthys* (complex fronto-intertemporal process, and a sensory canal branch traversing the parietal), but these are not known in other forms, and are assumed for the present to be autapomorphies.

The rhizodontiforms are the third major rhipidistian group, which until recently (Andrews, 1985; Long, 1989) were very poorly known with regard to skull structure. Jarvik (1972, 1980a) suggested a porolepiform relationship for the group, and Long (1985a) previously placed them as a sister-group to porolepiforms, actinistians and dipnoans on the evidence of the large ventral division of the cleithrum and subdermal anocleithrum (see Andrews, 1972). Ahlberg (1989) placed them in an unresolved trichotomy with tetrapods, and actinistians + porolepiforms + dipnoans, on the basis of an analysis of the paired fin skeleton. A more widely held opinion (e.g., Andrews, 1973; Long, 1989), provisionally followed here, is that they form a sister-group to osteolepiforms, or that group plus panderichthyids and tetrapods (Fig.47A). This is consistent with the many resemblances to *Eusthenopteron* in skull and braincase structure described above for *Notorhizodon* n.gen. The similarities in scale structure (with a median boss on the inner surface, as in eusthenopterids) are also well known, but on the evidence of cosmoid scales in canowindrids, megalichthyids and osteolepids (the presumed primitive condition) this must be interpreted as a parallelism (F1, Fig.47B).

The cheek of rhizodontids is poorly known, but can be reconstructed from preserved bones in *Strepsodus* and *Barameda* (Long, 1989: fig.5B). It shows the postorbital reaching the orbital margin, the assumed primitive condition. An alternative hypothesis discussed above (under character E4), that the condition in canowindrids is primitive, and not a synapomorphy of the group, would imply independent appearance of the postorbital forming part of the orbital margin at two positions on the cladogram in Figure 47B (with characters F1-4, and C1-3). This lack of parsimony influenced our decision regarding the polarity of E4 (see above). Characters 25 and 26 of Long (1989), used to unite osteolepiforms with tetrapods, are placed here at the base of the cladogram (A2, A3).

Andrews (1985: 85) diagnosed the family Rhizodontidae Traquair to include the genera *Rhizodus*, *Strepsodus*, *Sauripterus* and *Screbinodus*. The genera

Pycnoctenion and *Propycnoctenion* of Vorobjeva & Obrucheva (1977) are based on scale and tooth structure, and in view of the problems associated with the distribution of these characters in the better known Scottish forms, the status of these taxa is uncertain (Andrews, 1985). They have not been considered in this discussion, except to note that the form from Mansfield in Victoria described by Woodward (1906) as *Strepsodus decipiens* does not belong to *Pycnoctenion* as suggested by Vorobjeva & Obrucheva (1977), even though there are similarities in scale structure and ornament. Long (1989) described this form as a new genus, *Barameda*, which resembles *Notorhizodon* in several skull characters, although these may be symplesiomorphies. The only other described Devonian rhizodontiform is *Sauripterus* from the Upper Devonian of North America, which clearly belongs to the group on the evidence of shoulder girdle structure (Andrews & Westoll, 1970b), but is also too poorly known with regard to skull structure to be reliably placed in a phylogenetic scheme. However, as noted above, this form may show significant similarities in the pectoral fin skeleton to that of *Notorhizodon*.

