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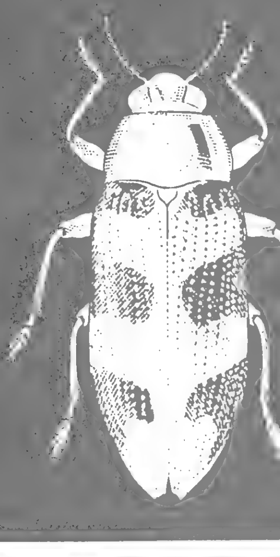

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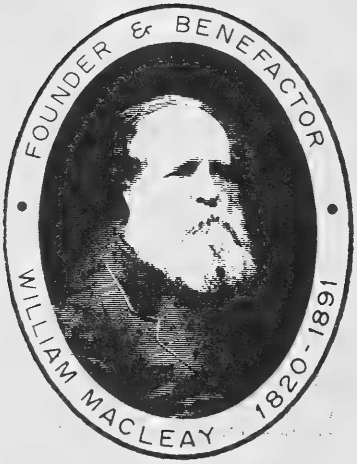

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Adapted by Len Hay from *Proc. Linn. Soc. N.S.W.* 55, 1930, plate IV(6).

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Palynological Evidence for Holocene Environmental Change and Uplift on Wireless Hill, Macquarie Island

D. R. SELKIRK, P. M. SELKIRK and K. GRIFFIN

SELKIRK, D. R., SELKIRK, P. M., & GRIFFIN, K. Palynological evidence for Holocene environmental change and uplift on Wireless Hill, Macquarie Island. *Proc. Linn. Soc. N.S.W.* 107 (1), (1982) 1983: 1-17.

Wireless Hill, at the northern end of subantarctic Macquarie Island, has a raised beach on its western edge at an altitude of about 100 m. The beach is overlain by a deposit of organic-rich sands grading upward into peat, the sequence having a basal date of approximately 5500 years BP. Palynological and other microfossil studies have revealed changes in the vegetation on the site, interpreted as indicating changes in the environment of the site rather than reflecting climatic change in the region.

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INTRODUCTION

The location of subantarctic Macquarie Island (158°57′E, 54°30′S) makes it a potentially sensitive recorder of Quaternary climatic and tectonic events. The island, a fault-bounded and cross-faulted block of ocean floor material (Varne and Rubenach, 1972) is a high point on the Macquarie Ridge, the junction of Indian-Australian and Pacific tectonic plates (Summerhayes, 1974). The area is seismically active. The Antarctic Convergence at present lies just south of the island but was north of it 18000 years BP (Hays, 1983). The climate today is hyperoceanic, cool, moist and windy.

The island was glaciated during the last glacial maximum, but the severity of glaciation is debated. The rather limited glaciations postulated by Colhoun and Goede (1974) and Löffler and Sullivan (1980) appear more likely than glaciation by an overriding ice sheet coming from the west (where there is now no land) as postulated in Mawson (1943). Taylor (1955) accepted the theory of ice-sheet glaciation and considered the island's present flora as due to long-distance recolonization in postglacial times. Bunt (1956) claimed to recognize fossil pollen remnants of a pre-glacial flora, differing from the present one, but suggested that some elements of this flora may have survived the glaciation in refugia on a then-larger Macquarie Island. The evidence for Bunt's conclusions is unclear. More limited glaciations described by recent authors would not have involved elimination of the biota, since substantial refugia would have occurred within the present limits of the island. Presence of similar refugia on South Georgia is suggested by Barrow (1978).

The timing of the island's emergence above sea level, and the rates of uplift of the island are also matters of uncertainty. McEvey and Vestjens (1973) dated penguin bones in beach deposits. Colhoun and Goede (1973) dated basal peats on marine terraces close to sea level. They assumed immediate peat formation on any area lifted above wave influence to calculate a maximum rate of terrace uplift of 4.5 m/1000 years. Using McEvey and Vestjens' penguin bone dates, they calculated a minimal rate of 1.5 m/1000 years, and suggested a mid to late Pleistocene emergence of the island. Blake (Mawson, 1943), from observation of wreckage on west coast terraces,

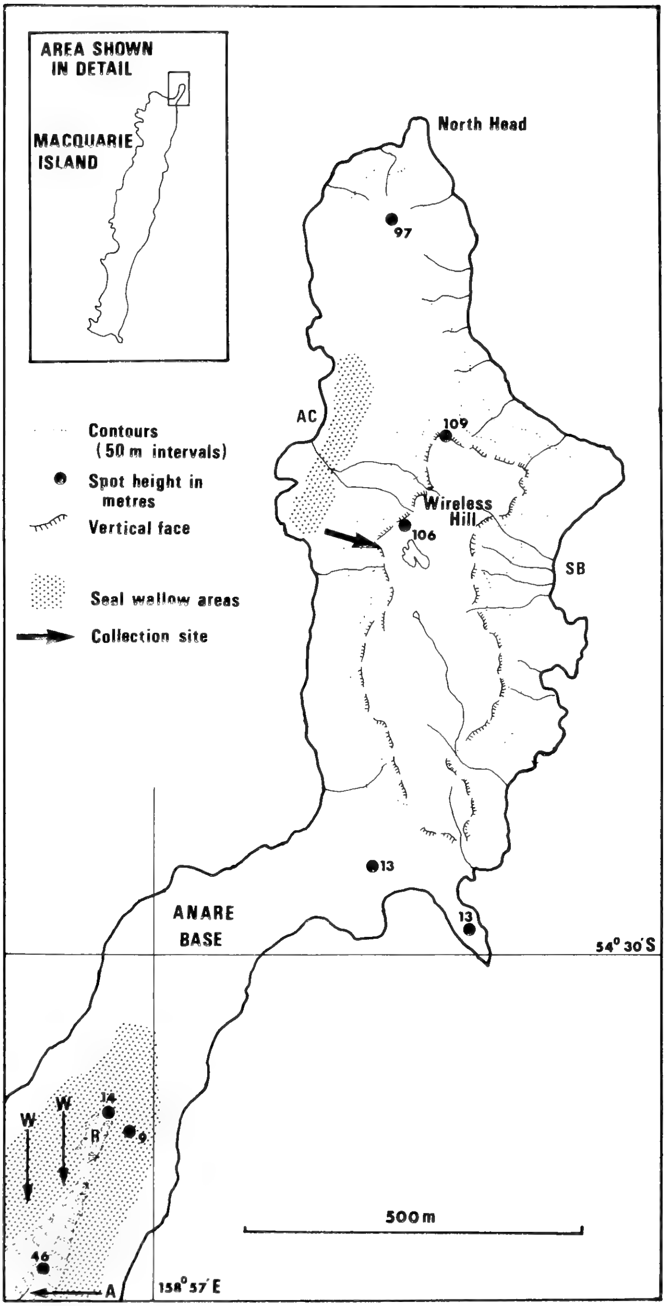

Fig. 1. Map showing location of collection site. AC = Aerial Cove; SB = Secluded Beach; A = Collection site of mat of *Amblystegium* on Doctor's Track; W = Seal wallow sampled for pollen analysis; R = Razorback Hill.

suggested that uplift was extremely rapid and probably measurable in the short term. Bunt (1956) had suggested the island dated from early Tertiary or even Mesozoic times. Miocene marine oozes on the island (Quilty *et al.,* 1973) make this unlikely.

Quaternary studies on Macquarie Island, apart from studies of glacial landforms (Colhoun and Goede, 1974; Löffler and Sullivan, 1980) and lakes (Peterson, 1975) have until recently been few, and there are as yet no clear indications as to whether any substantial vegetational change has occurred during the Holocene. Considerable interest is now being shown in the island's Holocene history. Selkirk and Selkirk (1983) reported early to mid Holocene ^{14}C dates for organic deposits from a number of sites and have described fossil mosses from two lacustrine deposits (Selkirk and Selkirk, 1982). Salas, Peterson and Scott (in preparation) are making palynological studies of two cores from Scoble Lake, near the northern end of the island. Ledingham and Peterson (in preparation) are studying raised beaches at several localities.

As the only land in a vast area of ocean, Macquarie Island supports huge breeding populations of seals and sea-birds which have a considerable effect on the vegetation over wide areas (Mawson, 1943; Taylor, 1955; Gillham, 1961; Jenkin, 1975). Evidence presented here of animal-modified vegetation preserved in Holocene deposits on top of Wireless Hill, suggests that Wireless Hill, a small fault-bounded segment of the island, appears to have undergone very rapid tectonic uplift at rates 3-4 times greater than the maximum proposed for marine terraces on the main island mass to the south. It therefore seems that uplift of Wireless Hill has been essentially independent of uplift of the island as a whole.

MATERIALS AND METHODS

The site

Samples analysed were collected from an exposure of peat and organic-rich sand on the western edge of Wireless Hill, a steep-sided headland whose flat top is mainly about 100 m a.s.l. (Figs 1, 2). The collection site is at the edge of the plateau, very close to the steep western seaward slope. Samples were collected from a face freshly cut into the exposure, the face extending downwards into a pit, at the bottom of which are beach cobbles. These cobbles clearly represent an extension beneath the deposit of the well-preserved raised beach (R. Ledingham, pers. comm.) which is exposed on the slope immediately north of the collection site (Figs 1, 3).

There are several vegetation types on and around Wireless Hill at present. In Aerial Cove (Fig. 1) there is a low-level beach terrace with *Poa foliosa* tussock and elephant seal wallows. At the base of the cliff behind Aerial Cove, and in sheltered parts of the steep slopes above Secluded Beach there is extensive growth of *Stilbocarpa polaris. Poa foliosa* tussock covers most of the slopes of the headland. The top of Wireless Hill is almost flat (Fig. 2) except for one small tarn and a wind-scoured area forming a slight depression at the head of a gully draining from the flat top to the eastern slopes. *Poa foliosa* grows over some of the plateau, and *Stilbocarpa polaris* occurs in sheltered spots near the slight depression. Most of the plateau surface supports a low herbfield which includes *Agrostis magellanica, Festuca contracta, Luzula crinita* and scattered plants of *Pleurophyllum hookeri.*

The isolated plateau of Wireless Hill is linked to the main island by a narrow (about 200 m wide) low-lying (mostly about 5 m a.s.l.) isthmus. During their breeding season numerous elephant seals occupy beaches on both sides of the isthmus and have created large wallow areas between the beaches and the ridge of Razorback Hill (Figs 1, 4). These wallow areas carry a mixed *Poa foliosa- Poa annua- Cotula plumosa- Callitriche antarctica* community with large bare areas (Figs 4, 5).

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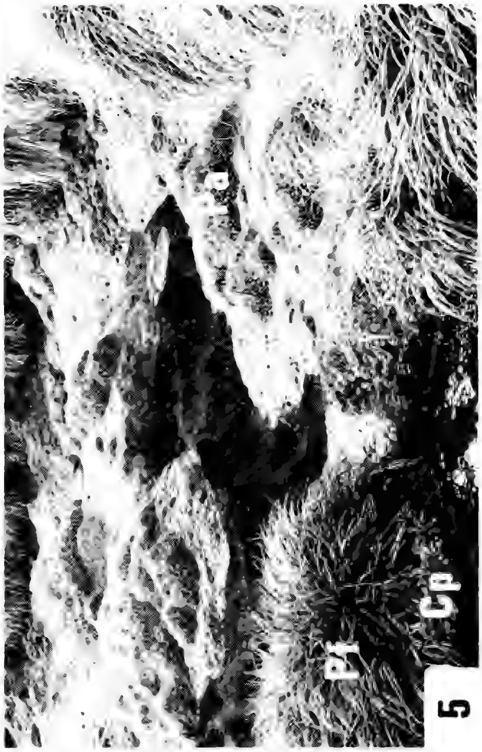

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Sample collection and treatment

The profile sampled totals almost 4 m, the top of the profile (0 cm in Fig. 6) being defined as the peat-soil surface under living vegetation at the site. This is very close to 100 m a.s.l. Samples from 0-270 cm were collected in plastic tubes, internal diameter 2.5 cm, pushed horizontally into the freshly exposed face. All other samples were removed with a spatula into plastic bags. Each sample represents about 2 cm vertical extent. Larger samples for ^{14}C dating (vertical extent shown to scale in Fig. 6) were transferred to plastic bags. A peat monolith straddling the 85 cm level was collected.

Each sample was divided into sub-samples for (1) pollen analysis, (2) analysis of the siliceous fraction, (3) total mineral content determination and (4) stratigraphic analysis.

For pollen analysis ca 5 cc of material were boiled in 10% KOH and then acetolysed using standard palynological techniques (Brown, 1960). Almost all pollen preparations required treatment with HF due to the high mineral content of most horizons and the presence of very abundant opal phytoliths, diatom fragments and chrysomonad cysts.

For analysis of the siliceous fraction ca 5 cc of material were boiled sequentially in concentrated hydrochloric, nitric and sulphuric acids, samples being centrifuged between successive acid treatments (Lacey, 1963). Coverslip strews of the siliceous fraction were mounted in Naphrax mounting medium for observation.

Total mineral content of 5 cc samples was determined by oven-drying at 80°C followed by ignition of the samples at 700°C. Qualitative estimates of the relative abundance of biogenic silica were made from strews of the siliceous fraction. No attempt has yet been made to determine quantitatively the ratio of biogenic silica to other mineral matter.

Stratigraphic analysis was carried out using ca 2 cc samples put in a petri dish with water and studied under a dissecting microscope. Identifiable plant remains and other components of the sample were recorded. Detailed analysis of the peat monolith spanning the 85 cm level was carried out in the same way. Results of these microscopic examinations appear in Figs 6, 7.

A subsample at 85 cm was boiled for one hour in concentrated nitric acid and then washed with 5% ammonium hydroxide as a charcoal verification test (Singh *et al.*, 1981). Macroscopic charcoal particles showing cellular structure were dissected from the matrix and studied with a scanning electron microscope.

A comprehensive reference collection of pollen, fruits, seeds and spores of the extant vascular flora was made during the summer of 1979-1980. Reference pollen samples, usually taken from anthers of several different plants of the species, were acetolysed and mounted in glycerine jelly.

RESULTS OF ANALYSIS

Three main stratigraphic divisions are distinguishable in the profile (Fig. 6). From 0-175 cm thin layers of well-humified peat alternate with layers of sandy peat. A thicker layer of well-humified peat occupies the 175-232 cm zone. Below 232 cm is a predominantly sandy matrix with interbedded layers of peat. The peat layers may well

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Fig. 2. Wireless Hill, photographed from the south east, from deck of ship.

Fig. 3. Raised beach at 100 m a.s.l. on western edge of Wireless Hill.

Fig. 4. Southern end of isthmus, from Doctor's Track. Note elephant seals on beach (arrow) and wallow areas amongst *Poa foliosa* tussocks, between beach and Razorback Hill and ridge.

Fig. 5. Seal wallow showing associated vegetation. Pf = *Poa foliosa,* Pa = *Poa annua,* Cp = *Cotula plumosa,* Ca = *Callitriche antarctica.*

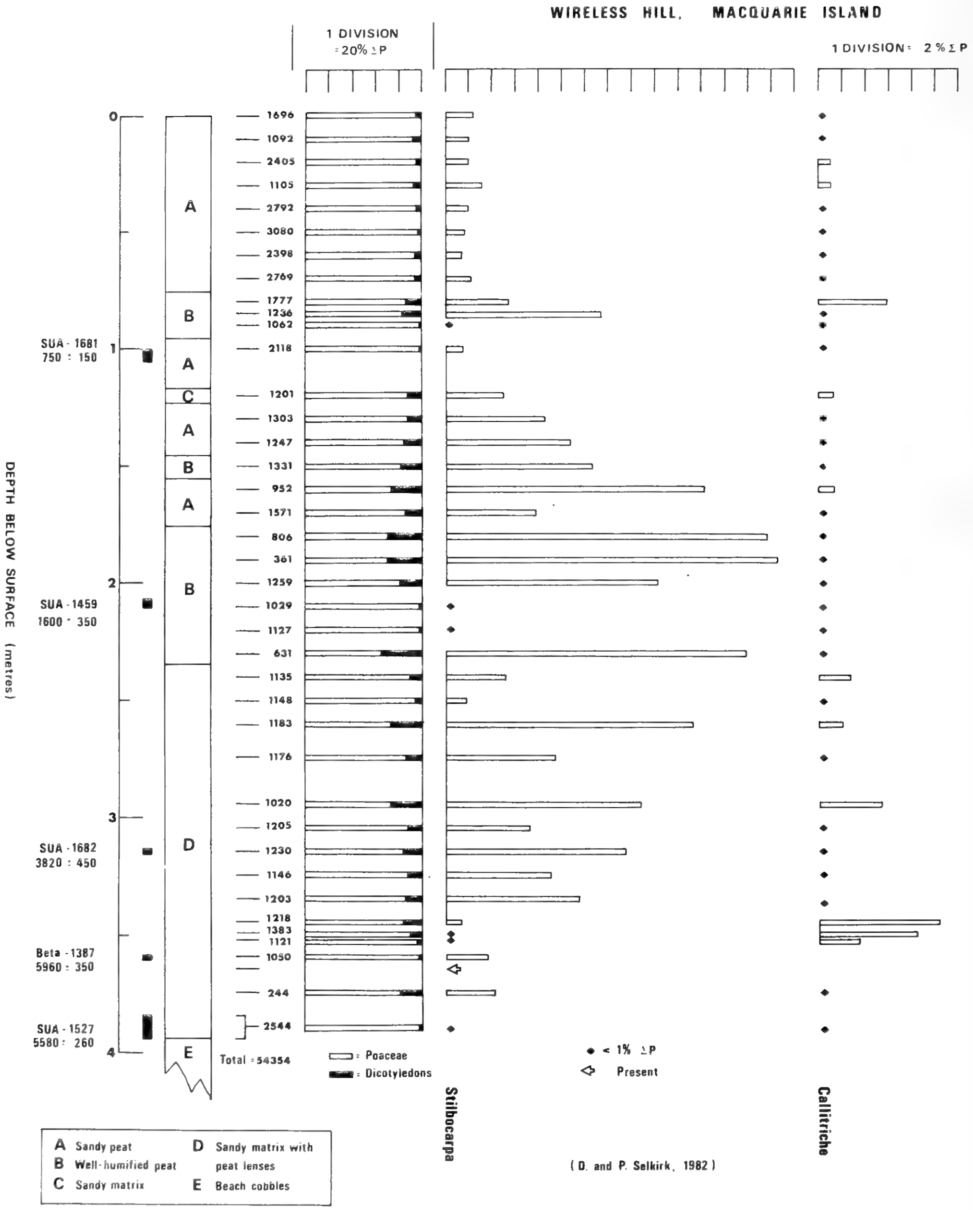


Fig. 6. Pollen diagram and stratigraphy of profile.

occur as lenses within the sandy matrix but have not been traced laterally to decide if this is so. From 384-394 cm the mineral matrix contains sand- to gravel-sized rounded balls of peat. The peat balls probably represent erosion of a pre-existing peat and incorporation of its fragments in the matrix. Whether erosion and redeposition occurred in situ or whether the peat balls were carried some distance by wind or water

Fig. 6. (Continued)

is unknown. Wind ablation of peat occurs on the island today during short relatively dry periods (J. Scott, pers. comm.).

Radiocarbon dates shown in Fig. 6 have been calibrated following Klein *et al.* (1982). Table 1 shows various radiocarbon dates obtained from the profile. There is no evidence in either the stratigraphy or dating of any prolonged hiatus in deposition since

TABLE 1

Depth (cm)	Code Number	Conventional Radiocarbon Age (years bp)	Calibrated Age (years BP, 95% confidence level)
384-394	SUA-1527	4880 ± 90	5580 ± 260
	SUA-1527 HA*	4610 ± 100	5300 ± 300
358-360	Beta-1387 (soluble fraction)	5140 ± 140	5960 ± 350
313-315	SUA-1682	3490 ± 210	3820 ± 450
206-210	SUA-1459	1600 ± 130	1600 ± 350
	SUA-1459 HA	1300 ± 90	1210 ± 160
100-105	SUA-1681	760 ± 100	750 ± 150

*HA = humic acid fraction

the profile began accumulating some 5500 years BP. There is some wash down through the peats of humic acids, as evidenced by the paired dates for insoluble and soluble fractions of SUA-1527 and SUA-1459.

At and below 274 cm there are large numbers of corroded and fragmented grass pollen grains. Only intact grass grains have been included in the pollen sum. In general, dicotyledon pollen appears to have been less susceptible to corrosion. *Callitriche* pollen, however, appears to corrode fairly rapidly, but remains identifiable even when corrosion is rather severe. No pollen was recoverable from the 110 cm sample. The pollen sum includes all local and exotic pollen grains, but excludes spores.

Results of the pollen analysis are given in Fig. 6. Exotic pollen grains occur throughout the profile, but in very small numbers, never more than 0.3% of the pollen sum. Podocarp grains are the most common exotic type, and there are occasional myrtaceous pollen grains. Several unknown types of exotic pollen were encountered. No attempt has been made to identify them because of the extremely small numbers involved. Fern spores occur even more rarely than exotic pollen. Of the thirteen encountered in a total of some 54000 spores and pollen grains counted, two are referable to *Hymenophyllum* and two to *Grammitis*. The rest are monolete spores which could represent *Polystichum* and/or *Blechnum*. All four fern genera are represented in the island's present flora. Spores of *Lycopodium* also occur rarely, and are present from the base of the profile. Because of the very low frequency of exotic pollen grains, fern and *Lycopodium* spores, they have not been included in the pollen diagram.

Grass phytoliths make up a significant proportion of the siliceous fraction of all samples. Diatoms and chrysomonad cysts are also common throughout. Diatoms are common on leaves of living *Poa foliosa* on Macquarie Island, and may well occur on leaves of most plants where conditions remain constantly moist. Chrysomonad cysts have been observed on the base of living *Poa foliosa* leaves and are common in samples of surface litter.

A survey of the diatoms in the profile (H. Brady, pers. comm.) shows close correspondence between preservation of diatoms and of pollen. At levels in which pollen is poorly preserved, diatoms are too broken for meaningful counts (e.g. 100-160 cm, 230-240 cm, 359-375 cm). These correspond with sandy layers in the stratigraphic column. Marine diatoms are present in low frequency (1-11% of the total diatom count) throughout the profile, presumably from wind-blown spray.

One diatom assemblage stands out in startling contrast to those in the rest of the profile. *Pinnularia atwoodii* is present throughout the profile in low frequency (0-4%) but at 394 cm, 344 cm and 294 cm, dominates the assemblage (12-19%). When

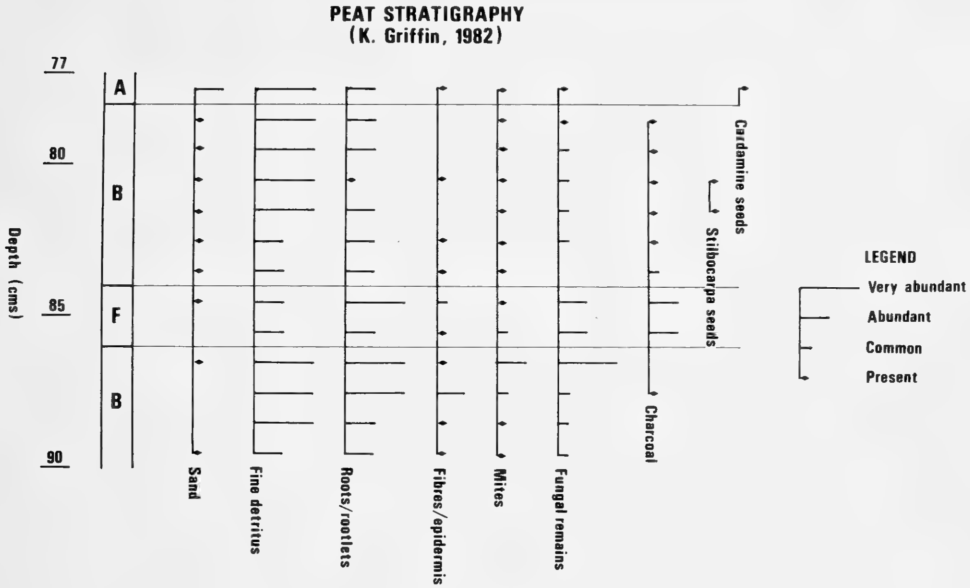
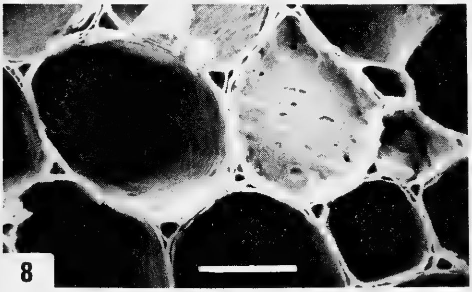


Fig. 7. Detailed stratigraphy of profile straddling charcoal layer at 85 cm. F = charcoal-rich layer. Other symbols as in Fig. 6.

samples from five modern seal wallows were examined it was found that in all five, there is only a small (less than 1 %) marine component. In three of the five, *P. atwoodii* is common, suggesting that this species thrives in a well-manured environment, such as seal and/or penguin-disturbed sites.

Plant macrofossils referable to specific genera occur most commonly in the well-humified peat layers above 200 cm. *Stilbocarpa* seeds first appear once pollen of that genus has reached its peak, but reappear throughout the upper part of the profile, even though *Stilbocarpa* pollen percentage declines.

Especially interesting is the occurrence in this profile from a hyperoceanic subantarctic island of two charcoal layers. There is a very distinct charcoal layer at 85 cm, and a less distinct charcoal layer at 30 cm. The layer at 85 cm has been traced a short distance laterally from the sampling site, but its full extent is unknown. A detailed



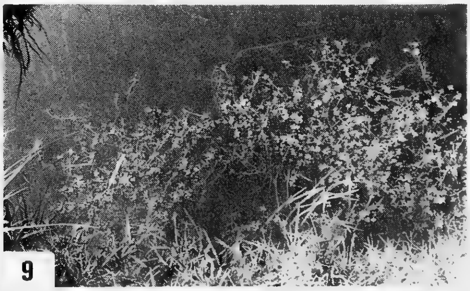


Fig. 8. Scanning electron micrograph of charcoal fragment from 85 cm depth. Note distinct layering of cell walls in cross-section. Scale line 25μm.

Fig. 9. Callitriche antarctica growing as an aquatic in an abandoned or little-used seal wallow.

stratigraphic study of the peat straddling the 85 cm zone is shown in Fig. 7. Movement of charcoal particles up and down the profile from the main layer is probably due to bioturbation. A test used to verify the presence of charcoal in palynological preparations (Singh *et al.,* 1981) indicates that the small black particles seen in the pollen preparations, and the macroscopic pieces visible in the peat, are indeed charcoal. The material even withstands the acid digestion technique used to prepare the siliceous fraction of samples for study. Macroscopic pieces are black, brittle, and have a characteristic sheen as seen in modern charcoal. Fig. 8 shows a scanning electron micrograph of a charcoal specimen, probably the remains of an axis such as a stalk of a *Poa foliosa* inflorescence. The specimen received no treatment other than the cutting of a flat face on the specimen with a razor blade and coating for scanning electron microscopy.

DISCUSSION

The profile analysed is likely to record vegetation change of a quite local nature. The site is on the western edge of Wireless Hill where, as is true for the whole island, winds are overwhelmingly north-westerly to south-westerly (Mawson, 1943: 30), blowing across thousands of kilometres of open ocean. Winds from other directions are uncommon, but when they do occur are usually gale force. There is no reason to assume major change in this wind pattern over the past 5000 years, so one could reasonably infer that pollen in peats on Wireless Hill would be derived mainly from vegetation close to the site or blown up to the site from the slopes and strand below. This inference appears to be justified since the pollen diagram shows an almost complete absence of a wide regional component. Barrow (1978) found that pollen in surface litter samples on South Georgia is principally derived from plants growing in communities very near sample sites. In the profile studied here *Azorella* pollen, for example, occurs only sporadically and in very low frequency, although *Azorella selago* is dominant in the feldmark community which covers about half the main part of Macquarie Island to the south, at altitudes above 250 m. *Azorella* pollen is common in surface samples in herbfield and feldmark situations on the main island (M. Salas, pers. comm.).

That the vegetation on or close to the site has been grass dominated for the past 5000 years or so is clear. Grass pollen is always present in huge quantities when compared with dicotyledon pollen, intact grass anthers have been encountered in all pollen preparations, and the relative abundance of immature grass pollen grains suggests a local source for the pollen. Grass phytoliths make up a significant proportion of the siliceous fraction of all samples. Phytoliths almost certainly represent grass growing on or close to the site, since they have little chance of becoming airborne once they rot out of the decaying foliage which has become incorporated in the surface litter layer. In dry, continental areas phytoliths may become airborne in dust, possibly being carried some distance (Baker, 1959a, b), but would be likely to remain in situ on Macquarie Island in the moist environments suitable for peat formation.

Vegetational changes recorded in the profile are not readily interpretable in terms of climatic variation. There are no major variations in ‘upland’ or ‘lowland’ components such as have allowed identification of climatic change on other subantarctic islands (Bellair and Delibrias, 1967; Bellair-Roche, 1972; Schalke and van Zinderen Bakker, 1971; Young and Schofield, 1973; Roche-Bellair, 1973, 1967a, b). Barrow (1978) could detect no evidence of major climatic variation over the past 10000 years on South Georgia by means of pollen analysis even though there was probably a readvance of valley glaciers about 5500 years BP (Stone, 1976).

The sequence of events recorded in the samples can most readily be interpreted in terms of localized vegetational changes resulting from uplift of the site from a position close to sea level to its present altitude. That the cobbles underlying the deposit are those of an ocean beach rather than a lake-shore beach is clear. Only a substantial lake at 100 m would allow sufficient wave action to form a well-developed beach, and such a beach would be best developed at the lake's eastern end, due to prevailing winds. Interpretation of the cobbles as those of a lakeside beach would imply loss of an extensive area of land to the west of the present Wireless Hill. For this there is no evidence. The basal sequence of the profile gives a clear indication of animal-disturbed vegetation, and taken together, both pollen and diatoms present in the basal samples point to elephant seals as the most likely cause of this disturbance.

The peaks in *Callitriche* pollen between 120 and 352 cm almost certainly represent periods of modification of the vegetation by animals. On Macquarie Island at present, *Callitriche* appears only to be locally abundant where there is animal disturbance and manuring of the vegetation. It is most common around elephant seal wallow areas, growing both on the ground between wallows, and as an aquatic plant in the water of abandoned and infrequently used wallows (Figs 5 and 9). Taylor (1955) described *Callitriche* as growing on very wet soils and in pools at low elevations, commonly colonizing abandoned seal wallows. Gillham (1961) pointed out the close association between *Callitriche* and animals, recording it as most common on and near seal wallows, and common in wet gentoo penguin rookeries on the 'featherbed' at Handspike Point. J. Scott (pers. comm.) reports *Callitriche* and *Poa annua* as locally luxuriant near abandoned gentoo nesting sites close to the sea, and notes that such sites are also commonly disturbed by elephant seals. At higher altitudes, similar but less luxuriant growth of *Callitriche* and *Poa annua* occurs in association with giant petrel colonies, although both plants are rare in the surrounding undisturbed tussock grassland (J. Scott, pers. comm.). *Callitriche* can occur also in small quantities in rockhopper penguin rookeries which may be at considerable altitude. Whether *Callitriche* can be associated with albatross nests on Macquarie Island is still unclear. Although *Callitriche* acts as a colonizing species on peat surfaces bared by landslip, providing 15-20% cover eighteen months after slippage, it appears to be absent from old well-vegetated slip sites (J. Scott, pers. comm.).

On other subantarctic islands, *Callitriche* also seems closely linked with animal disturbance. On South Georgia, *Callitriche* is almost entirely confined to seal wallow areas in *Poa* tussock grassland, but also occurs in 'meadow' bogs enriched by bird excreta (Smith, 1981). On Marion and Prince Edward Islands, *Callitriche* is locally important in areas manured by seals, rockhopper penguins and albatrosses, forming part of a community called by Huntley (1971) a biotic complex. Croome (1971) studied effects of albatross manuring on Marion Island, and found *Callitriche* abundant near albatross nests. Smith (1978) found that *Callitriche* occurred only in manured sites on Marion Island. Schalke and van Zinderen Bakker (1971) interpreted *Callitriche* peaks in their pollen diagrams as due to albatross nesting.

The peaks in *Callitriche* pollen at 20, 30 and 80 cm (Fig. 6) may represent bird activity. Black browed albatrosses and giant petrels have nested on Wireless Hill quite recently (G. Johnstone, pers. comm.) and could cause local flushes of *Callitriche*. However the peaks in *Callitriche* at 30 and 80 cm are also associated fairly closely with charcoal layers in the peat, discussed below.

If *Callitriche* pollen is to be used as an indicator of environmental conditions at a very localized site, then it is necessary to establish that its pollen is not transported far from its origin. The possibility of large inputs of windborne pollen needs to be eliminated. Analysis of pollen in a surface litter sample, a moss mat and a modern seal wallow (Fig. 10) indicates that *Callitriche* peaks in the pollen record almost certainly represent vegetation on or close to the site. The surface litter sample was collected from the top of the profile analysed. *Callitriche* contributes less than 1% of total pollen and only 10% of total dicotyledon pollen. On the coast below and to the west of the collection site is a seal wallow area (Fig. 1) which provides a source of *Callitriche* pollen which has, however, not been blown the 100 m up to the site on prevailing winds. Similarly, analysis of a mat of *Amblystegium* at 80 m a.s.l. on the Doctors Track (Fig. 1), above extensive seal wallow areas on both sides of the isthmus (Fig. 4) yielded *Callitriche* at levels of less than 1% on both a total pollen and dicotyledon-only basis. The *Amblystegium* mat was collected when extensive swards of *Callitriche* in the wallow areas were in full flower, and when prevailing winds were favourable for pollen transport.

Both the litter and the moss mat samples, taken in conjunction with an analysis of pollen from a modern seal wallow (Fig. 10), indicate that most *Callitriche* pollen is deposited very locally, and that transport to other sites is very minor. This is perhaps not surprising for a plant which grows as a low mat on very wet soils, or as an aquatic (Fig. 9) in a hyperoceanic environment with almost daily precipitation.

We interpret the main *Callitriche* peak at 344-352 cm as representing seal wallow conditions on or very close to the site. In these samples *Callitriche* pollen is markedly more abundant than elsewhere in the profile, and accounts for 65-88% of total dicotyledon pollen (Fig. 10). In modern wallows (Fig. 10) *Callitriche* reaches 95% of total dicotyledon pollen with *Cotula, Stilbocarpa* and other dicotyledons present in small amounts. On a dicotyledon-only basis the 294 cm sample is much poorer in *Callitriche* (20% of total dicotyledons), while at 80 cm it reaches 45% of total dicotyledons. The occurrence in the 394 cm, 344 cm and 294 cm samples of diatom suites rich in *Pinnularia atwoodii* is consistent with the interpretation from the pollen evidence, that

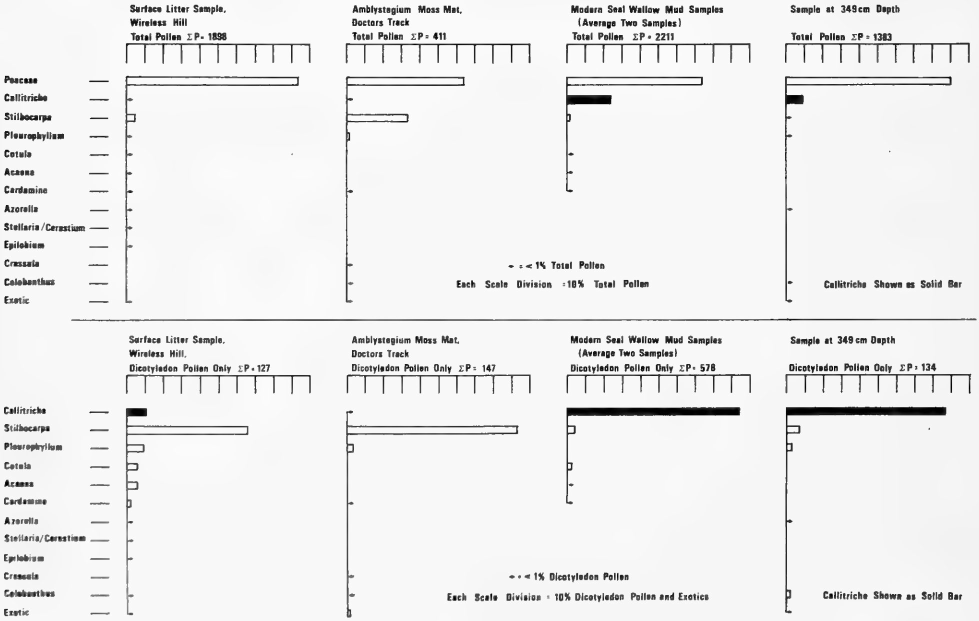


Fig. 10. Pollen diagram comparing analysis of a surface litter sample, *Amblystegium* moss mat, modern seal wallow mud and sample at 349 cm depth in profile. Upper diagrams show % total pollen. Lower diagrams show % based on total dicotyledon plus exotic pollen only.

the basal sequence of the profile represents an animal-disturbed area, most probably a seal wallow.