Several characters in the diagnosis of Andrews (1985) do not apply to *Barameda* Long (1989) and *Notorhizodon* as described above. The growth centre of the parietal ('postparietal') is posteriorly placed in a juvenile specimen of *Barameda*. It is provisionally assumed that this is not the condition in adults (with differential growth to give a longer posterior division of the bone in larger specimens; see Schultze, 1984) because of incongruence with character F5 (structure of the humerus) in our cladogram. Although an elongate humerus is also known in *Panderichthys* (Vorobjeva, 1975), which might suggest that this character is unreliable, Ahlberg (1989: 160) has argued on the basis of fin skeleton structure in other osteolepiforms that peculiarities in the structure of the humerus in *Panderichthys* are likely to be autapomorphies. The presence of an extratemporal, and contact between the extratemporal and intertemporal are assumed primitive, on the evidence of skull roof pattern in other osteichthyan groups (Fig.46B,D,E). In both *Barameda* and *Notorhizodon* the postotic sensory canal passes straight back through the intertemporal and supratemporal, also assumed symplesiomorphic on the basis of outgroup comparisons. These features place both forms outside the family Rhizodontidae (defined by characters F9,10 in Fig.47B). The structure of the shoulder girdle in *Pycnoctenion* (poorly known, but with a rhizodontid-like reduced dorsal division of the cleithrum) and shoulder girdle and fins in *Barameda* suggest a sister-group relationship to rhizodontids *sensu stricto*. *Notorhizodon*, which may resemble *Sauripterus* in its more primitive shoulder girdle shape (but with the characteristic reverse overlap of the cleithrum and clavicle), can be placed as the most primitive known rhizodontiform. This is based on the apparently similar shape of the humerus in the two Devonian forms, which Andrews & Westoll (1970b) regarded as specialised in *Sauripterus* on functional grounds, but which we suggest may be the primitive condition. This leaves four

characters (F5-8), concerned with the special structure of the humerus and dermal shoulder-girdle, as synapomorphies of all higher (Carboniferous) rhizodontiforms.

In conclusion, we acknowledge that Figure 47B represents only one possible scheme of inter-relationships for the included taxa, which will change as new information on their structure becomes available. We reiterate that the shared derived characters used here must be regarded as provisional synapomorphies at present, because their polarisation is difficult to establish by outgroup comparison in the absence of a robust higher level phylogeny (e.g., Forey, 1987; Panchen & Smithson, 1987; Ahlberg, 1989).

Biogeographic Relationships

The vertebrate fauna from the Aztec Siltstone occurs within the 'East Gondwana Province' of Young (1981). The biogeographic significance of the new forms described above can be considered in the context of biogeographic patterns indicated by other groups from the fauna.

The Aztec fish fauna has provided evidence supporting the hypothesis (e.g., Young, 1981, 1984, 1987b) that some early vertebrate taxa may have originated in the Gondwana region, and subsequently dispersed into other areas, including the Euramerican landmass of the Middle Palaeozoic. In this respect the crossopterygian fishes have a special interest because of their presumed close relationship to early tetrapods, a group for many years only represented in Devonian rocks by the ichthyostegids and acanthostegids from the latest Devonian of east Greenland (e.g., Jarvik, 1980a). However, tetrapod footprints and other remains are now documented from the Middle and Late Devonian of the Gondwana areas of eastern Australia and South America (summarised in Young, 1987a), and possibly in the Early Devonian of Victoria (Warren *et al.*, 1986). This evidence shows that early tetrapods were widespread in Gondwana during the Devonian, and they were also present in Euramerica during the Late Devonian.

The 'East Gondwana Province' of Young (1981) differs markedly in its Early to Middle Devonian fish faunas from those of Europe and North America in the complete absence of such major groups as the osteostracan and heterostracan agnathans. The only Euramerican agnathan group known from the Aztec fauna, and the East Gondwana region generally, is the Thelodontida. On the other hand, some close resemblances have been noted between the vertebrate faunas of Late Devonian age in non-marine deposits of Euramerica and East Gondwana (e.g., Young, 1987b), to which various placoderms such as phyllolepisids, *Bothriolepis* and *Groenlandaspis* are common taxa. All three occur in the Aztec fauna, but the evidence suggests that these may be slightly earlier occurrences (late Middle Devonian) than in Euramerica. A pattern of older and/or more primitive occurrences in East Gondwana

than in Europe has been suggested for several groups, such as xenacanth sharks (Young, 1982), and phyllolepid and bothriolepid placoderms (Young, 1988, 1989a). Both the earlier biostratigraphic occurrence, and the application of 'Hennig's progression rule', that the distribution of the most primitive members of a group indicates its centre of origin (e.g., Patterson, 1981), suggest a Gondwana origin for these groups, and subsequent dispersal to produce the characteristic Late Devonian and Early Carboniferous fish faunas of Euramerica.