Since the basal *Callitriche* peak appears to represent seal wallow conditions, developed only at low altitudes, the pronounced peak in *Pleurophyllum* at 374 cm could appear anomalous, since *Pleurophyllum hookeri* is very common in subglacial herbfield (Taylor, 1955) at altitudes of about 200 m or more. *Pleurophyllum,* however, is also a major component of communities on the raised beach terrace at the northern end of the west coast of the island. Taylor (1955) mentions elephant seal destruction of *Pleurophyllum* patches at numerous places on this terrace. The pollen record could well represent elephant seal invasion of such an established community, close to the sea.

If the basal portion of the sequence represents the local presence of seal wallows, there are important implications in the record for the tectonic history of Wireless Hill. Seal wallows on top of the hill at its present altitude of 100 m are impossible. So steep are the slopes to the flat top that fixed ropes are provided to assist people in the climb. Seals could only wallow in the area if it were close to sea level. Wallows on Macquarie Island and other subantarctic islands occur on flat areas relatively close to the ocean, and elephant seals probably do not regularly go more than 15-20 m above sea level. If one accepts 20 m as the probable upper limit of elephant seal-modified vegetation, the conclusion seems plausible that, at about 5500 years BP, the Wireless Hill site, now at 100 m, can have been no more than about 20 m above sea level. Uplift of the site relative to sea level at average rate of 14.5 m/1000 years over the past 5500 years is implied. This rate is 3-4 times the maximum rate of uplift calculated for the marine terraces on the main part of the island (Colhoun and Goede, 1973).

The increase to a maximum, followed by a decrease, of *Stilbocarpa* pollen is explicable in terms of steady uplift of the site. On Macquarie Island, *Stilbocarpa polaris* is very common in a rather narrow altitudinal band at the base of the scarps which bound the island and on their lower slopes. Higher up the scarps as on the western side of Wireless Hill, *Stilbocarpa* gives way to dense stands of *Poa foliosa* tussock. The upper limit of this pure tussock grassland occurs at the scarp-plateau transition and may extend beyond it in favoured conditions. *Stilbocarpa* is particularly common in soil-slip and other bare areas on steep slopes (Taylor, 1955). Taylor regarded the presence of a mixed *Poa* tussock-*Stilbocarpa* community as a stage in succession to pure *Poa foliosa* tussock. One can imagine *Stilbocarpa* as having been common on steep, unstable slopes which could have developed on Wireless Hill during uplift, and then declining in importance at higher altitude as *Poa* tussock stands became more common at the top of the slope and on the edge of the plateau.

Radiocarbon dating of the base of organic deposits overlying a raised beach does not of itself provide dating of the uplift since there may be a considerable and unpredictable time lapse between uplift and establishment of vegetative cover. Colhoun and Goede (1973) commented on the probability, in a hyperoceanic environment such as that of Macquarie Island, of the immediate development of vegetation on any land surface lifted above the limit of marine erosion. With this we agree. Stone (1979) reports thin peat deposits on an 8 m raised beach on South Georgia. The ^{14}C dates for the Wireless Hill site imply development of vegetative cover only some 5500 years ago. Had the site been anywhere near its present altitude before that time, one would expect peat accumulation to have begun earlier. At 100 to 150 m altitude at both Finch Creek and Green Gorge peat was accumulating considerably earlier (about 10000 and 6900 years bp respectively) (Selkirk and Selkirk, 1983). The likelihood of peat accumulation at the same altitude on Wireless Hill being delayed several thousand years is remote. It is difficult to envisage complete removal of an older peat which originally overlay the cobbles and its replacement at a later stage by another peat. Erosion by wind and/or water is unlikely to have removed peat from a flat-topped hill while peat accumulated elsewhere. Landslip would not remove material from an almost flat surface in any quantity, while landslip on the steep slopes near the site is unlikely to have left the beach deposit intact. It seems more likely that peat accumulation on what is now the top of Wireless Hill only began some 5500 years ago because it was only then that the site became clear of overwhelming marine influence.

The postulated rapid uplift of the Wireless Hill site can only be due to tectonic activity on the Macquarie Ridge. There is no evidence of any but slight relative sea-level changes in the period under consideration (Clark and Lingle, 1979). Large-scale isostatic readjustment following removal of an ice sheet can be ruled out, if glaciation of Macquarie Island has been moderate (Colhoun and Goede, 1974; Löffler and Sullivan, 1980). Glacio-isostatic readjustment is probably responsible for some low-level raised beaches on other subantarctic and antarctic islands. On South Georgia there is a series of Holocene raised beaches up to 7 m above sea level (Clapperton, 1971; Stone, 1974, 1976), and a series of raised beaches at higher levels (up to 52 m) which are much older, clearly predating a glaciation (Sugden and Clapperton, 1977; Clapperton *et al.*, 1978). Clapperton *et al.* suggest a date for the 7 m raised beach somewhere between 9500 and 4000 years BP. John and Sugden (1971) described high-level residual beaches, overridden by till, at altitudes up to 275 m in the South Shetland Islands block, possibly structurally linked to Patagonia, where late Tertiary tectonism produced raised marine features. Low level raised beaches occur on Marion Island series of lower raised beaches, the beaches at about 6 m dating at approximately 640 radiocarbon years (Sugden and John, 1973). On West Falkland raised beach deposits occur up to 69 m (Clapperton and Sugden, 1976), and it is suggested that the most likely explanation for the high-level beaches is tectonic movement of the Falkland Islands block, possibly structurally linked to Patagonia, where late Tertiary tectonism produced raised marine features. Low level raised beaches occur on Marion Island (Hall, 1978). The raised beach on Wireless Hill at 100 m, almost certainly Holocene, and overlain by deposits dating at about 5500 years BP appears to be in striking contrast with other subantarctic raised beaches.

The suggested rate of uplift for the Wireless Hill site is high. Movement along the fault line which separates Wireless Hill from the isthmus (Varne and Rubenach, 1972) must have been frequent, although there has been no reported movement on the fault line since discovery of the island. Single large earthquakes have been associated with uplift of the order of 10 m over small areas (Plafker, 1965).

Rates of tectonic movement quoted in the literature are lower than the postulated 14.5 m/1000 years for Wireless Hill. Suggate (1978) quotes uplift of about 10 m/1000 years at the Paring River locality on the Alpine Fault of New Zealand, the Alpine Fault being regarded as a northward extension of the Macquarie Ridge. Chappell (1974) and Chappell and Veeh (1978) used emergence of coral reefs above sea level to study tectonic movement in New Guinea and Timor. Rates of uplift in the Timor area range from 0.5 m/1000 years to 0.03 m/1000 years (Chappell and Veeh, 1978).

The presence of the distinct charcoal layer at 85 cm and the less pronounced charcoal band at 30 cm appears to be the first direct evidence for natural, rather than man-made, fire in the subantarctic. Barrow (1978) states that South Georgia has suffered no fire, while vegetation on the Falkland Islands has suffered from both fire and grazing pressure for some time. Further research on South Georgia may, of course, eventually give evidence of fire there. Fires have certainly occurred on Macquarie Island since sealing began there and Cumpston (1968) refers to several deliberately-lit fires. However, there is no reference to the effect of fires on vegetation. G. Copson (pers. comm.) has seen vegetation on Wireless Hill continue to burn after having been accidentally lit, and believes a peat fire could burn for some time once started. J. Jenkin (pers. comm.) reports having watched fire from a burning rubbish heap on the main island spread into tussock vegetation, heat from the fire drying out the vegetation in front of it as it was fanned by wind. The only agent likely to cause natural fire on Macquarie Island is lightning, which Copson states is recorded on average at least once a year. A dry spell coupled with lightning strike offers the best possibility for fires. Although such events would be rare, over a period of thousands of years a number of such events could occur.

Macroscopic charcoal pieces from the 85 cm layer when viewed under scanning electron microscopy do not meet the criteria for charcoal put forward by Cope and Chaloner (1980). Cope and Chaloner, dealing with woody tissue, regarded the presence of homogeneous cell walls without visible layering as diagnostic of wood charcoal under the scanning electron microscope. Cell walls of the putative charcoal from Macquarie Island (Fig. 8) are clearly not homogeneous. However, very little is as yet known about charcoal pieces derived from herbaceous plants, and it is probable that tissues other than wood, charred under wet conditions, may give a charcoal differing rather radically from the type of wood charcoal usually encountered in sediments.

It is interesting that both fire events appear to correlate with an increase in *Callitriche* pollen. *Callitriche* may not only be coprophilous, but may also act as a colonizer of wet bare areas with high nutrient levels such as would occur after fire in tussock grassland. As there are no direct observations of recolonization by plants of burnt areas on Macquarie Island, it is not possible to be sure of this, however, as bird disturbance of vegetation may also account for the increase in *Callitriche* pollen at both 80 and 30 cm.

In summary, sediment, palynological, diatom and plant macrofossil analysis of samples from this profile show evidence of changing vegetation on the site. Having considered the possible alternatives, we feel that the available evidence is most appropriately interpreted as suggesting that this site was at or close to sea level about 5500 years ago when it began accumulating vegetation; that the plant communites, when close to sea level, were animal-, probably seal and/or gentoo penguin, disturbed; and that the sequence of vegetation changes in the profile reflects changes due to altitude as the site was uplifted.

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Estuarine Flora and Fauna of Smiths Lake, New South Wales

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(Communicated by L. W. C. FILEWOOD)

ROBINSON, K. I. M., GIBBS, P. J., BARCLAY, J. B., & MAY, J. L. Estuarine flora and fauna of Smiths Lake, New South Wales. *Proc. Linn. Soc. N.S.W.* 107 (1), (1982) 1983: 19-34.

Data on the distribution of benthic invertebrates and aquatic macrophytes in Smiths Lake were collected during the summer of 1979/1980. These data are discussed in relation to information on past distributions and hydrological conditions. Qualitative data on the lagoon's fish community are presented.

The distribution of aquatic macrophytes has varied over recent years, probably as a result of salinity changes associated with opening or closure of the lagoon entrance. Under the present salinity regime, seagrass distribution is probably limited by the degree of light penetration and wave action.

Benthic invertebrate communities are related to substrate type and vegetation. Seagrass and sand habitats support more diverse and abundant communities than mud sediments.

Both the benthic and fish communities recorded in Smiths Lake are typically estuarine, and resemble communities in other lagoons along the N.S.W. coast. The absence of several benthic and fish species commonly associated with N.S.W. estuaries is attributed to intermittent closure of the lagoon to oceanic influence.

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INTRODUCTION

In recent years there has been an accumulation of ecological data on the aquatic flora and fauna of New South Wales coastal lagoons. Although some data have been published (MacIntyre, 1959; Thomson, 1959; Wood, 1959; Higginson, 1965, 1970; Weate and Hutchings, 1977; Hutchings *et al.,* 1978; Powis and Robinson, 1980; Harris *et al.,* 1980; Collett *et al.,* 1981; Atkinson *et al.,* 1981), much still remains in the form of theses and student reports. This paper combines unpublished data on Smiths Lake with surveys of the macrobenthic fauna and flora of that lagoon undertaken in the summer of 1979/1980.

STUDY AREA

Smiths Lake is a marine-dominated coastal lagoon (32°24′S, 152°22′E), 130 km north of Newcastle, N.S.W. The lake is 10 km^2 in area with its catchment extending just beyond its perimeter (Bell and Edwards, 1980). Freshwater input is provided by swamps on the southern shore, and during rainy periods by several small creeks (Fig. 1). The median annual rainfall in nearby Bulahdelah is 1251 mm, the wettest months being in late summer and early autumn (Atkinson *et al.,* 1981).

The lagoon is divided into two main regions by a sandbar at Simons Point. The seaward end comprises a wide shallow lagoon (1-2 m deep) with deeper holes (3-4 m) at its northern and southwestern extremities. The western region of the lagoon is twice the area of the seaward region with an average depth of 3-4 m and a maximum depth of 5 m off Big Island.

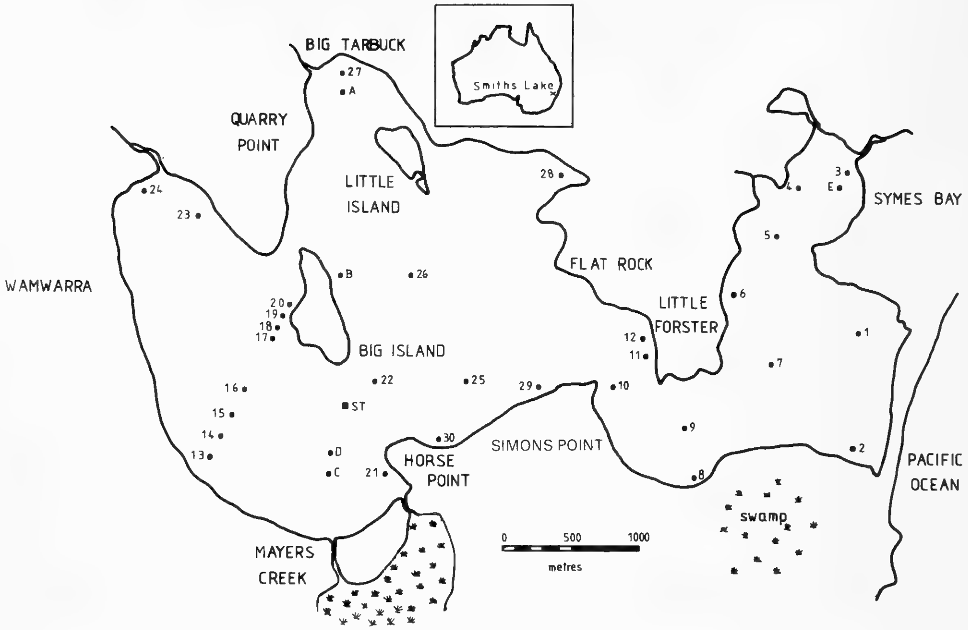

Fig. 1. Smiths Lake showing benthic fauna and salinity/temperature sampling sites (1-30), *Zostera* abundance sites (A-E) and two-year salinity and temperature sampling site (ST).

Smiths Lake is one of many lagoons on the southeast coast of Australia that are closed to the sea by sand barriers. It is opened naturally to the sea when the pressure of flood waters after heavy rain causes the sandbar to give way (Bird, 1967). Since early this century fishermen have periodically opened the sandbar at Smiths Lake to allow the movement of fish from the sea into the lagoon; more recently (1959) it has been breached artificially to prevent flooding. Since 1932, the lagoon has been opened to the sea on an average of once every 1.5 years, with the longest closure being 4 years and the shortest one month. Depending upon the weather conditions, the lagoon has remained open to the sea for periods ranging from one to 11 months.

HYDROLOGY

Materials and Methods

In December 1979, surface and bottom temperatures and salinity readings were recorded at 30 sites (Fig. 1) throughout the lagoon using a salinity — temperature bridge (Hamon, 1956). During this survey the lagoon was closed to the sea, and its waters were approximately one metre above sea level. The most recent connection to the sea occurred between June and August 1978. For two years prior to this survey, surface temperature and salinity readings were recorded monthly at one station (Fig. 1).

Light penetration through the water was measured with a Secchi disc. Between December 1979 and October 1980 Secchi extinction depths were recorded approximately every six weeks at four sites in Smiths Lake (Fig. 1). No readings were taken at Site D because of its close proximity to Site C.

Results and Discussion

The mean and standard deviation of surface and bottom temperatures during

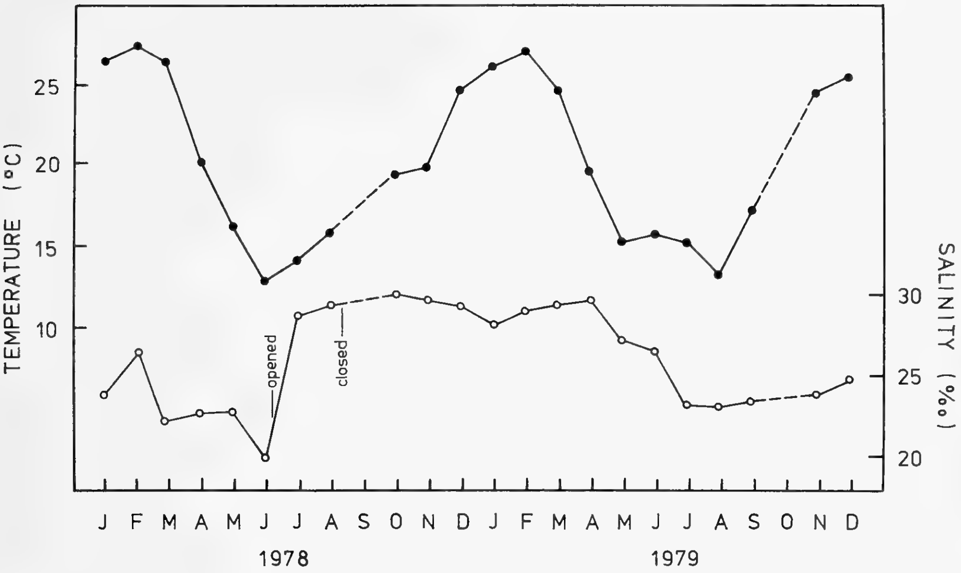

Fig. 2. Salinity and temperature readings at site ST taken over a two-year period.

December 1979 were 26.0 ± 0.67°C and 25.7 ± 0.67°C respectively; salinities were 25.28 ± 0.13$^{0}/_{00}$ and 25.25 ± 0.15$^{0}/_{00}$. This shows that the lagoon was homogeneous with regard to salinity and temperature at that time. However, when the lagoon has been open, salinity and temperature have varied with depth. Haloclines particularly have occurred due to the intrusion of oceanic water (e.g. 25$^{0}/_{00}$ salinity on surface, 31$^{0}/_{00}$ on bottom during February 1973) (U.N.S.W. unpublished student reports).

The monthly surface temperature and salinity readings for 1978-1979 are given (Fig. 2). Seasonal changes in temperature were observed with a maximum of 27°C occurring in February and winter minima of 12°C in June 1978 and 13°C in August 1979. Surface salinity fluctuated between 20-30$^{0}/_{00}$ throughout this period due to rainfall, evaporation and the opening of the lagoon. Minima of 8.5°C and 10$^{0}/_{00}$ have been recorded during the winter of 1967 (Dixon, 1975).

Heavy rainfall prior to June 1978 resulted in a drop in salinity (20$^{0}/_{00}$) and a rise in water level of approximately one metre. Breaching of the sandbar in June 1978 caused an abrupt change. The water level dropped by approximately 2 m and the salinity increased from a minimum of 20$^{0}/_{00}$ to a maximum of 29$^{0}/_{00}$ within 7 weeks.

Light penetration readings ranged between 2.1 m and 2.4 m at the three western sites, but were much higher (3.8 m) at the northeastern site (Table 1). The implications of this for plant growth will be discussed in the next section.

AQUATIC MACROPHYTES

Materials and Methods

In mid December 1979 the occurrence of vegetation was recorded by a SCUBA diver towed on a manta board along transects both perpendicular and diagonal to the shore line. The minimum and maximum depths at which species were found were noted. In February 1980, the abundance of the seagrass *Zostera capricorni* Aschers. was estimated by two methods:

TABLE 1

Estimates of Zostera *abundance in Smiths Lake in February 1980, and Secchi extinction depth taken from December 1979 to October 1980*

Site	N	Depth (m)	Density (shoots/m^2) Mean ± S.E.	Leaf Height (m)	Mean Biomass g/m^2 (dry wgt)				Secchi Extinction Depth m. Mean ± S.E.
					Living leaf	Detritus	Root	Total	
A.	24	1	379 ± 45	—	—	—	—	—	2.2 ± 0.1
B.	24	2	207 ± 233	0.50	60	20	118	198	2.1 ± 0.2
C.	24	2	281 ± 16	0.25	30	30	71	131	2.4 ± 0.2
D.	12	3	115 ± 28	0.30	12	10	6	28	—
E.	24	2	186 ± 15	0.55	72	12	176	260	3.8 ± 0.7

(1) Density (number of upright shoots) was determined in 24 quadrats (0.25 × 0.25 m) randomly distributed in 2.0 m of water at each of 3 sites, 3.0 m at one site and 1.0 m at another (Fig. 1). Comparisons between sites were made using a l-way Analysis of Variance. A test for homogeneity of variance was not significant so untransformed data were used. At each site leaf heights of the longest intact leaves were measured to the nearest 50 mm.

(2) The biomass of *Zostera* was estimated at 4 of the 5 sites from three samples taken at each site with a cylindrical corer, 0.03 m^2 and 100 mm deep. The samples were pooled and sorted into living leaf, detritus and root material. Wet weights were measured to the nearest gram and expressed as dry weight (gm^{-2}) using conversion factors (live leaf × 10.5%; detritus × 8.2%; roots × 9.6%) determined by Barclay (1978).

Results and Discussions

A conspicuous feature of the macrophytic community of Smiths Lake is the abundance of the seagrasses *Zostera capricorni* Aschers. and *Halophila ovalis* (R. Br.) Hook f. *Ruppia* sp. which can tolerate waters of high salinity (Aston, 1973) is also present. The algal flora of the lagoon is dominated by a species of *Dictyota* (Phaeophyta) which resembles most closely *D. furcellata* (C. Agardh) J. Agardh. *Laurencia* spp., *Sargassum* sp. and *Chaetomorpha* sp. occur in some shallow areas, however the taxonomy of these groups is not definitive.

Distribution: The macrophytes were restricted to the soft sediments of the lagoon perimeter and exhibited a general zonation pattern of *Dictyota, Zostera* and *Halophila* with increasing depth (Fig. 3). *Zostera* formed dense beds in the western sector of the lake and in Symes Bay but was absent from the eastern sandflat. *Ruppia* was found at the mouth of both Mayers Creek and the creek in Symes Bay. Clumps of *Dictyota* and *Laurencia* occurred infrequently on the extensive shallow (0.6 m depth) sandflat in the eastern end of Smiths Lake. *Dictyota* also occurred as a continuous band along the southwestern shore. *Laurencia, Sargassum* and *Dictyota* covered the rocks adjacent to Horse Point.

The shallowest occurrence of *Zostera* was 1.1 m in the lee of Little Island and along the northeastern shore (Quarry Pt to Little Forster); along the southwestern shore (Simons Pt to Wamwarra) the minimum depth was 2.0 m. *Zostera* grew to its maximum depth (3.4 m) in Symes Bay and in the southwest region *Halophila* generally occurred as a narrow band 0.5 m deeper than the *Zostera* but extending to 4.0 m depth off Little Island.

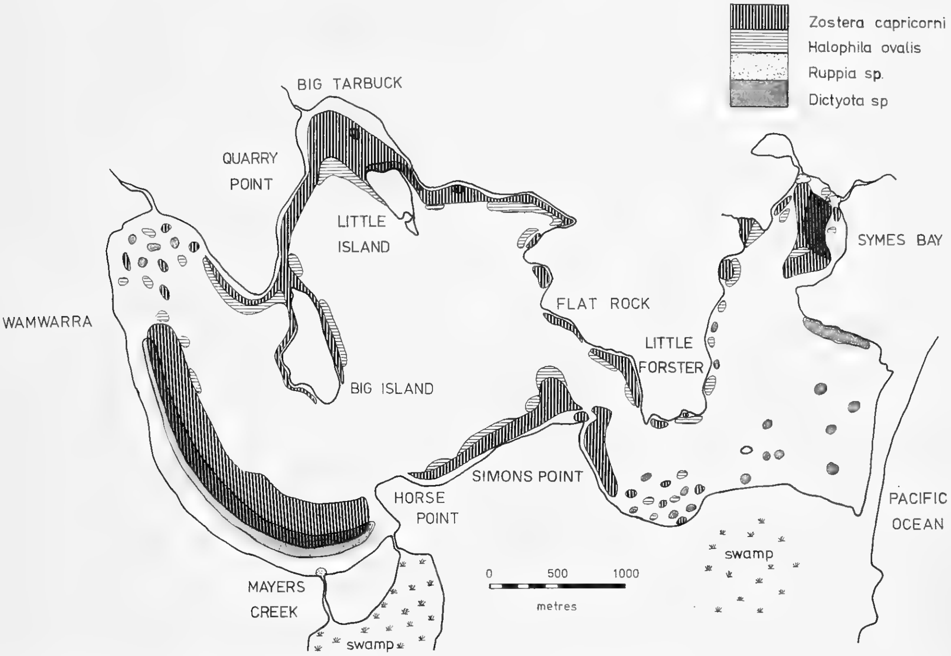

Fig. 3. Distribution of aquatic macrophytes in Smiths Lake, summer 1979/1980.

Local fishermen have reported a change in the distribution of seagrass species over the last 30 years. Before 1960, *Zostera* dominated the steppe (shallow perimeter of the southwestern sector of the lake at a depth of 3.5 m). In the mid 1960s the *Zostera* beds declined and *Ruppia* became the conspicuous angiosperm. Fishermen related this change to a lower salinity for an extended period. In summer 1968, *Ruppia* was the dominant macrophyte on the steppe (U.N.S.W. unpublished student reports), but it was not until February 1970 that the exact distribution of aquatic vegetation was first mapped. This showed that *Zostera* was present in the deeper water and as sparse patches amongst the more dominant *Ruppia* (U.N.S.W. unpublished student reports).

In mid 1970s the *Ruppia* beds disappeared and the steppe was devoid of vegetation for some years, although some *Zostera* was present near Big Island around this time (Dixon, pers. comm.). Fishermen reported the recolonization of the rest of the lake by *Zostera* in the late 1970s and, in February 1979, *Zostera* beds were recorded to a depth of 2.5 m around Big Island (U.N.S.W. unpublished student reports).

Abundance: Shoot density readings of *Zostera* at Site A (one metre deep) were excluded from the ANOVA as they were very much greater than the readings from the 2 m and 3 m sites (Table 1). The 1-way ANOVA of the remaining 4 sites indicated a highly significant difference (9.835, $p < 0.001$) in shoot density. A Student-Newman-Keuls test showed shoot density at the 3 m site (Site D) was less than those at both Sites B and E which in turn were less than that at Site C. The biomass estimate at the 3 m deep site (Site D) was also much less than all the other sites but Sites B and E both had a greater biomass than Site C. Sites B and E were similar in shoot density and total biomass although Site B had a higher detrital biomass and lower root biomass than Site E.

It has been suggested that there is a relationship between *Zostera* abundance and water turbulence and turbidity in N.S.W. coastal lagoons such as Tuggerah

(Higginson, 1965, 1967) and Illawarra Lakes (Harris *et al.,* 1980). Strong north-easterly winds and associated water turbulence occurred prior to the seagrass biomass sampling and if this impeded the normal growth of seagrass, it is likely that sampling took place during a period of regrowth. This would account for the high detrital stock, short leaf lengths and high shoot densities. Site E was protected from the prevailing winds and had the lowest detrital and highest living leaf biomass. Site B, while not as exposed as Site C, seemed to show some effects of the wind in that living leaf biomass was greater and detrital biomass less than at Site C.

Wave action may be a determining factor controlling the inshore limit to which seagrass can grow by not allowing propagating material of seagrass to establish at shallow depths. Thus, the absence of seagrass on the eastern sandflat and the lower depth to which *Zostera* was found on the southwestern shore is possibly due to the prevailing northeasterly winds.

It has been suggested that the availability of light may determine the maximum depth to which *Zostera* grows (Higginson, 1965; Harris *et al.,* 1980). This may account for *Zostera* growing to its greatest depth in the less turbid waters of Symes Bay and the southwestern region of the lagoon. Also, *Zostera* was less abundant at site D, perhaps due to the increase in depth and presumably a decrease in light. *Halophila,* in contrast, was still present at 4 m. This ability of *Halophilia* to tolerate a lower light intensity than *Zostera* has also been observed in Tuggerah Lakes (Higginson, 1965, 1967; Barclay, 1978) and in Lake Macquarie (Barclay, 1978).

On the southwestern shore, the upper distribution of *Zostera* may also be limited by reduced light due to the prolific growth of *Dictyota* forming a blanket across the bottom. This appears to be a spring and summer phenomenon and coincides with the major growth period of *Zostera.*

MACROZOOBENTHOS

Materials and Methods

Two 200 mm diameter sediment cores were taken at each of 30 sites (Fig. 1) in the lagoon during December 1979. Each core was washed through a one-millimetre sieve, the residue sorted and identified as far as possible to species level. Sediment type, seagrass cover and depth were recorded for each site.

A hierarchial monothetic divisive method (DIVINF-Williams, 1976) was used to classify sites using information gain as a dissimilarity index. This indicates the degree of similarity of sites based on presence/absence of species.

The community indices species number (S), number of individuals (N) and evenness (J') (Pielou, 1975) were calculated for each site.

As the faunal classification provided groupings that could be related to habitat types (see Results), the three community indices for each of six randomly chosen sites from each habitat type were compared using 1-way ANOVA. The null hypothesis was that there was no significant difference between habitat types for each of the indices. Tests for homogeneity of variances required N values to be log transformed. For S and J' untransformed data were used.

To provide a more extensive characterization of the fauna of each habitat, the 6 sites from each were lumped and S, N and J' determined for the lumped data in each habitat type. The numerically dominant species in each habitat were also determined.

Results and Discussion

43 species of macrozoobenthos were recorded in this survey (Appendix 1), but many were present only in low numbers or in few sites.

The dendrogram of the classification is shown as Fig. 4 and the classification site

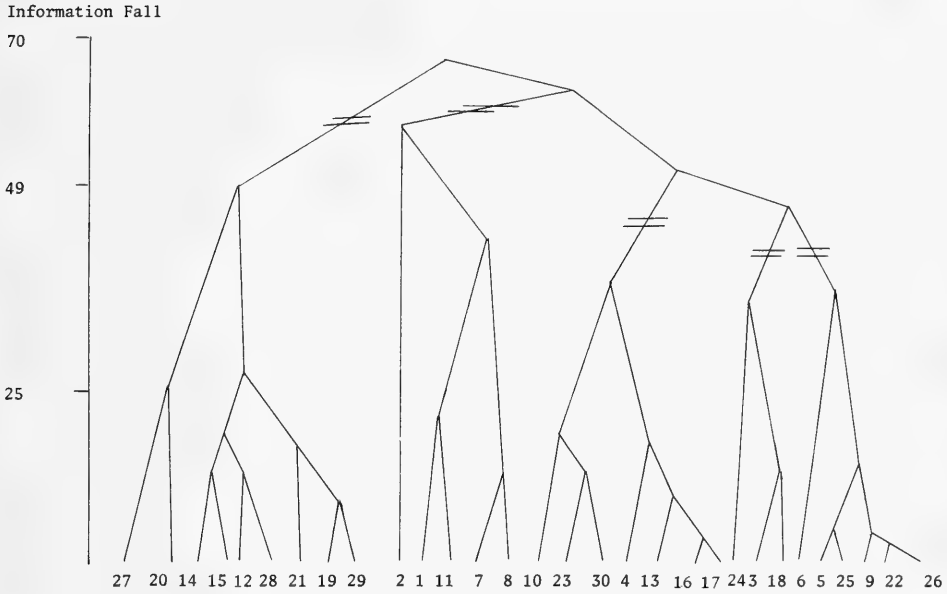

Fig. 4. Dendogram showing macrozoobenthic site groupings.

groupings, habitat type, location, divisive species and other species common to each site group are shown in Table 2. Site groupings were split into 5 groups on the basis of faunal characteristics and these groupings corresponded with habitat type.

Site groups I, II and V showed a very pronounced habitat preference by the fauna. Groups III and IV, however, were evidently quite distinct from the main habitat groups defined by I, II and V. The sand sites in site group II were from the eastern side of the lake whereas the sand sites in site group III were from the central and western areas. The mud in the site group III and the seagrass sites in group IV were both from outlying areas compared with mud in group V and the seagrass sites in Group I.

The separation between sand sites was due to the polychaete *Scoloplos simplex* and the filter feeding bivalve *Sanguinolaria donacioides,* neither of which appeared in the central or western sand sites. The geographical separation amongst seagrass and amongst mud sites was due mainly to the presence or absence of numerically unimportant species. Both seagrass site groups have the same characteristic species regardless of where they were located in the lagoon, as did both mud site groups.

Means and standard errors of community indices for each habitat are shown in Table 3. 1-way ANOVA between habitat types for species number was significant (6.759, $p< 0.01$). S-N-K test showed mud sites to have significantly fewer species than either sand or seagrass sites, while there was no difference between sand and seagrass. N also showed a significant difference (21.674, $p< 0.001$), mud having significantly fewer individuals than sand, which in turn had significantly fewer than seagrass sites. Although the ANOVA for evenness was significant (5.075, $p< 0.05$), the only significant difference was between mud and seagrass sites, the former being greater. High numbers of *Velacumantus australis* in seagrass beds probably accounted for the low evenness.

Table 4 shows community indices and dominant species for lumped data in each

TABLE 2

Macrobenthic Site Groupings

(Z = *Zostera;* H = *Halophila;* S = sand; M = mud; R = *Ruppia*)

Site Group	Site	Habitat	Site Location	Comment
I	27	Z	Mostly seagrass sites in west or central part of lagoon. 21 in area adjacent to seagrass. 12 at junction of central/east.	Presence of *Marphysa sanguinea* separating characteristic. Other common species *Velacumantus australis, Notomastus torquatus, Owenia fusiformis, Nassarius burchardi.*
	20	H, gravel		
	14	Z		
	15	Z		
	28	Z		
	19	Z, H		
	29	Z		
	21	S		
	12	M/S		
II	2	S, some H	All eastern side of lagoon.	Presence of *Scoloplos simplex.* Others common: *Sanguinolaria donacioides, N. burchardi.*
	1	S		
	11	S		
	7	S		
	8	S		
V	6	M	Central and east side of lagoon.	Absence of *O. fusiformis.* Common species: *Tellina deltoidalis, Notospisula trigonella, N. burchardi.*
	5	M		
	25	M		
	9	M		
	22	M		
	26	M		
III	10	S	Central and western areas of lagoon.	Presence of nemerteans. Others common: *V. australis, N. burchardi, Tellina deltoidalis, N. trigonella.*
	23	M/S sparse Z		
	30	S		
	13	S		
	16	M		
	17	M		
	4	M	— N.E. arm.	
IV	24	H, M/S	— N.W. corner	Presence of *O. fusiformis* Others common: *V. australis, T. deltoidalis, N. burchardi.*
	3	H, R, S	— N.E. corner	
	18	Z, H	— West	

habitat type. Total species number in sand and seagrass areas are the same and very much higher than in mud, while evenness in seagrass is reduced compared with the other habitats.

Habitat appeared to play a major part in the structure of infaunal benthic communities within the lagoon. The communities in each of the three main habitat types comprised species which displayed differences in relative abundances, although there was considerable overlap in that a number of species, while dominating one habitat type, could still be found in small numbers in other habitats. This same pattern is found in a number of N.S.W. coastal lagoons (Powis and Robinson, 1980; Robinson, 1982; Gibbs, unpub. data).

Reduced species diversity and/or density in mud habitats have been recorded in N.S.W. coastal lagoons (MacIntyre, 1959; Hutchings *et al.,* 1978; Powis and Robinson, 1980; Robinson, 1982) and elsewhere (cited in Gray 1974; Rhoads, 1974). A variety of theories has been provided to account for this (see Gray, 1974; Rhoads,

TABLE 3

Mean ± standard error of mean for Species Number (S), *Number of Individuals* (N) *and Evenness* (J') *for 6 sites in each habitat*

Habitat type	N	Community Indices	Mean ± S.E.
Seagrass	6	S	9.00 ± 0.73
	6	N	58.83 ± 9.38
	6	J'	0.65 ± 0.04
Sand	6	S	8.50 ± 1.23
	6	N	32.33 ± 5.71
	6	J'	0.77 ± 0.05
Mud	6	S	4.67 ± 0.67
	6	N	10.83 ± 2.21
	6	J'	0.84 ± 0.04

1974), the most often cited being related to habitat diversity. It is possible that limited habitats available in the mud zone provide fewer niches in which species can coexist.

Common species: The gastropod *Nassarius burchardi* was common in all habitats in the lagoon in this (up to 144 specimens per m^2) and past surveys (Hutchings *et al.,* 1978; U.N.S.W. unpub. student reports). A very similar species *N. jonasi,* was found at two sites near the entrance. In the past there has been some confusion in identifying these two species, and often no attempt was made to separate them (Hutchings *et al.,* 1978). *N. jonasi* is more marine than *N. burchardi* and has been found near the entrances to a number of other coastal lagoons (Gibbs and Robinson, unpub. data).

The two bivalves *Tellina deltoidalis* and *Notospisula trigonella* both appeared in a variety of habitats, although they were more abundant in muddy areas (up to $134/m^2$ and $32/m^2$ respectively). Student reports over the last 12 years confirm this distribution. *T. deltoidalis* was always common, although the numbers of *N. trigonella* were variable. Hutchings *et al.* (1978) did not record *N. trigonella* in Smiths Lake, although it was present there at that time (Dixon, pers. comm.) and in nearby Wallis Lake.

TABLE 4

Community Indices and dominant species for the three habitat types

(S = No. of species; J' = evenness index; N = No. of individuals)

Habitat	Seagrass	Sand	Mud
S	22.0	22.0	12.0
J'	0.58	0.78	0.78
N	301.0	176.0	51.0
Dominant species. (ranked in order of dominance)	1. *V. australis* 2. *O. fusiformis* 3. { *N. torquatus* *N. burchardi* 5. *T. deltoidalis*	1. *Tanytarsus* sp. 2. *S. simplex* 3. *S. donacioides* 4. *N. torquatus* 5. { *V. australis,* *N. burchardi*	1. *T. deltoidalis* 2. *V. australis* 3. *N. trigonella* 4. *N. torquatus* 5. *N. burchardi*

TABLE 5

The dominant fish species in Smiths Lake, listed in taxonomic order

Species
Harengula abbreviata
Hyporhamphus ardelio
Centropogon australis
Platycephalus fuscus
Sillago ciliata
Pomatomus saltatrix
Acanthopagrus australis
Rhabdosargus sarba
Girella tricuspidata
Mugil cephalus
Achlyopa nigra
Monacanthus chinensis
Torquigener hamiltoni

The potamid whelk *Velacumantus australis* was common, particularly in shallow water and seagrass beds (up to 900/m^2). This same habitat preference was also recorded in past years (U.N.S.W. unpub. student reports), although taxonomic problems related to distinguishing juvenile *Pyrazus ebeninus* from *V. australis* have complicated the issue. In the present survey no definite records of *P. ebeninus* were noted, probably due to limited sampling in habitats preferred by this species, i.e. shallow sand/mud flats.