For crossopterygian fishes and tetrapods similar suggestions have been made. Panchen (1977) first proposed a Gondwana origin for tetrapods on the evidence of Late Devonian trackways from Victoria (Warren & Wakefield, 1972), and Janvier (1978) suggested a widespread osteolepiform common ancestor from which tetrapods evolved in Gondwana, and eusthenopterid rhipidistians evolved in Laurasia, during the Middle Devonian. Janvier, Termier & Termier (1979) suggested a Gondwana origin for the large osteolepiform *Megalichthys*, which is common in the Early Carboniferous of Europe, and this is supported by the new evidence of *Mahalalepis*, interpreted above as a primitive and early megalichthyid from East Gondwana. Young (1989a) has suggested (based on the assumed Givetian-early Frasnian age for the Aztec fauna) that rhizodontid crossopterygians, also best known from the Coal Measures of Europe, may show the same pattern (see also Long, 1990). The earliest record of rhizodontids (*sensu stricto*) in Euramerica is *Sauripterus* from the Famennian of eastern North America. These forms typically occur in non-marine deposits, although recently marine rhizodontids have been recorded from Turkey (Janvier *et al.*, 1984) and north-western Australia (Long, 1989: 15). Because such postulated dispersals are based mainly on an apparent earlier occurrence for the groups concerned in the fossil record of the Gondwana regions they must be viewed with caution. However, the preliminary phylogenetic support is provided for rhizodontids by the assessment presented above that the East Gondwanan taxa *Notorhizodon* and *Barameda* may be relatively primitive or stem taxa within the Rhizodontiformes.

Two additional patterns have been exhibited by other groups from the Aztec fauna, which might also be expected to manifest themselves for crossopterygians. East Gondwana endemism is shown at the specific level for the shark *Antarctilamna* (Young, 1982), perhaps for some species groups of the antiarch *Bothriolepis* (Young, 1988), and at the generic level for the acanthodian *Culmacanthus* (Young, 1989a,b). The new osteolepiform family Canowindridae described above with representatives in southern Victoria Land, eastern Victoria, and New South Wales, is another clear example of this pattern. The possible close relationship of *Platyethmoidia* described above to the osteolepids described from the Hatchery Creek fauna of New South Wales (Young & Gorter, 1981), is consistent with the fact that this and the Aztec fauna are the only ones so far known in which turiniid thelodonts and bothriolepid antiarchs are associated (Young, 1988).

A second pattern is the biogeographic affinity shown by some bothriolepid antiarchs to those from the Middle Devonian of South China (Young, 1988), but there is as yet no evidence of such affinities amongst the crossopterygians. In the osteolepiform *Koharalepis* described above some primitive features were noted as resemblances shared with the Early Devonian *Youngolepis* from South China, but also with *Powichthys* from Arctic Canada, so this is not evidence of South Chinese affinity. Since crossopterygians of comparable age to the Aztec fauna (late Middle Devonian) have not yet been reported from South China, the presence or absence of such a pattern remains to be determined if and when such forms are described. It is noteworthy, however, that two Russian genera (*Megistolepis*, *Thysanolepis*) are shown in our scheme of relationships as plesiomorphic sister-groups to Antarctic taxa (in the case of megalichthyids with an advanced and more widespread Early Carboniferous subgroup). *Thysanolepis* occurs in the Upper Devonian - ?Lower Carboniferous Viluchian and Emiaxin Suites of the Ygyatta depression in eastern Siberia, which on some reconstructions (e.g., Scotese, 1986) is palaeogeographically remote from Gondwana in high northern palaeolatitudes. *Megistolepis* occurs in the Frasnian of the Minusinsk Depression in the Tuva region, regarded by Young (1981) as a separate biogeographic province in the Early Devonian on the basis of endemic agnathans (see Afanassieva & Janvier, 1985). Of interest in the present connection is the fact that poorly known placoderms from Tuva suggest affinity with the quasipetalichthyids of South China (Young, 1990). It may be therefore that specific biogeographic relationships to South China just alluded to are confined to antiarchan placoderms, with crossopterygians showing other (but related) connections, perhaps resulting from different areas of origin caused by much earlier vicariance events in gnathostome evolutionary history.

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APPENDIX I

Table 1. Summary of the geographic distribution of rhipidistian remains described in this paper from 17 vertebrate localities in the Aztec Siltstone. Locality numbers refer to Figure 2. (T = type locality; X = occurrence; ? = identification uncertain).

LOCALITY	2	4	8	9	10	11	12	13	14	15	16	17	19	20	21	23	24
SECTION	-	-	L2	L1	-	-	P1	M1	M2	-	A2	A1	-	-	-	A5	A4
(Askin <i>et al.</i> , 1971)																	
SECTION	-		H6	-	-	-	10	-	9	-	8	7	6	5	4	3	-
(Barrett & Webb, 1973)																	
<i>Koharalepis jarviki</i>						T										
<i>Mahalalepis resima</i>						T										
<i>Platyethmoidia antarctica</i>						X										
<i>Vorobjevia dolonodon</i>						T										
<i>Notorhizodon mackelveyi</i>						X	X	X	T				
porolepiform indet.						X	X	X	X				
osteolepids indet. a	X	X	X	X	X	X	X	X	X
osteolepids indet. b						X	X								
eusthenopterid indet.	?	X													
rhizodontiform indet.												X	?		

Table 2. Data matrix for characters used in constructing the cladogram of Figure 47B. Character polarity is considered in discussion. For list of characters see caption to Figure 47. (0 = primitive character state; 1 = derived character state; - = character state unknown; ? = character state uncertain; X = character inapplicable or neither condition shown).

Character	A	1	2	3	4	5	6	B	1	2	3	C	1	2	3	D	1	2	3	4	5	6	7	8	9	E	1	2	3	4	F	1	2	3	4	5	6	7	8	9	10	11	G	1
Notorhizodon	1	-	-	1	1	-	.	-	-	-	0	-	-	-	-	0	-	-	-	0	-	0	-	-	1	1	1	-	0	0	0	0	-	0	0	-	-							
Barameda	1	1	1	1	1	1	-	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	?	1	1	1	1	1	0	0	0	0								
Screbinodus	1	1	-	-	-	-	-	-	0	1	-	-	-	-	-	-	0	0	0	-	-	1	1	1	1	1	1	1	1	1	1	1	0	0										
Rhizodus	1	1	-	1	1	1	-	-	0	-	0	-	-	-	-	-	-	1	0	0	-	-	1	1	1	1	1	1	1	1	1	1	1	1	-									
Strepsodus	1	1	-	1	1	1	0	0	0	-	0	0	-	-	-	-	0	0	0	-	0	1	1	1	1	1	1	1	1	1	1	1	1	0										
Koharalepis	1	-	1	-	-	-	1	1	-	0	0	0	-	0	0	-	1	-	1	1	1	1	0	-	-	0	-	-	-	-	0	0	0	-										
Beelarongia	-	1	1	1	1	1	1	1	0	0	0	-	0	-	-	-	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0										
Canowindra	1	-	1	-	-	-	1	1	1	0	0	0	-	0	-	-	0	0	1	1	1	1	1	1	-	0	0	-	0	0	0	0	0	0										
Thysanolepis	1	1	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	1	-	-	-	-	0	-	-	-	-	-	-	-	-	0	0	-									
Vorobjevaia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-									
Megistolepis	-	-	-	-	-	-	-	1	-	-	-	1	1	-	-	1	0	-	0	0	-	-	0	-	0	-	-	-	-	-	-	0	0	-										
Mahalalepis	-	-	-	-	-	-	-	-	1	-	-	-	-	1	1	?	-	0	-	0	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-									
Ectosteorhachis	1	1	1	-	-	1	1	1	1	0	1	-	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0										
Megalichthys	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0										
OSTEOLEPIDS	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0										
Marsdenichthys	1	-	1	-	-	-	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	-	0	0	0	0	1	-								
Platycephalichthys	1	1	1	-	-	-	-	1	-	-	1	1	0	0	0	0	0	0	0	0	0	0	0	0	-	1	-	0	-	-	0	0	0	0	0	1	1							
Eusthenopteron	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1								
PANDERICHTHYIDS	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	-	0	1	0	0	0	0	0	0	0	0	0									
TETRAPODS	X	1	1	1	1	1	X	1	X	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	?	0	0	?	0	0	0	0	0	0								