Two common filter feeders, the bivalve *Sanguinolaria donacioides* (up to 160/m^2) and the polychaete *Owenia fusiformis* (up to 800/m^2) were found in sand and seagrass habitats respectively, indicating a distinct preference for areas where a filter feeding life style would be less affected by fine sediments.

The only other common species was a chironomid larva *Tanytarsus* sp. (up to 430/m^2). The polychaete *Ceratonereis mirabilis* and the molluscs *Ostrea angasi* and *Eumarcia fumigata* have been recorded previously from the lagoon (Hutchings *et al.*, 1978), but were not collected during this study.

FISH FAUNA

Materials and Methods

Fish records for Smiths Lake were obtained from the following sources:

(i) University of N.S.W. Summer School Reports (1968-1979),

(ii) Specimens obtained from commercial fishermen, 1978-1979,

(iii) Occasional fishing between 1978-1979.

Between 1968-1979 the fish were sampled in all habitats using gill, seine and dip nets and a miniature otter trawl. As gear and effort varied between collections, only presence or absence of each species is recorded here. The fish species were grouped, according to their frequency of occurrence, as: common (present in greater than 70% of collections); frequent (20% to 70%); rare (less than 20%).

Results and Discussion

Seventy-eight species of fish were recorded in Smiths Lake (Appendix 2). Of these, 13 species (16.6%) were common, 21 species (27%) frequent, and 44 species (56.4%) rare. The 13 common species (Table 5) are all representative of a typically estuarine fish fauna with warm-temperate (Peronian) zoogeographic affinities. Only seven tropical (Solanderian) and four cool-temperate (Maugean) fish species were recorded in the lagoon (Appendix 2).

The fish fauna of Smiths Lake is similar to that of Tuggerah Lakes (Henry and Virgona, 1981) and to that of the *Zostera* seagrass beds in Lake Macquarie (Friedlander, 1980), with the same common species present. It differs, however, from the fish fauna of these and other N.S.W. estuaries (Young, 1981; State Pollution Control Commission, 1981; Paxton, Gibbs, Young and Collett, unpub. data), in the absence of many tropical (e.g. *Leiognathus moretoniensis, Lethrinus nebulosus, Chaetodon* spp., *Heniochus accuminatus* and *Pomacentrus coelestris*) and cold temperate species (e.g. *Gymnapistes marmoratus, Arripis trutta, Neodax semifasciatus* and *Ammotretis rostratus*).

GENERAL DISCUSSION

In their study of the Myall Lakes system, Atkinson *et al.* (1981) discussed the possibility of there being characteristic lagoon benthic species, but concluded that this was not the case. The species of benthic fauna present in that study were related to salinity, aquatic vegetation and sediment type and were generally found in other N.S.W. estuaries with similar conditions. Similarly, in Smiths Lake the distribution and abundance of benthic fauna within the lagoon is strongly influenced by the vegetation and sediments. The benthic flora and fauna are also present in other N.S.W. estuaries and no species appear characteristic of Smiths Lake or of coastal lagoons generally.

Although the absence of some species common in other estuaries would be due to the generally low salinity of Smiths Lake, some euryhaline species common in other estuaries, e.g. the polychaete *Barantolla lepte,* have also been consistently absent. Hutchings *et al.* (1978) suggested this was due to the species having pelagic larvae and the sand barrier preventing entrance of these larvae into the lagoon at the appropriate time. This probably applies to other benthic species, however little is known about the breeding behaviour of estuarine benthic fauna.

Similarly, the absence of many estuarine fish species is probably due to the sand barrier restricting migration. The lagoon is usually opened to the sea during midwinter or sometimes in midsummer, but rarely during Autumn or Spring (May, unpub. data). Hence, species that spawn at sea during these latter periods have little opportunity to colonize the lagoon. Even if spawning coincides with the opening, colonization by post-larvae, especially tropical species, would be dependent upon suitable oceanic currents (see Jeffrey, 1981).

Not only are sediment type, vegetation and salinity associated with composition and distribution of biota within Smiths Lake, but also the periodic opening of the sand barrier is important, indirectly by altering salinity and hence vegetation and directly by controlling migration of species into the lagoon.

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APPENDIX 1

Macrofaunal Species List

Phylum PORIFERA
- Unknown species 1

Phylum CNIDARIA
- Unknown species 1

Phylum ANNELIDA
- Class POLYCHAETA
  - *Australonereis ehlersi* (Augener, 1913)
  - *Ceratonereis* sp.
  - *Marphysa sanguinea* (Montagu, 1815)
  - *Phyllodoce novaehollandiae* Kinberg, 1866
  - *Sigambra parva* (Day, 1963)
  - *Nephtys australiensis* Fauchald, 1965
  - *Lumbrineris latreilli* Audouin & Milne Edwards, 1834
  - *Scoloplos (Scoloplos) simplex* (Hutchings, 1974)
  - *Magelona dakini* Jones, 1978
  - *Notomastus torquatus* Hutchings & Rainer, 1979
  - *Armandia intermedia* Fauvel, 1902
  - Family Cirratulidae Unknown species 1
  - *Owenia fusiformis* delle Chiaje, 1841-1844

Phylum NEMERTINEA
- Unknown spp.

Phylum MOLLUSCA
- Class GASTROPODA
  - *Velacumantus australis* (Quoy & Gaimard, 1834)
  - *Nassarius burchardi* (Dunker in Phillipi, 1849)
  - *Nassarius jonasi* (Dunker, 1846)
  - *Bedeva hanleyi* (Angas, 1867)
- Class BIVALVIA
  - *Anadara trapezia* (Deshayes, 1840)
  - *Xenostrobus securis* (Lamarck, 1819)
  - *Saccostrea commercialis* (Iredale & Roughley, 1933)
  - *Laternula tasmanica* Reeve, 1818
  - *Tellina (Macomona) deltoidalis* Lamarck, 1818
  - *Sanguinolaria donacioides* (Reeve, 1857)
  - *Notospisula trigonella* (Lamarck, 1818)
  - *Theora fragilis* (A. Adams, 1855)

Phylum ARTHROPODA
- Class CRUSTACEA
- Order Decapoda
  - *Metapenaeus bennettae* (Racek & Dall, 1965)
  - *Callianassa arenosa* Poore, 1975
  - *Amarinus laevis* (Targioni Tozzetti, 1877)
- Order Amphipoda
  - *Megamphopus* sp.
  - *Melita* sp.
  - *Oediceropsis* sp.
  - *Victoriopisa australiensis* Karaman & Barnard, 1979
  - *Cymadusa* sp.
  - Family Aoridae Unknown species 1
- Order Isopoda
  - *Cyathura* sp.
  - Family Sphaeromidae Unknown species 1
- Class INSECTA
  - Family Chironomidae
  - *Tanytarsus* sp.

Phylum UROCHORDATA
- Class ASCIDIACAE
  - *Styela plicata* Lesueur, 1803

Phylum CHORDATA
- Class PISCES
  - *Parkraemaria ornata* (Whitley, 1951)
  - *Urocampus carinorostris* Castelnau, 1872

APPENDIX 2

Checklist of fishes collected in Smiths Lake

S = Tropical (Solanderian);
P = Warm temperate (Peronian);
I = Introduced;
M = Cold temperate (Maugean);
C = Common;
F = Frequent;
R = Rare.

SCIENTIFIC NAME	COMMON NAME	OCCURRENCE	ZOOGEOGRAPHIC AFFINITY
ANGUILLIDAE			
Anguilla australis Schmidt, 1928	Short finned eel	F	M
Anguilla reinhardti Steindachner 1867	Long finned eel	F	P
ELOPIDAE			
Elops australis Regan, 1909	Giant herring	R	S
CLUPEIDAE			
Harengula abbreviata Valenciennes, 1847	South herring	C	P
Hyperlophus translucidus McCulloch, 1917	Translucent sprat	R	P
Hyperlophus vittatus (Castelnau, 1875)	Sandy Sprat	R	P
ENGRAULIDAE			
Engraulis australis (Shaw, 1790)	Australian anchovy	R	P
SYNODONTIDAE			
Trachinocephalus myops (Schneider, 1801)	Painted grinner	R	S
GONORHYNCHIDAE			
Gonorhynchus greyi (Richardson, 1845)	Beaked salmon	R	P
BATRACHOIDIDAE			
Batrachomoeus dubius (Shaw, 1790)	Frogfish	R	P
ANTENNARIIDAE			
Antennarius striatus (Shaw, 1794)	Anglerfish	R	P
HEMIRHAMPHIDAE			
Hyporhamphus ardelio (Whitley, 1931)	River garfish	C	P
BELONIDAE			
Tylosurus macleayanus (Ogilby, 1886)	Stout long tom	F	S
POECILIIDAE			
Gambusia affinis (Baird & Girard, 1854)	Mosquito fish	F	I
ATHERINIDAE			
Atherinosoma microstoma (Gunther, 1861)	Small mouthed hardyhead	F	M
Pranesus ogilbyi Whitley, 1930	Ogilby's hardyhead	F	P
Pseudomugil signifer Kner, 1867	Blue-eye	F	P
FISTULARIDAE			
Fistularia petimba Lacepede, 1803	Smooth flute-mouth	R	P
SYNGNATHIDAE			
Syngnathus altirostris Ogilby, 1890	Steep nosed pipefish	R	P
Syngnathus margaritifer Peters, 1869	Mother-of-pearl pipefish	R	P
Urocampus carinirostris Castelnau, 1872	Hairy pipefish	F	P
Hippocampus whitei Bleeker, 1855	Common seahorse	R	P
SCORPAENIDAE			
Centropogon australis (White, 1790)	Fortesque	C	P
Notesthes robusta (Gunther, 1860)	Bullrout	R	S
TRIGLIDAE			
Chelidonichthys kumu (Lesson & Garnot, 1826)	Red gurnard	R	P
PLATYCEPHALIDAE			
Platycephalus arenarius Ramsay & Ogilby, 1886	Sand flathead	R	P
Platycephalus fuscus Cuvier, 1829	Dusky flathead	C	P
AMBASSIDAE			
Priopodichthys marianus (Gunther, 1880)	Yellow perchlet	R	P
Velambassis jacksoniensis (Macleay, 1881)	Perchlet	R	P
THERAPONIDAE			
Pelates quadrilineatus (Bloch, 1829)	Four lined trumpeter	F	S
Pelates sexlineatus Quoy & Gaimard, 1824	Six lined trumpeter	R	P
APOGONIDAE			
Siphamia roseigaster (Ramsay & Ogilby, 1866)	Pink breasted siphonfish	R	P

APPENDIX 2 (Continued)

Checklist of fishes collected in Smiths Lake

S = Tropical (Solanderian);
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F = Frequent;

SCIENTIFIC NAME	COMMON NAME	OCCURRENCE	ZOOGEOGRAPHIC AFFINITY
SILLAGINIDAE			
Sillago ciliata Cuvier, 1829	Sand whiting	C	P
Sillago maculata Quoy & Gaimard, 1824	Trumpeter whiting	F	P
POMATOMIDAE			
Pomatomus saltatrix (Linnaeus, 1766)	Tailor	C	P
CARANGIDAE			
Trachurus mccullochi Nichols, 1920	Yellowtail	R	P
Caranx georgianus (Macleay, 1881)	Trevally	R	P
GERREIDAE			
Gerres ovatus Gunther, 1859	Silver biddy	F	P
SPARIDAE			
Acanthopagrus australis (Gunther, 1859)	Yellowfin bream	C	P
Chrysophrys auratus (Bloch & Schneider, 1801)	Snapper	F	P
Rhabdosargus sarba (Forskal, 1775)	Tarwhine	C	P
MONODACTYLIDAE			
Monodactylus argenteus (Linnaeus, 1758)	Silver batfish	R	P
KYPHOSIDAE			
Girella tricuspidata (Quoy & Gaimard, 1825)	Luderick	C	P
SCORPIDIDAE			
Microcanthus strigatus (Cuvier, 1831)	Stripey	R	P
ENOPLOSIDAE			
Enoplosus armatus (Shaw, 1790)	Old wife	R	P
CHEILODACTYLIDAE			
Cheilodactylus fuscus Castelnau, 1879	Red morwong	R	P
MUGILIDAE			
Aldrichetta forsteri (Valenciennes, 1836)	Yellow-eye mullet	R	M
Liza argentea (Quoy & Gaimard, 1825)	Flat tail mullet	F	P
Mugil cephalus Linnaeus, 1758	Sea mullet	C	P
Mugil georgii Ogilby, 1897	Fantail mullet	R	P
Myxus elongatus Gunther, 1861	Sand mullet	F	P
Myxus petardi (Castelnau, 1875)	Freshwater mullet	R	P
SPHYRAENIDAE			
Sphyranella obtusata (Cuvier, 1829)	Striped sea pike	R	P
LABRIDAE			
Achoerodus gouldii (Richardson, 1843)	Blue groper	F	P
ODACIDAE			
Heteroscarus acroptilus (Richardson, 1846)	Rainbow fish	R	M
URANOSCOPIDAE			
Ichthyscopus lebeck (Bloch & Schneider, 1801)	Stargazer	R	S
CLINIDAE			
Cristiceps australis Cuvier & Valenciennes, 1836	Crested weedfish	R	P
CALLIONYMIDAE			
Callionymus calcaratus Macleay, 1881	Spotted stinkfish	F	P
GOBIIDAE			
Arenigobius bifrenatus (Kner, 1865)	Bridled goby	F	P
Favonigobius exquisitus Whitley, 1950	Exquisite goby	R	S
Favonigobius lateralis (Macleay, 1881)	Goby	F	P
Favonigobius tamarensis (Johnston 1883)	Tamar river goby	R	P
Gobiopterus semivestita (Munro, 1949)	Goby	R	P
Parkraemaria ornata (Whitley, 1951)	Goby	R	P
Pseudogobius olorum (Sauvage, 1880)	Goby	P	P

APPENDIX 2 (Continued)

Checklist of fishes collected in Smiths Lake

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I = Introduced;
C = Common;
R = Rare.
P = Warm temperate (Peronian);
M = Cold temperate (Maugean);
F = Frequent;

SCIENTIFIC NAME	COMMON NAME	OCCURRENCE	ZOOGEOGRAPHIC AFFINITY
ELEOTRIDAE			
Philypnodon grandiceps (Krefft, 1864)	Flat headed gudgeon	R	P
BOTHIDAE			
Pseudorhombus arsius (Hamilton Buchanan, 1822)	Large toothed flounder	F	P
Pseudorhombus jenynsii (Bleeker, 1855)	Small toothed flounder	R	P
SOLEIDAE			
Achlyopa nigra (Macleay, 1881)	Black sole	C	P
MONACANTHIDAE			
Meuschenia freycineti (Quoy & Gaimard, 1824)	Variable leatherjacket	R	P
Meuschenia trachylepis (Gunther, 1870)	Yellow finned leatherjacket	F	P
Monacanthus chinensis (Osbeck, 1765)	Fanbellied leatherjacket	C	P
Scobinichthys granulatus (Shaw, 1790)	Rough leatherjacket	R	P
TETRAODONTIDAE			
Torquigener glaber (Freminville, 1873)	Toado	R	P
Torquigener hamiltoni (Gray & Richardson, 1843)	Toado	C	P
Torquigener pleurogramma (Regan, 1903)	Toado	R	P
Torquigener squamicauda (Ogilby, 1910)	Toado	R	P
DIODONTIDAE			
Dicotylichthys myersi Ogilby, 1910	Porcupine fish	R	P

The Re-establishment of the Ostracod Fauna of Llangothlin Lagoon after a Drought

J. M. BACKHOUSE and K. G. McKENZIE

BACKHOUSE, J. M., & MCKENZIE, K. G. The re-establishment of the ostracod fauna of Llangothlin Lagoon after a drought. *Proc. Linn. Soc. N.S.W.* 107 (1), (1982) 1983: 35-40.

Within three months of refilling after a period of drought a fauna of up to seven species of Ostracoda was re-established in Llangothlin Lagoon. These species belong to six genera: *Cypretta, Newnhamia, Ilyodromus, Candonocypris, Heterocypris,* and *Gomphodella.* Five species of the first four genera were commonly found but *Heterocypris* disappeared from the fauna within six months of inundation and only one individual of *Gomphodella* was found. Brief descriptions and ecological notes for each species are given.

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INTRODUCTION

Llangothlin Lagoon is a shallow, freshwater lake approximately 18 km NNE of Guyra on the New England Tablelands of New South Wales. It lies at an elevation of 1,350 m above sea level. It has a surface area of approximately 400 ha when full and the maximum depth is probably no more than 1.6 m (Briggs, 1976). Average annual rainfall at Guyra is 900 mm with summer rainfall predominating. The years 1979 and 1980 had well below average rainfall with totals of only 687 and 591 mm respectively being recorded. The early part of 1981 was also abnormally dry but significant rains fell in May and June and the total for the year was near, but still below, average.

Although generally regarded as a permanent water body Llangothlin Lagoon was dry for an unverifiable period in the summer and autumn of 1980-81 (probably not more than seven months) but it began filling again in early June 1981. In July, 1982, its surface area was roughly 0.75 of 'normal', i.e. about 300 ha. Complete drying out of this lagoon is infrequent, occurring possibly once every thirty years or so. It has proved impossible to get a consensus on the matter from local inhabitants.

Monthly sampling of the invertebrate fauna was begun in August 1981. Four species of ostracod were present at the first sampling. The maximum number of species, seven, was present in November.

Data for this paper were collected as part of a detailed ecological investigation of four lagoons in the Guyra region currently being undertaken by one of the authors (J.M.B.) for a Masters thesis at the University of New England.

METHODS

Open water, vegetation, and mud samples, were taken from each of a number of submerged transect points at the southern end of the lagoon. Samples were collected between August, 1981, and July, 1982, inclusive. The maximum mean depth along the transect was 46 cm recorded in April, 1982. From time to time additional samples were collected from sites other than the fixed transect points.

Duplicate open water samples were collected at each point using a perspex tube 4.5 cm in diameter allowing a column of water of known volume to be taken. Samples included species from all depths, from the mud-water interface to the surface. Any predators were removed from the samples in the field.

Vegetation was clipped from 30 cm^2 quadrats at each point and all plant material above approximately 1 cm from the bottom was collected. The clipped vegetation was placed in plastic bags with sufficient water to prevent dehydration of either plants or animals during transport to the laboratory. In the laboratory all plant material was washed thoroughly and inspected for the removal of all animals. The water in which the plants were washed was collected and filtered through a fine terylene cloth; any animals remaining in the filtrate were added to the sample.

Mud cores to a depth of 5 cm were taken with a split corer of 5.2 cm diameter. Due to technical problems, mud samples were not collected in August, 1981, or May, 1982.

All samples were taken back to the laboratory, packed in ice in the summer, within a few hours of collection. They were then refrigerated until they could be sorted. Sorting was completed within three or four days of collection.

All animals were removed live from the sample with the aid of a desk magnifier and preserved in 80% alcohol for later identification. This method allows for the detection of any specimen greater than 0.2 mm in size.

Specimens are currently held at the University of New England but will be deposited with the Australian Museum.

RESULTS AND DISCUSSION

(a) *The Habitat*

Apart from a period of approximately seven to ten days in late February, 1982, all regular sampling points, except one in the middle of the transect, were submerged from early July, 1981. The one point that was not, was above water level in September, 1981, and early February, 1982, but in neither instance did the bottom mud dry out.

At the beginning of the sampling period the dominant macrophyte along the transect was water meadow grass, *Glyceria* sp., with *Myriophyllum propinquum* as co-dominant at the transect point furthest from the shore. At that time vegetation cover was much less than 50%. As the water meadow grass died off *Myriophyllum* replaced it and was dominant from October, 1981, providing 80-100% of the botanical composition. Other macrophytes in the sample area were *Eleocharis sphacelata* and *Potamogeton* sp.

Vegetation cover at all regular sampling points was greater than 90% from November, 1981. From March to the end of sampling in July, 1982, all sites had 100% cover.

b. *The Ostracod Fauna: Species Description and Ecological Notes*

1. Cypretta minna (King, 1855)

Size: females 1.0 mm; males 0.85 mm. Figs 1, 2.

The genus is cosmopolitan (McKenzie, 1980) and this species is yellowish with green patches when mature. It is hairy and has distinct radial septa in both valves. Juveniles are a vivid green.

C. minna is an active swimmer and is found both in open water and in association with plants, but more frequently the latter. However, the relationship appears to be with the algae that are associated with the macrophytes rather than with the larger plants themselves. The species was present throughout the sampling period with both adults and juveniles collected on most occasions except in March, 1982, when virtually

TABLE 1

Mean Monthly Densities of Ostracods 1981-82

	C. minna[a]		*N. fenestrata*[a]		*Ilyodromus* spp.[b]		*C. candonioides*[b]		*H. vatia*[b]	
	$\bar{x}$	s.d	$\bar{x}$	s.d	$\bar{x}$	s.d	$\bar{x}$	s.d	$\bar{x}$	s.d
Aug	4.2	4.6	—	—	P		—	—	P	
Sep	5.4	7.7	5.4	7.5	P		—	—	2700	2225
Oct	4.9	3.6	18.2	23.0	1167	1366	—	—	2785	1799
Nov	49	108	37.4	33.8	9150	9869	1444	2068	444	391
Dec	9.9	16.0	134	128	9500	8660	83	204	—	—
Jan	13.4	9.1	2.4	3.7	23916	27855	—	—	—	—
Feb	11.2	7.6	4.9	5.2	11750	10093	928	2029	—	—
Mar	15.9	16.1	11.1	9.0	3750	3029	83	204	—	—
Apr	9.1	5.6	2.2	2.6	3583	4329	—	—	—	—
May	16.3	5.8	1.2	2.5	—	—	—	—	—	—
Jun	3.9	3.2	P*		467	533	83	204	—	—
Jul	3.1	2.3	0.2	0.6	554	816	—	—	—	—

a = no/litre
b = no/metre^2
P = present, but sample unquantified. Density expressions are related to sampling methods
* See text

no adults were present. This sampling immediately followed the brief period during which the transect was above water.

Mean densities for *C. minna* and all other species except *Gomphodella australica,* are given in Table 1.

2. *Newnhamia fenestrata* (King, 1855)

Size: females 0.85 mm, males 0.80 mn; Fig. 3.

Mature individuals of this species are dark brownish to almost black. They have a ribbed and flattened ventral surface, plus 2 distinctive eye tubercles. The genus is endemic to the Australian Zoogeographical Region.

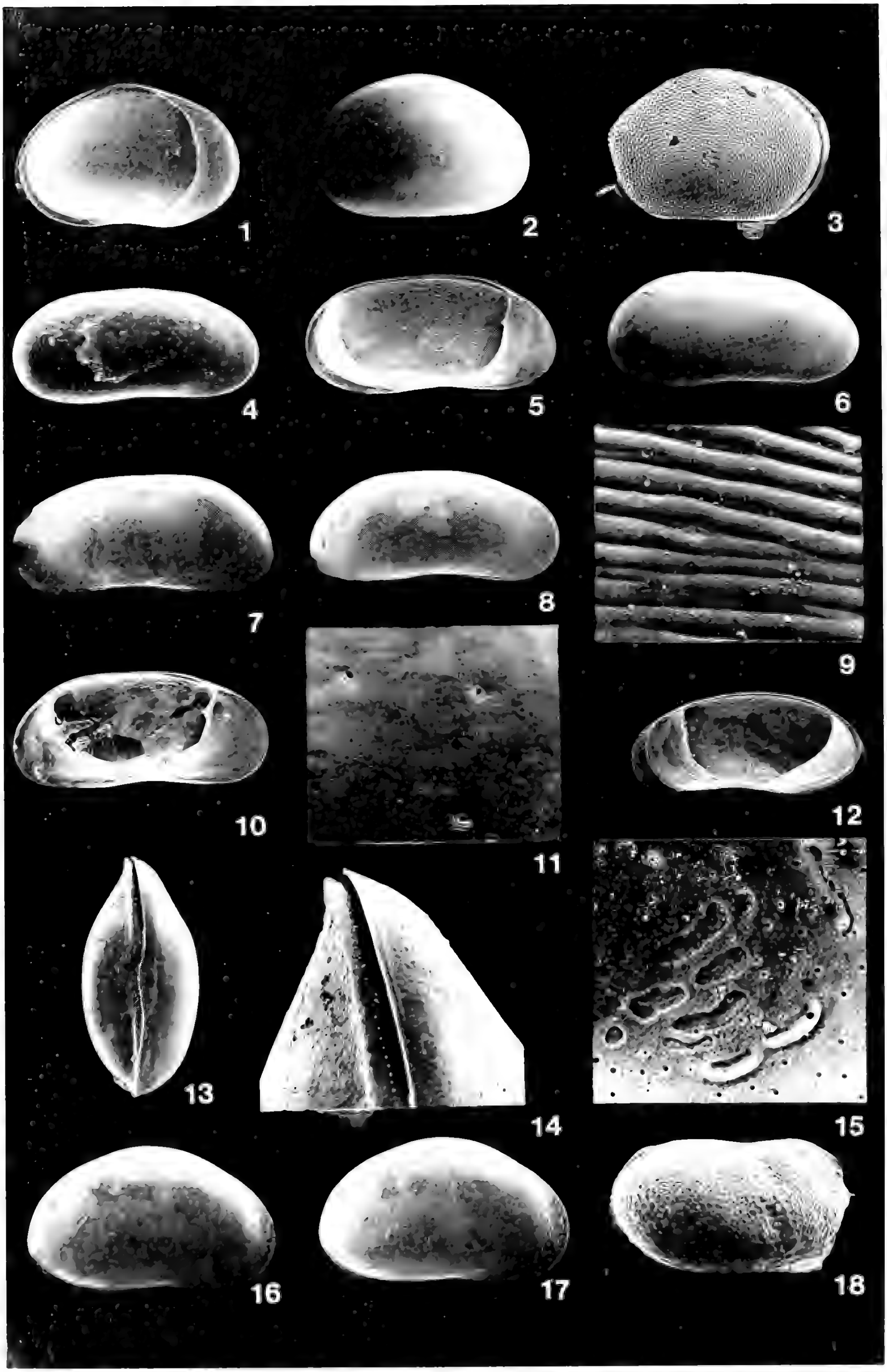
N. fenestrata is a very active swimmer and was most often found in open water less than 30 cm deep near the edge of the lagoon where it reached densities of up to 300/litre. Unlike *C. minna* it was rarely collected in association with dense growths of vegetation.

N. fenestrata did not appear until September, 1981, but from then all life stages were present although, when the lagoon was at its maximum depth (46 cm in the sampling area) and there was a lush growth of *Myriophyllum,* the species was not commonly found at the regular sample sites. It was, however, present at high densities on the edge of the lagoon in areas of relatively low turbidity. This suggests that open, clear waters of depths less than 0.5 m are its preferred habitat. As with *C. minna* few adults were present in March, 1982.

3. *Ilyodromus varrovillius* (King, 1855); *Ilyodromus viridulus* (Brady, 1886).

Size: females 1.7 mm and 1.3 mm; males 1.6 mm and 1.2 mm respectively; Figs 4-11.

Ilyodromus was formerly considered to be endemic to the Australian Zoogeographical Region but recently females of the genus have been found in the Philippines (Victor and Fernando, 1981). It also occurs in some European ricefields, but only as parthenogenetic populations (Fox, 1965). Thus, it seems probable that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bisexual populations remain confined to the Australian Region. The significance of this pattern was discussed by McKenzie (1971).

Ilyodromus varrovillius is dark greenish when mature and has distinct surface striations on both valves, whereas *Ilyodromus viridulus* has smooth valves and is a paler colour. These two species occur together in several localities, presumably occupying different ecological niches but just what that difference is was not revealed by the sampling methods used in this study. Both occurred regularly in mud samples where they were found burrowed into the mud and also on the mud surface. During sorting they were seen moving freely through the mud on the surface of the container but they were not seen swimming. They were also found in both water and vegetation samples but they had almost certainly been picked up from the mud-water interface in both instances.

4. *Candonocypris candonioides* (King, 1855).
Size: females 1.8 mm, males not found; Fig. 12.

Candonocypris candonioides belongs to another genus endemic to the Australian Zoogeographical Region and when mature it is greenish and has an elongated bean-shape. There is a distinct selvage in the right valve. It is much less common than any of the species already mentioned and was only collected on five, non-consecutive occasions over the twelve months suggesting that, at least since its first appearance in November, it was always present but at much lower densities than the other species.

Adult *C. candonioides* were most frequently found in mud samples where they had burrowed into the mud. Again, they also occurred in water and vegetation samples but, as in the case of the two other benthic species, they were probably picked up from the mud surface. According to De Deckker (1981a) the adults are not known to swim but the juveniles swim quite strongly.

C. candonioides may be a junior synonym of *C. novaezelandiae* (Baird), as suggested by De Deckker (1981a), but the Australian species name is preferred here.

5. *Heterocypris vatia* (De Deckker, 1981)
Size: females, 2.2 mm; males 1.9 mm; Figs 13-17.

Mature individuals of this species are brownish-orange and have weak crenulations on the ventral right valve.

H. vatia was found in shallow water towards the edge of the lagoon at depths of less than 0.5 m and also in isolated shallow pools on the mud flats around the edge of the lagoon. It was seen in large numbers crawling rather sluggishly over the mud surface but was not observed swimming. By November the density had declined and it had disappeared by December. It was not seen after that time except for one individual found in a sample collected near the edge of the lagoon in July, 1982, at a site which was first inundated in mid-March of the same year. This is perhaps indicative of *H.*

Figs 1-18 **1.** *Cypretta minna* (King) male, internal left valve (LV), x46. **2.** *C. minna;* female, external right valve (RV), x38. **3.** *Newnhamia fenestrata* (King) female, external RV, x42. **4.** *Ilyodromus viridulus* (Brady) female, external RV, x32. **5.** *I. viridulus;* male, internal LV, x28. **6.** *I. viridulus;* male, external LV, x34. **7.** *Ilyodromus varrovillius* (King) male, external LV, x28. **8.** *I. varrovillius;* female, external RV, x24. **9.** *I. varrovillius;* female, external LV, detail of striation, x54. **10.** *I. varrovillius;* female, external RV, x24. **11.** *I. viridulus;* male, external LV, detail of normal pores, x54. **12.** *Candonocypris candonioides* (King) female, internal RV, x24. **13.** *Heterocypris vatia* (De Deckker) female, ventral view, x20. **14.** *H. vatia;* female detail of RV anteroventral denticulation, x58. **15.** *H. vatia;* female, internal LV, detail of central muscle field, x96. **16, 17.** *H. vatia;* female, external RV stereo pair, x20. **18.** *Gomphodella australica* (Hussainy) female, external broken RV, x48.

SEM micrographs by the Electron Microscope Unit, University of New England, Armidale.

vatia being a pioneer species. Its appearance and disappearance coincided within one month of two other pioneer species: the notostracan *Lepidurus viridis* and a conchostracan species. Neither of these is mentioned in two previous studies of the lagoon invertebrate fauna (Timms, 1970, and Maher, 1976). As these two studies were undertaken at times when the lagoon had not been dry for some years it seems probable that the eggs of both those species require a period of desiccation before hatching can occur. A similar explanation would account for the records of *H. vatia.*

6. *Gomphodella australica* (Hussainy, 1968).
Size: female 0.85 mm; males not found; Fig. 18.

When mature, *Gomphodella australica* is brownish-purple with a heart-shaped carapace. It has a cytheracean, as distinct from a cypridacean, anatomy with three post-abdominal lobes.

Only one individual of this species was found. It was collected in November in a vegetation sample, which contained associated algae, from water 14 cm deep. This agrees quite well with De Deckker's (1981b) statement that it is usually found crawling amongst filamentous algae at depths of 0.5-1.0 m. De Deckker placed this species in the new genus *Gomphodella* because of the lack of the peripheral lateral ridge around the flat base of the valves which is characteristic of *Gomphocythere* Sars, 1924, to which it was referred previously.

All of the ostracod species found in Llangothlin Lagoon are considered indicative of good quality waters (McKenzie, 1980). This will make them useful indicator species when monitoring the effects of management plans to be implemented in the future.

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A Review of Reproduction and Development in the Fork-tailed Catfishes (Ariidae)

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RIMMER, M. A., & MERRICK, J. R. A review of reproduction and development in the fork-tailed catfishes (Ariidae). *Proc. Linn. Soc. N.S.W.* 107 (1), (1982) 1983: 41-50.

Available data on a number of aspects of reproduction of ariids are presented with emphasis on recent information. Gonad structure, secondary sex characters, spawning movements and behaviour, eggs, development and parental care are discussed. Evolution of buccal incubation as a reproductive strategy is briefly considered.

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INTRODUCTION

The family Ariidae is estimated to comprise 150 species inhabiting freshwater, estuarine and marine environments in tropical and sub-tropical regions throughout the world (McDowall, 1981). Despite unresolved speciation problems, it is apparent that a radiation of ariids has occurred in Australasia; approximately 40 species are known to occur in New Guinea and 18 in Australia (Kailola, 1981).

Ariid reproduction has previously been reviewed by Gudger (1916, 1918, 1919) and Breder and Rosen (1966); the objective of this paper is to complement those earlier surveys by presenting recent information, especially data relating to Australasian species. The information now available indicates that all species practise oral incubation. Gudger (1918), Breder (1935) and Breder and Rosen (1966) dismissed suggestions that gastric incubation and even viviparity were to be found in ariids, although suggestions of these latter modes occasionally still appear in literature (Nikolsky, 1963).

Bancroft (1924) noted a specimen of *Arius australis* with ova in the mouth, but Semon (1899) reported that this species laid eggs (3-4 mm in diameter) in a nest about one metre in diameter, composed of gravel and small stones. This latter observation was repeated by Wiedersheim (1900), Stead (1906), Whitley (1941, 1957), Breder and Rosen (1966) and Balon (1975) but was rejected by Lake and Midgley (1970). The authors consider that Semon's original description resulted from misidentification of the nest of the sympatric freshwater plotosid catfish *Tandanus tandanus,* which builds nests of the type described (Lake, 1978; Merrick and Midgley, 1981).

The 6 parts of this review summarize and attempt to interpret all the available information; detailed published data on reproduction and development in ariids are listed in Table 1. Generic nomenclature, where applicable, follows Wheeler and Baddokwaya (1981), all other epithets listed are those used in individual publications.

LITERATURE DISCUSSION

Gonad Structure

Because of the large and spectacular eggs found in ariids, most gonad descriptions have dealt with the ovaries. Gudger (1919) described the ovaries of *Bagre marinus* in detail; other species for which ovary descriptions have been published are: *A. manillensis*

(Mane, 1929), *A. felis* (Merriman, 1940; Gunter, 1947), *A. heudoloti* (Tobor, 1969), *A. thalassinus* and *A. dayii* (Dmitrenko, 1970, 1974) and *A. dussumieri* (Vasudevappa and James, 1980).

Generally, three size classes of eggs are found in ariid ovaries: (a) large yolky eggs which are the group fertilized at spawning, and which in *A. felis* may have a small (0.5 mm) stellate micropyle present during later stages of maturity (Gunter, 1947), (b) smaller yolky eggs, and (c) small (ca. 1-2 mm) hyaline eggs in vast numbers. Mane (1929), Dmitrenko (1970, 1974) and Vasudevappa and James (1980) detailed diameters of oocyte classes of *A. manillensis, A. thalassinus* and *A. dayii,* and *A. dussumieri* respectively. Mature ovaries may take up most of the body cavity, compressing the stomach and intestine and precluding feeding prior to spawning (Gudger, 1916, 1919; Smith, 1945; Pantulu, 1963; Tobor, 1978), although gonadal development in *A. heudoloti* does not reach this extreme (Tobor, 1969).

Fecundity values (listed in Table 1) are low (14-184), by teleost standards, while mature oocyte diameters are large (9.5-25.0 mm). Several workers have investigated relationships between fecundity and body length, body weight and gonad weight (Pantulu, 1963; Tobor, 1969; Etchevers, 1978; Vasudevappa and James, 1980) but findings have been variable.

Gabaeva and Ermolina (1972) detailed changes in the follicular epithelium of ovum membranes during oogenesis of *A. thalassinus* and observed that the small hyaline oocytes differed considerably from the larger yolky oocytes in the cell structure of the follicular epithelium during the later stages of oogenesis. Stott *et al.* (1980, 1981) provided micrographs of ovarian sections of *A. felis,* together with a general description of histology of both ovaries and testes in this species. The mature testes of ariids are reported to be small, elongated straps which vary little seasonally (Lee, 1937; Tobor, 1969; Bishop *et al.,* 1980) and which in *A. leptaspis* contain small quantities of colourless milt (S. H. Midgley, pers. comm., 1980).