APPENDIX II

Abbreviations used in Figures

II	foramen for optic nerve	f.mdVII	foramen for mandibular rami of facial nerve
V	foramen for trigeminal nerve	f.mk	foramina leading to meckelian fossa
acan	acanthodian scales	fo.add	adductor fossa
a.pal	groove for palatine artery	fo.br	fossa bridgei
ar.exp	smooth exposed area of lateral side of entopterygoid	f.occ.lat	lateral occipital fissure
ar.latd	possible attachment for latissimus dorsi muscle	fo.nt	notocordal pit
ar.li1,2	ligament attachment areas	Gu	gular
art	articular surface	gp.so	pores for cutaneous sensory organ
art.dep	articular pit	gr	groove
art.ptm	articulation for paratemporal process of palatoquadrate	gr.ju	groove for jugular vein
		groen	plate of groenlandaspid arthrodire
		gr.p	posterior groove
bli	blisters in the cosmine surface	H	humerus
b.sc	basal scales of fin lobe	Hy	hyomandibula
bsl	basal scute of fin	hc.sc1,2	hemicylindrical scales protecting leading edge of fin
bs.sdf	basal scute of second dorsal fin	hyd	dorsal articular surface for hyomandibula
		hyv	ventral articular surface for hyomandibula
Clav	clavicle	Id1-3	first - third infradentary
Clm	cleithrum	It	intertemporal
ca.H	articular head of humerus	ioc	infraorbital sensory canal
cav.cr	cranial cavity	Ju	jugal
cd.art	articular condyle for mandibular joint	juc	jugal sensory canal
cdf	caudal fin	La	lachrymal
c.ju	canal for jugular vein	Lj	lower jaw
c.pal	foramen for palatine branch of facial nerve	lac	lateral commissure
c.o.lat	foramen for ramis ophthalmicus lateralis	la.Co	tooth-bearing coronoid lamina
c.ot	foramen for ramis oticus	lc	main lateral line sensory canal
cvf	ventral portion of caudal fin lobe	ld.It	dorsal lamina of intertemporal
		le.so	suborbital ledge
De	dentary	lig	ligamentous attachment area
Dpl	dermopalatine	l.Esc	lateral extrascapular
Ds	dermosphenotic	lv.Ent	lateral lamina of entopterygoid
Ds1,2	anterior and posterior dermosphenotics	Mk	meckelian cartilage
dep	depression	Mx	maxilla
dfr	dermal fin ray	mc	mandibular sensory canal
dlr1-12	dorsolateral scale rows 1 to 12	m.depr	process, possibly for attachment of depressor mandibulae muscle
dma1,6	median dorsal scales 1, 6	m.Esc	median extrascapular
		m.Pq	ventral margin of (commissural lamina of) palatoquadrate
Ect	ectopterygoid	Na.p	posterior nasal
Ent	entopterygoid	n	notch
Ent.dp	entopterygoid dental plate	n1,2	mesial and lateral notches on median
Esc	extrascapular bone or series	n.La	extrascapular
Et	extratemporal	n.Po	lachrymal notch
ec.c	ectepicondyle of humerus	n.spir	postorbital notch
en.c	endepicondyle of humerus	Op	spiracular notch
end	endocranial fragment	od	opercular
		od.Clm	overlap area
Fr	frontal		overlap area for cleithrum
Fr1,2	anterior, posterior frontals		
FrS	fronto-ethmoidal shield		
f1,2	foramina leading to sensory canal		
f.art	articular fossa for mandibular joint		
f.bhp	buccohypophysial foramen		
fe.exa	anterior external nasal opening		
fe.v	basicranial fenestra		
f.ioc	foramen for nerve fibres to infraorbital canal		