Secondary Sex Characters

Sexually dimorphic pelvic fins have been found in *B. marinus* (Merriman, 1940), *A. felis* (Lee, 1931, 1937), *A. australis* (Whitley, 1941, 1957) and *A. leptaspis* (Bishop *et al.,* 1980). In these cases the female pelvic fins were longer and more rounded than those of the male. In addition, the pelvic fin base is broader in females than in males (P. Kailola, pers, comm., 1982). Breder (1935) reported that Hubbs found no sexual dimorphism in *A. aquadulce.*

The development of a hook-like thickening on the inner dorsal surface of the pelvic fins of female ariids appears to be closely associated with the reproductive cycle, as these 'claspers' (Smith, 1945) increase in size as the breeding season progresses and are resorbed following spawning (Lee, 1937). These secondary modifications are found in the genera *Arius* (Mane, 1929; Hardenberg, 1935; Lee, 1931, 1937; Smith, 1945; Dmitrenko, 1970; Morley, 1981), *Hemipimelodus* (Smith, 1945), *Potamarius* (Hubbs and Miller, 1960), *Selenaspis* (Luengo, 1973), *Brustiarius, Cochlefelis* and *Nedystoma* (P. Kailola, pers. comm., 1982) but are absent in *Bagre marinus* (Gudger, 1916) and *Cinetodus froggatti* (P. Kailola, pers. comm., 1982). The degree of maximum development and the shape of the claspers appears to vary between species (P. Kailola, pers. comm., 1982).

Mane (1929), Lee (1937) and Smith (1945) suggested that the claspers were used to hold the eggs as they were extruded and the male picked them up one at a time from the basket thus formed. Hardenberg (1935) suggested that the male attached himself to these hooks in order to fertilize the eggs internally or at the moment they were extruded. However, there is no record of any specializations necessary for internal fertilization amongst ariids, nor of any corresponding developments of the pelvic fins of the male which would enable such attachment. Dmitrenko (1970) suggested that these fin modifications assist in holding the egg mass close to the urogenital orifice as further oocytes are extruded.

Gudger (1916) considered the distension of the branchial region of incubating male *B. marinus* to be a secondary sex character developed prior to spawning, since he took several specimens of this species with enlarged buccal cavities which were not carrying eggs. However, Breder and Rosen (1966) suggested that these fish may have released or lost their offspring and that the enlarged buccal cavity may thus be the result of, rather than a modification for, carrying a large volume of eggs or young. Lee (1937), Dmitrenko (1970) and Luengo (1973) noted similar changes in the branchial region of several other ariid species.

Other reported changes associated with breeding are reductions in tooth patches and changes in the structure of the oral epithelium. Willey (1910) found that male *A. falcarius* brooding eggs had greatly reduced tooth patches compared to females and non-incubating males. Thistlethwaite (1947) found that the oral epithelium of female *A. felis* contained no goblet cells, while that of non-brooding males contained scattered goblet cells in the surface layer. During the brooding process the proportion of goblet cells in the oral epithlium increased sharply, as did folding of the epithelium, reaching a peak approximately midway through the egg development period. As Di Conza (1970) found serum immunoglobulins to be present in *A. australis* mucus secretions, modifications to the oral epithelium, apparently associated with increased mucus production during buccal incubation, may have an important protective role in maintaining eggs and larvae.

Migrations

Little detailed information is available on movements of ariid populations: however, among estuarine and marine species anadromous movements associated with breeding have been reported in *A. felis* (Lee, 1937; Gunter, 1947; Harvey, 1972a, b), *Osteogeneiosus militaris* (Pantulu, 1963) and *A. heudoloti* (Tobor, 1969). *A. australis* shows a marked seasonal pattern of abundance in estuarine creeks in southern Queensland (Ellway and Hegerl, 1972; Stephenson and Dredge, 1976; Quinn, 1980) which may be related to its breeding season. Two references refer to movements in freshwater species: Mane (1929) reported that *A. manillensis* began schooling in deep water in Laguna de Bay at the beginning of the breeding season, and newly-released juveniles migrated to shallower portions of the lake, close inshore; Roberts (1978) suggested that *A. acrocephalus* may move upstream into highland habitats of the Fly River to spawn.

Spawning

Generally ariids have a single annual spawning corresponding to the beginning of the wet season in tropical species (P. Kailola, pers. comm., 1982), and spring in subtropical species (Table 1). However, there is evidence of biannual spawning in *A. caerulescens* although fish may be observed in reproductive condition throughout the year (Gonzalez, 1972; cited by Warburton, 1978). No detailed analyses of environmental stimuli on spawning in ariids have been published although Dmitrenko (1970, 1974) notes that *A. thalassinus* and *A. dayii* breed at surface water temperatures of 25 to 28°C, while Lake (1978) reported that *A. leptaspis* commenced spawning when water temperatures exceeded 26°C. Spawning season duration varies but can be up to seven months in the case of *A. heudoloti* (Tobor, 1969). Etchevers (1978) observed that older female *A. spixii* have a more protracted breeding season than younger females. Gonadal development may be extremely rapid, the bulk of development taking place in the few months prior to spawning (Merriman, 1940; Ward, 1957; Etchevers, 1978; Bishop *et al.*, 1980).

TABLE 1

Summary of Published Reproductive Data for the Family Ariidae

Genus and Species	Spawning		Mature oocyte diameter: Range (Mean)	Fecundity[1]: Range (Mean)	Buccal Incubation			Source(s)
	Sites, Movements	Season, Locality			Period	No. eggs in mouth	Development Notes[2]	
Arius								
A. caelatus			11-15 mm ovulated			33-68 (2 spec.)		Sekharan & Mojumder, 1974
A. dussumieri	-	Annual: Dec-Mar, Peak activity Feb; India	13-17 mm	105-184 (141)				Vasudevappa & James, 1980
A. felis	Coastal bays, salinities down to 13.6%	Annual: Jun-Jul; East coast U.S.	12-14 mm 14-18 mm ovulated	40-62	6-8 wks	Usually 10-30, Max. 48	Young at release: 40-49.5 mm. Begin feeding while in mouth	Lee, 1937; Merriman, 1940; Gunter, 1947; Ward, 1957
A. gambiensis			10-20 mm (13.5 mm)	70-90 (78)		15-22	Max. size found in mouth: 100 mm. Begin feeding while in mouth	Tobor, 1978
A. heudoloti	Migration to breeding grounds in Nov, depart Aug.	Annual: Nov-Jun, Peak activity Mar-Apr; Nigeria	10-19 mm	22-45	7 wks	Max. 20	Young at release: 90 mm. Begin feeding while in mouth	Tobor, 1969
A. jella			9.5-11.5 mm (10.5 mm)	ca.50	8 wks	Usually 30-40		Chidambaram, 1941
A. leptaspis	Freshwater billabongs; 26°C	Annual: Nov-Dec; Australasia	11.9-15.7 mm (13.8 mm)	26-70 (42)	8 wks	1-62 (28)	Incubated egg dia. 14.0 mm. Max. size found in mouth 60 mm.	Bishop *et al.*, 1980; Lake, 1978
A. maculatus		Annual: Jul; Java	12 mm	19-22		Usually 25-35		Hardenberg, 1935
A. manillensis	Freshwater lake: School at start of breeding season, disperse afterwards	Annual (4 spawning runs): Feb-May; Philippines	10.75 mm		8 wks		Young at release: 30-44 mm	Mane, 1929; Aldaba, 1931
A. sagor			11-12 mm			39 (+ 4 larvae) -48 (2 spec.)		Smith, 1945

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Summary of Published Reproductive Data for the Family Ariidae

Genus and Species	Spawning		Mature oocyte diameter: Range (Mean)	Fecundity[1]: Range (Mean)	Buccal Incubation			Source(s)
	Sites, Movements	Season, Locality			Period	No. eggs in mouth	Development Notes[2]	
A. spixii		Annual: Jul-Oct; Venezuela		14-38			Young at release: 42-44 mm	Luengo, 1973; Etchevers, 1978
A. thalassinus /*A. dayii*[3]	20-60 m depth over silt substratum; 25-28°C	Annual: Jun-Aug; (*A. thalassinus*); Nov-Mar (*A. dayii*); Arabian Sea.	15-20 mm Usually 16 mm	160, in 4 batches; each batch 23-67		1-47	Young at release: 64 mm. Each male incubates a single batch of eggs	Dmitrenko, 1970, 1974; Al-Nasiri and Hoda, 1977
Bagre *B. marinus*	Over mud substratum	Annual: May-Jun; East Coast U.S.	15-25 mm Usually 19-20 mm	25-68	9 wks	1-55 Usually 10-30	Egg weight 3.5 g; Young at release: 9.0 g, 85-100 mm	Gudger, 1916, 1919; Merriman, 1940
Nedystoma *N. dayi*	Freshwater		10 mm			20 (1 spec.)		Roberts, 1978
Osteogeneiosus *O. militaris*	Lower estuarine areas, after migration up estuaries in late winter, Jan-Feb.	Annual: Mar-May; India	9.8-12.0 mm (10.45)	18-63				Pantulu, 1963
Selenaspis *S. herzbergii*			9.5-11.0 mm	54 (1 spec.)				Luengo, 1973
Sciadeichthys *S. proops*						20-28	Young at release: 69-73 mm	Luengo, 1973

1. Sample sizes are variable — where an estimate is based on a very small sample, the sample size is given.
2. Unless otherwise stated lengths are assumed to be total length.
3. A number of observations of the reproductive biology of *A. thalassinus* (Dmitrenko, 1970) were later found to be based on two species, *A. thalassinus* and *A. dayii* (Dmitrenko, 1974); thus it is uncertain to which species quantitative information refers.

No details of spawning behaviour in ariids are available but a few general observations have been recorded. Atz (1958) noted that spawning in *A. felis* was apparently preceded by females vigorously chasing the males. Gudger (1916) and Gunter (1947) noted that stripped female *B. marinus* and *A. felis* extruded clumps of oocytes, both yolky and hyaline, which were held together by an adhesive substance which broke down when exposed to water for a few hours. Similar clusters were reported by Chidambaram (1941) and Smith (1945). Gudger (1918) quoted a report of *A. felis* depositing the egg mass in a depression in sand where it was fertilized and then picked up by the male. Dmitrenko (1970, 1974) found similar clusters of oocytes of *A. thalassinus* and *A. dayii* on the substratum of the Arabian Sea and postulated that the function of the positively buoyant hyaline eggs was to prevent the egg mass sinking into the silt before it could be ingested by the male. As several males of these two species were found to have stomach contents which included empty follicular membranes and hyaline eggs, Dmitrenko further suggested that males swallowed the egg mass. He postulated that the adhesive denatured under enzyme action, and that mature eggs were then regurgitated to the buccal cavity. However, it is difficult to accept that the fertilized eggs would remain undamaged by either the stomach enzymes or regurgitation process. Sekharan and Mojumder (1974) observed that unfertilized oocytes in an egg mass carried by *A. caelatus* decomposed soon after spawning.

Most authors have reported a single spawning per season; however, Mane (1929) and Dmitrenko (1970) found egg classes corresponding to separate spawning runs in *A. manillensis* and *A. thalassinus* respectively, although this observation for the latter species appears to have been due to some taxonomic confusion (Dmitrenko, 1974). Merriman (1940) suggested that *A. felis* may be polygamous, as individual fecundity exceeds the number of eggs generally carried by a single male, but Dmitrenko (1970, 1974) found *A. thalassinus* and *A. dayii* to be apparently monogamous.

Development

All published reports, with one exception, note that the male carries the eggs and larvae; Mane (1929) reported that in a sample of 250 *A. manillensis* a single female was found to be carrying eggs. Assessing numbers of eggs held orally is difficult as carrying males often drop or swallow eggs when captured (Gudger, 1916, 1918; Lee, 1931; Breder, 1935; Luengo, 1973); this phenomenon at least partly explains the wide range of mouth egg counts recorded (1-68). Lake and Midgley (1970) found 123 eggs in the mouth of a male ariid from the Dawson River, Queensland; however, the specific identification of this specimen is now uncertain. Generally, all the eggs or juveniles are at the same stage of development, although Smith (1945) found a male *A. sagor* carrying a newly-spawned egg mass as well as four postlarvae 40 mm in length, suggesting that some individuals may incubate more than one brood per season.

During the incubation period the male does not feed; the stomach shrinks greatly and contains only a small quantity of mucus (Willey, 1910; Gudger, 1918, Hardenberg, 1935; Lee, 1937, Merriman, 1940; Chidambaram, 1941; Smith, 1945; Tobor, 1969, 1978; Luengo, 1973; Bishop *et al.,* 1980). Lee (1937) noted that the testes of male *A. felis* carrying eggs were much more developed than those of non-carriers. Recorded incubation periods range from 6 to 9 weeks and during the latter part of the carrying period the young may commence feeding on plankton (Merriman, 1940; Tobor, 1969, 1978). Gudger (1918) and Luengo (1973) reported observations of young leaving the male's mouth for short periods and returning when alarmed, a behaviour pattern also observed in other mouthbrooders (Oppenheimer, 1970; Merrick and Green, 1982). The size of young at release varies from 30 to 44 mm for *A. manillensis* (Mane, 1929) to 85 to 100 mm for *B. marinus* (Gudger, 1918).

Chidambaram (1941) noted that embryos of *A. jella* hatched head-first through a tear in the egg membrane, and Fowler (1942) concluded that secretory cells in the epidermis of the head region of *A. felis* embryos were responsible for the thinning of the embryonic membrane just prior to hatching. Hatching generally takes place approximately mid-way through the incubation period (Merriman, 1940; Chidambaram, 1941).

Evolution of Reproductive Strategies

Gudger (1918) and Breder (1935) speculated on the evolution of buccal incubation as a reproductive mode in siluroids. Both authors suggested that buccal incubation evolved from a nest-building mode as seen in modern ictalurid catfishes. The nest-building *Ictalurus nebulosus* may rearrange its eggs by 'mouthing' the egg mass and may even retain the eggs in the mouth for short periods (Breder, 1935). Such an evolutionary trend, from nesting to oral incubation, is seen in the Cichlidae (Oppenheimer, 1970; Balon, 1977). It has also been suggested that territorial behaviour, such as nest guarding, may pre-adapt a species for the evolution of male parental care by optimizing the level of paternity (Werren *et al.,* 1980).

The evolution of parental care in fishes has generally resulted in decreased fecundity and increased egg size (Oppenheimer, 1970), and this is particularly evident in the Ariidae. The ariids are also notable for the length of time the eggs and young are retained — generally 6 to 8 weeks — which is far longer than is found in most other mouthbrooders (Oppenheimer, 1970; Merrick and Green, 1982).

The advantages of buccal incubation involve minimizing mortality in the vulnerable egg and larval stages by optimizing physiological conditions (e.g. water temperature, dissolved oxygen) and by limiting predation during incubation as well as after release due to the production of large well-developed offspring (Oppenheimer, 1970; Lowe-McConnell, 1975). An example of physicochemical influences on oral incubation was noted by Harvey (1972a, b) who found incubating male *A. felis* with embryos in salinities from 8.33 to 12.78 p.p.t., while those brooding larvae were found in salinities from 16.66 to 28.32 p.p.t.; Harvey suggested that this was a response to limited salinity tolerances of the embryo until kidney development could cope with osmoregulation in higher salinities.

Balon (1977) noted that the buccal cavity may often be an oxygen deficient environment due to the limited amount of water movement possible when much of the mouth is blocked by eggs. Recent evidence suggests that the evolution of bright yellow, orange or red eggs, commonly found in fishes with well-developed parental care strategies, may be due to the use of the carotenoid pigments in endogenous oxygen metabolism (Nikolsky, 1963; Balon, 1977, 1979).

The mode of reproduction found in ariids is undoubtedly an important aspect of their success in fluviatile, estuarine and marine environments. Buccal incubation does not necessitate specific substrata or water quality criteria as the mobile adults are able to select the environmental conditions necessary for developing eggs and larvae. This feature, in addition to apparently wide physiological tolerances, has enabled ariids to colonize a wide range of habitats in tropical and sub-tropical regions.

CONCLUSIONS

Whilst further information is required on all aspects of ariid reproduction and development, this survey summarizes data on 28 species representing 11 genera. From the current knowledge a number of general points can be drawn to form the basis for future detailed investigations, either of individual species or groups.

Ariids are dioecious, oviparous and possess paired functional cystovarian gonads of an unlobed hollow type. Sexual dimorphism is confined to pelvic fin structural differences and seasonal changes in the oral epithelium of the male and the 'claspers' of the female.

Anadromous and limnodromous movements associated with breeding have been observed in several species. Most ariids have a single annual spawning associated with the wet monsoon (tropical species) or spring (sub-tropical species); the few water temperatures reported during the spawning season have ranged from 25° to 28°C.

The external fertilization involves small numbers of large demersal eggs together with large numbers of small non-functional eggs apparently laid in clusters onto the substratum. Development is protracted; buccal incubation, undertaken by the male, may continue for up to 9 weeks before the offspring are released as well-developed, actively feeding juveniles.

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The male of *Progradungula carraiensis* Forster and Gray (Araneae, Gradungulidae) with Observations on the Web and prey Capture

M. R. GRAY

GRAY, M. R. The male of *Progradungula carraiensis* Forster and Gray (Araneae, Gradungulidae) with observations on the web and prey capture. *Proc. Linn. Soc. N.S.W.* 107 (1), (1982) 1983:51-58.

The male of *Progradungula carraiensis* is described. Notes are given on the structure of the webs of female spiders and of the cribellate silk used in the prey 'catching ladder'. Prey catching and avoidance behaviour are described.

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INTRODUCTION

Progradungula carraiensis Forster and Gray is the only cribellate representative of the hypochiloid family Gradungulidae. A description, based on female and juvenile specimens from Carrai Bat Cave, New South Wales, and a discussion of the phylogenetic significance of the genus was given in Forster and Gray (1979).

Recently, a penultimate male spider was collected from a web in Carrai Bat Cave. The web consisted simply of a sparse network of non-cribellate silk spanning a wall recess. The spider was subsequently reared to maturity in the laboratory.