od1,2Ds	mesial and lateral overlap areas for dermosphenotic	pr.Co	dorsal process on coronoid lamina
od.It	overlap area for intertemporal	pr.conn	processus connectens of ethmosphenoid
od.Ju	overlap area for jugal	pr.d	dorsal process of meckelian cartilage
od.La	overlap area for lachrymal	pr.delt	deltoid and/or supinator process of humerus
od.m.Esc	overlap area for median extrascapular	pr.Ect	posterior lateral process of ectopterygoid
od.Op	overlap area for opercular	proc	preorbital corner
od.Pa	overlap area between parietals	pr.pd	posterdorsal process of ethmosphenoid
od.Po	overlap area for postorbital	pr.sp	suprapterygoid process
od.Ps	attachment surface for parasymphysial dental plate	ptoc	postorbital corner
od.Rbr	overlap area for branchiostegal ray	p.vot	pit which received vomerine tusk
od.So	overlap area for supraorbital	Qj	quadratojugal
od.Sop	overlap area for subopercular	Rbr	branchiostegal ray
od.St	overlap area for supratemporal	ri	ridge
orb	orbit	ri.lig	ridge for ligamentous attachment
orc	oral sensory canal	r.lab	labial ridge
ov1,2It	mesial and lateral areas overlapping intertemporal	Sclm	supracleithrum
ov.Pa	area overlapping parietal	So1,2	anterior and posterior supraorbitals
ov.Po	area overlapping postorbital	Sop	subopercular
ov.So	area overlapping supraorbital	Sq	squamosal
Pa	parietal	St	supratemporal
PaS	parietal shield	sa.Ect	replacement socket for anterior tusk of ectopterygoid
Pmx	premaxilla	s.Co1-3	socket for coronoid replacement tusk
Po	postorbital	s.De	socket for dentary replacement tusk
Pop	preopercular	s.Dpl	socket for dermopalatine replacement tusk
Pq	palatoquadrate	sdf	second dorsal fin
Pq.dm	dorsomesial thickening on margin of palatoquadrate	sh.ot	otic shelf of otoccipital
Prart	prearticular	snc	subnarial corner
Prart.dp	prearticular dental plate	soc	supraorbital sensory canal
Ps.dp	parasymphysial dental plate	sp.Co3	replacement socket for posterior tusk of third coronoid
Psp	parasphenoid	sp.Ect	replacement socket for posterior tusk of ectopterygoid
Pt	post-temporal	stcc	supratemporal cross-commissure
Ptr	postrostral	sym	sympophysial pit on meckelian bone
p.dplt	pit which received dermopalatine tusk	Te.p	posterior tectal
pi	pineal foramen	ta.Co3	anterior tusk of third coronoid
pin	pineal plate	ta.Ect	anterior tusk on ectopterygoid
pl	pitline	t.Co1,2	tusk of first or second coronoid
pl.Esc	extrascapular pitline	t.De	dentary tusk
pl.Fr	frontal pitline	t.Dpl	dermopalatine tusk
plh.Id	horizontal infradentary pitline	tlj	marginal tooth row of lower jaw
pl.Id2	pitline of second infradentary	tp.Co3	posterior tusk of third coronoid
pl.p	posterior parietal pitline	tp.Ect	posterior tusk on ectopterygoid
pl.Pop	preopercular pitline	tuj	marginal tooth row of upper jaw
plPs	postero-lateral division of parasymphysial dental plate	Ul	ulna
pl.Qj	quadratojugal pitline	v.font	vestibular fontanelle
pl.Sq	squamosal pitline	vma1	median ventral scale of first scale row
pl.tr	transverse parietal pitline	vot	vomerine tusk
plv.Id	vertical infradentary pitline	zd.Co3	marginal denticulate zone of third coronoid
po.m	postorbital margin	zd.Ect	marginal denticulate zone of entopterygoid
pr.ad	anterodorsal process of postorbital		
pr.asc	ascending process of parasphenoid		
pr.bp	basipterygoid process		
pr.Clav	ascending process of clavicle		