The basic structure of the *Progradungula* male palp (Figs 3, 4) resembles both that seen in the related ecribellate genus *Gradungula* Forster (Davies, 1969; Forster, 1955) and the Tasmanian hypochiloid genus *Hickmania* Gertsch (Hickmaniidae) in which the conductor and embolus are fused and the bulb is inserted basally on the cymbium. In the other hypochiloid genera a discrete conductor and embolus is present and, in *Hypochilus* Marx and *Ectatosticta* Simon, the bulb is inserted apically upon the cymbium (Gertsch, 1958). However, in *Thaida* Karsch the bulb is basally inserted as it is in the Gradungulidae and *Hickmania.* The presence of a notch on the tibial bothria of *Thaida* and *Hickmania* seems to represent a significant synapomorphy between these genera (Forster and Gray, 1979). The gradungulid bothria are elaborately notched or crenellated, rather more so in the ecribellate species than in *Progradungula.*

GENUS *PROGRADUNGULA*

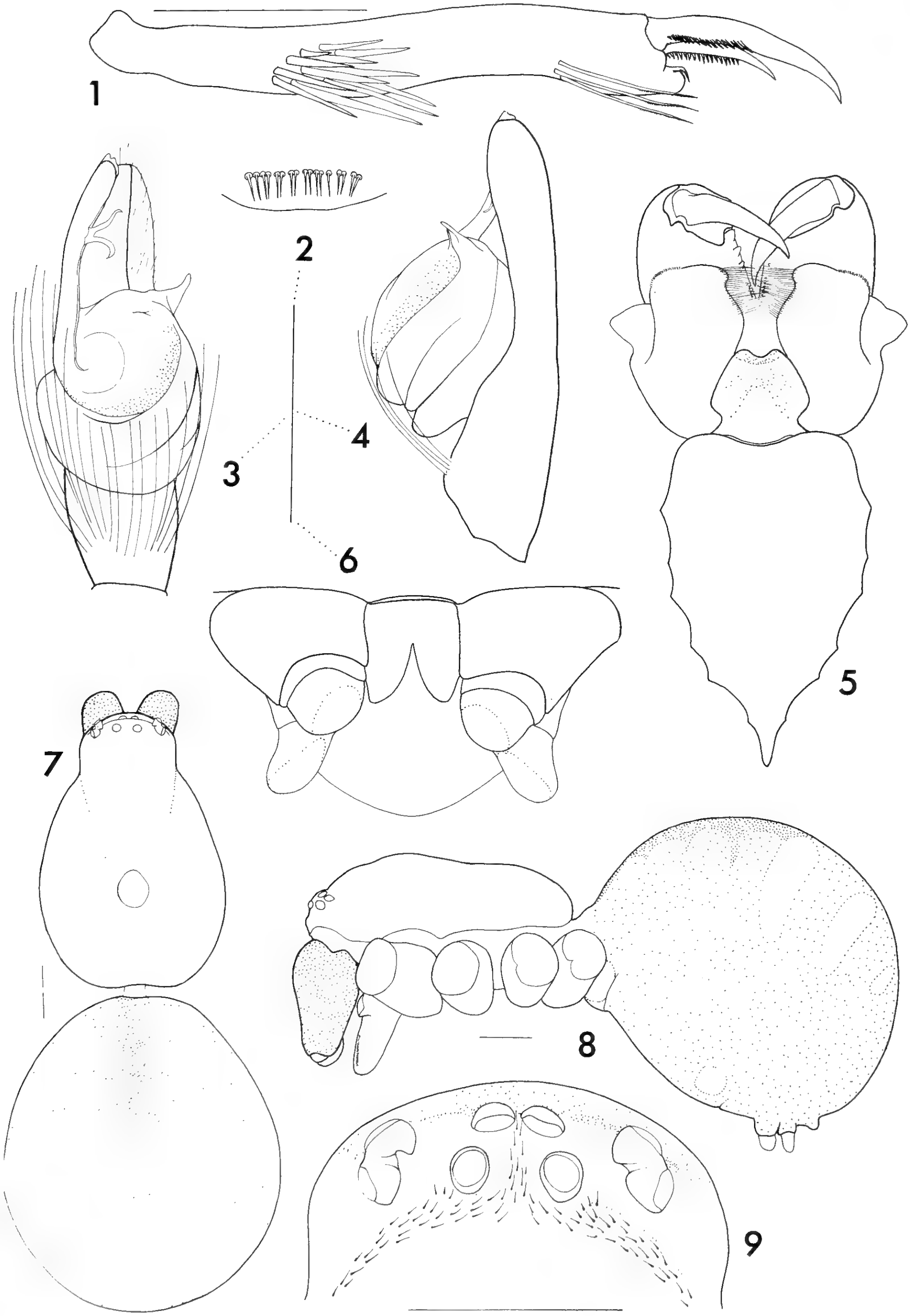
Progradungula Forster and Gray, 1979: 1051.

Type species: *Progradungula carraiensis* Forster and Gray.

Diagnosis: Four lunged, cribellate spiders with enlarged prolateral superior tarsal claws on legs 1 and 2. Female genitalia consisting of six receptacula placed in two widely separated groups of three each; thin ducts, associated with secretory cells, connect them to a common copulatory bursa. Male palp with a ventrally furrowed cymbium, bulb attached basally. Embolus rod-like, fused with conductor, with two curved, spine-like processes arising close together near its middle.

Progradungula carraiensis Forster and Gray

Types: Holotype female: New South Wales, Carrai Bat Cave, Carrai State Forest, 19.vii.1971, M. Gray; in Australian Museum, Sydney (KS 1583). Paratypes: 2 females, coll. 24.iv.1974, other data as above; in Otago Museum, Dunedin. 1 juvenile,



Figs 1-9. Progradungula carraiensis, male. **1,** tarsus, first leg, proventral. **2,** epiandrous glands. **3-4,** male palp: 3, ventral; 4, retrolateral. **5,** cephalothorax, ventral. **6,** spinnerets. **7-8,** cephalothorax and abdomen: 7, dorsal; 8, lateral. **9,** eyes, dorsal. Scale lines 1.0 mm.

locality as above, coll. 1.vii.1970, J. A. Harris; in American Museum of Natural History.

Description of male (Figs 1-9)

Measurements (mm) — Carapace length 5.03, width 3.41. Abdomen length 11.0, width 9.5.

Colour pattern (Figs 7, 8) — carapace, sternum and legs light fawn-brown, legs slightly darker. Chelicerae dark brown. Abdomen light brown with an indistinct, greyish, mid-dorsal stripe followed by three pairs of paler dorso-lateral chevron markings.

Carapace (Figs 7, 8) — longer than wide in ratio 1:0.68. Cephalic area prominent, anterior margin strongly recurved; profile domed. Ocular area delimited in front and behind by transverse grooves. Fovea a broad, shallow, rounded pit. Clypeus convex, projecting over the chelicerae; clypeus height 3.5 times the diameter of an AME.

Eyes (Fig. 9) — lateral eyes on a common, low prominence. All eyes with complete tapeta. ALE > PME > PLE > AME in ratio 1:0.85:0.79:0.69. Interdistances (mm): AME–AME 0.10, AME–ALE 0.29, ALE–PLE 0.08, PLE–PME 0.35, PME–PME 0.23. M.O.Q. length 0.38 mm, anterior width 0.36 mm, posterior width 0.58 mm. Posterior eye row slightly longer than anterior eye row in ratio 1:0.95. Eye row curvatures: from above both rows are slightly recurved; from in front the anterior row is straight to slightly procurved, posterior row slightly procurved.

Chelicerae (Fig. 5) — boss absent, fang groove long and narrow with 4 large, evenly-spaced prolateral teeth; and 7 retrolateral denticles in basal half of groove.

Maxillae (Fig. 5) — length 1.56 mm, width 0.86 mm. Linear serrula of 60-70 teeth on antero-ectal border.

Labium (Fig. 5) — length 0.79 mm, width 0.82 mm. Not fused with sternum. Margin rebordered.

Sternum (Fig. 5) — length 2.68 mm, width 1.69 mm. Long, extending to level of posterior margins of coxae 4.

Palp — Spination: femur d 5 (apical third), p 1-3 (apical), r 1-3 (apical), v 100; patella d 11, r 1, p 1, (all weak); tibia d 11, p 010, r 011. Cymbium ventrally furrowed, bulb attached basally (Figs 3, 4). Tegulum with a fixed retrolateral process. Embolus and fused conductor form a gently sinuous rod running below the cymbial furrow. Two slender, spine-like, curved processes arise retrolaterally from the embolus at the junction of its central and distal thirds. Embolus apex blunt, indented, non-sclerotized.

Legs — 1423. Long and slender. Length (mm), legs 1-4: 37.37, 29.91, 24.87, 30.01. Spination: Leg 1, femur p seventeen in single row, r 12121101100, d 102(1111111, all retrolateral) 2, v 121221210; patella p 1, r 1; tibia p 111111, r 101111, d 010001, v 221222; metatarsus p 11101, r 1010101, v 2221; tarsus v fourteen (proximal). Leg 2, femur p thirteen (in single row), r 1120000, d 12(11111, all retrolateral)02, v 222220; patella p 1, r 1; tibia p 111111, r 10111, d 00101, v 22222; metatarsus p 11112, r 110102, v 22121; tarsus v eleven (proximal). Leg 3, femur p ten (in single row, dorsal), r 1111000, d 221111113, v 1222121; patella p 1, r 1; tibia p 11111, r 111111, d 01101, v 21222; metatarsus p 11112, r 11102, v 22121; tarsus v 010. Leg 4, femur p 101111101, r 00011111, d 2111110001, v 212211211; patella p 1; tibia p 11111, r 111111, d 10001, v 221112; metatarsus p 11112, r 10112, v 211221; tarsus v 010. Legs 1 and 2 with short, curved, ventrally concave tarsi, ventral spines bunched proximally and prolateral superior claws enlarged (Fig. 1). Empodium prominent with a slender inferior claw. Teeth on superior tarsal claws (legs 1-4): prolateral 19, 18, 10, 11, retrolateral 25, 19, 11, 11; on inferior tarsal claws, 1-2. Ventral tarsi with several toothed hairs (14-16 pectinations in distal half) arising subdistally. Trichobothria: tarsus, none; metatarsus, 1 distal (legs 1 and 2), 1 subdistal (legs 3 and 4); tibia (legs 1-4), prodorsal, 2 in distal third to fifth, 8-9 in proximal quarter, retrodorsal 9-10 in distal half to two thirds. Bothria crenellated on antero-internal margin. Trochanters shallowly notched. Calamistrum reduced to a short row of weak hairs.

Abdomen (Figs 7, 8) — A broad common spiracle, placed near spinnerets opens into an atrium leading to the posterior lung books. Posterior lung books placed closer to spinnerets than to genital groove. Epiandrous glands present in a single row along the anterior border of the epigastric fold (Fig. 2). Cribellum reduced.

Collection Data: Male, Carrai Bat Cave, Carrai State Forest, N.S.W., M. Gray, 21.2.1980; KS 6740, Australian Museum.

WEB STRUCTURE

All of the webs so far observed have been found in cave environments. However, it seems reasonable to assume that *Progradungula* may also occur in suitable epigean habitats e.g. within rotting logs or moist rock/soil cavities.

Notes on web structure based upon a vertically elongated web were given in Gray (1973) and Forster and Gray (1979). Further observation of the webs of female spiders at Carrai Bat Cave indicates that webs are generally more compact than this, most ranging from 20 to 50 centimetres overall in both vertical and horizontal extent. The webs are built between adjacent rocks or under rock overhangs, usually near the cave walls. They are not particularly associated with bat roosting areas but occur sporadically throughout the twilight and dark zones.

The structure of the *Progradungula* web (Fig. 10) may be summarized as follows: a narrow, cribellate catching ladder (a) is suspended low down between two semi-vertical lateral support lines (b) which run from an irregular retreat network (d) above to ground attachments below. These attachments may be to soil or rocks on the cave floor or, less commonly, to the cave wall.

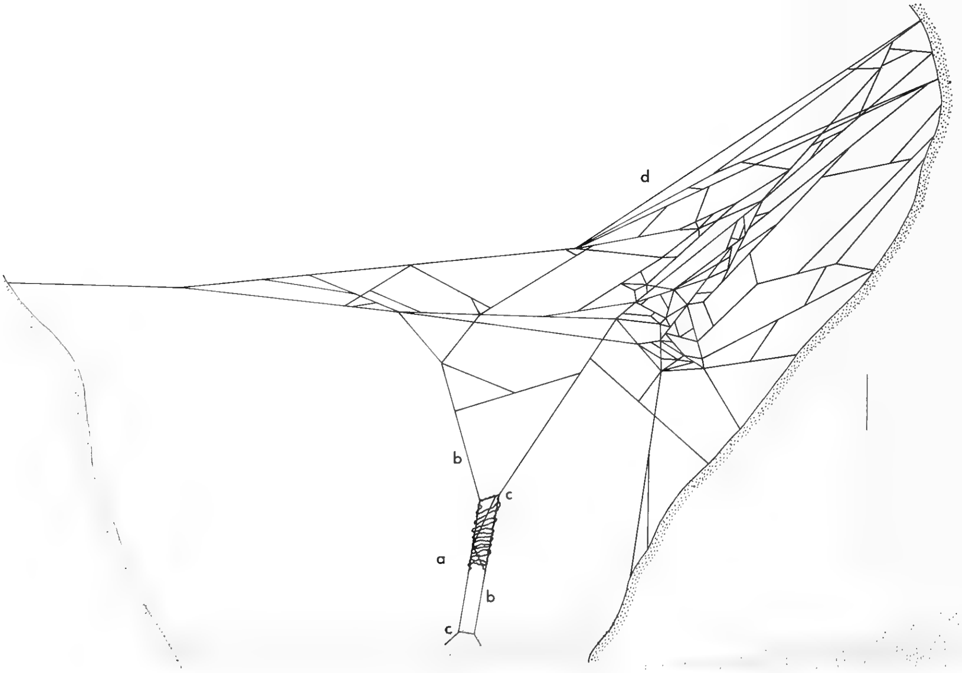
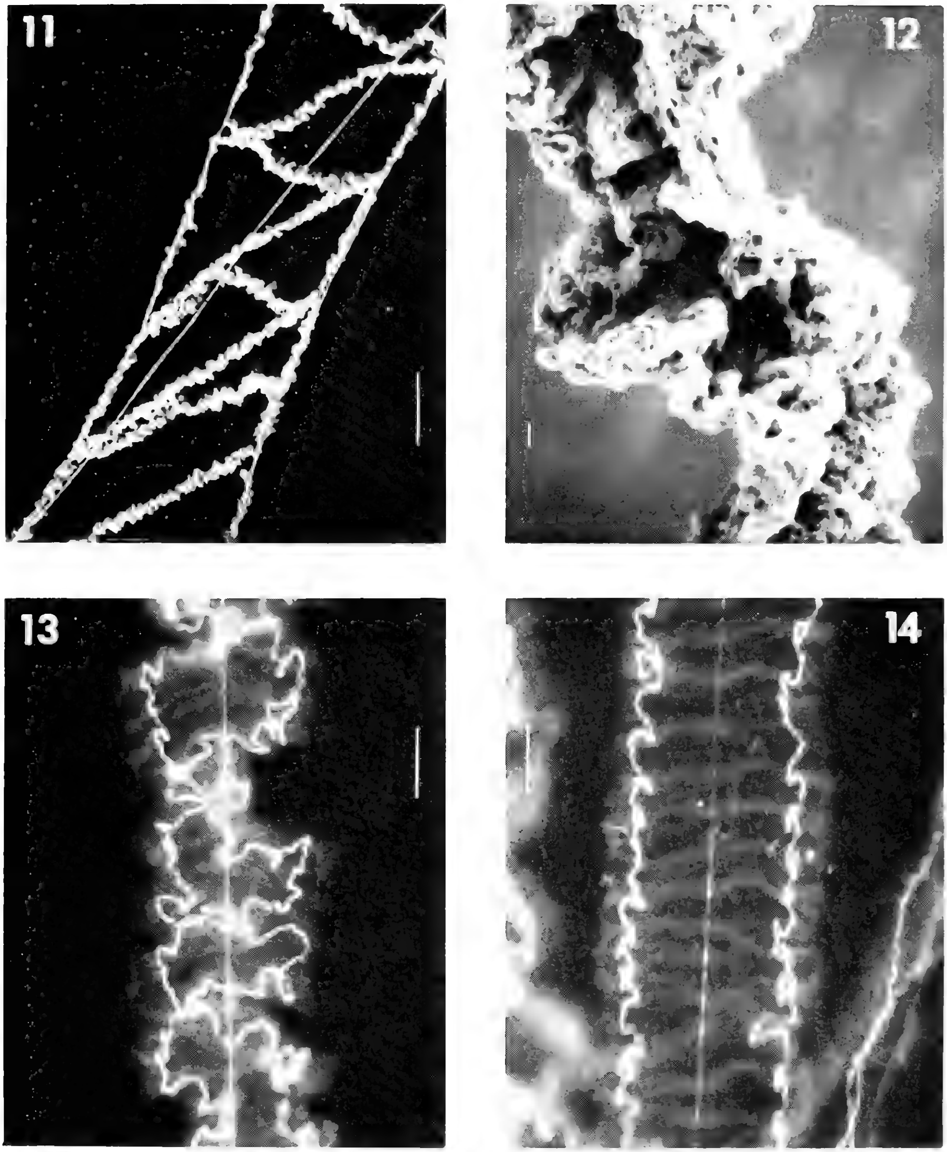


Fig. 10. Web of *Progradungula carraiensis* — (a) prey catching ladder; (b) lateral support lines; (c) bridge lines; (d) retreat network. Scale line 2.5 cm.



Figs 11-14. Progradungula carraiensis, catching ladder. **11,** part of ladder showing non-cribellate support and cribellate catching lines. Scale line 3.0 mm. **12,** cribellate line showing dense, fibrillar surface structure. **13-14,** structure of cribellate silk line. 13, relaxed; 14, stretched. Scale lines 0.15 mm.

The most unusual feature of the web is the subvertical prey-catching ladder (referred to as the catching 'platform' in Forster and Gray, 1979; 'ladder' is more accurately descriptive). The catching ladder is delimited by transverse upper and lower bridge lines (c, Fig. 10) set some 50 to 120 millimetres apart. With one or two diagonal brace/support lines, they hold the main lateral support lines in place at a near parallel separation of 5 to 8 millimetres. An upper diagonal line is always present below the upper bridge line; the lower diagonal line is usually shorter and may be replaced by a secondary cribellate line. The lower bridge line is placed from 5 to 20 millimetres above ground level; rarely there may be two lower bridge lines or none at all.

Only the upper part of the catching ladder receives an application of cribellate silk, the lower part being left open. A continuous line of cribellate silk is applied in a series of loose loops back and forth across the lateral and diagonal support lines, often overlapping the laterals, to form a zig-zag, ladder-like structure (Fig. 11). In adult webs the number of cross loops varies from 14 to 25. Cribellate silk is also applied to the adjacent parts of the lateral support lines and often to the diagonal and upper bridge lines as well.

The webs of other cribellate hypochiloid spiders are very different in structure. For example, *Hypochilus* Marx makes a short, slightly tapered cylindrical web ('lamp-shade'-shaped) while the web of *Hickmania* Gertsch takes the form of a large sheet (Shear, 1969; Hickman, 1967). The cribellate part of the *Progradungula* web, the catching ladder, may be homologous with the simple, zig-zag element which forms the basis of many, more elaborate cribellate webs. The web is probably derivative, resulting from simplification of web structure in association with both space-restricted habitats and specialized feeding behaviour.

CRIBELLATE SILK STRUCTURE

The cribellate silk laid down across the support lines of the catching ladder is only loosely adherent to them. Each cribellate line consists of a thick, irregularly twisted network of fine, curling microfibrils (Fig. 12). The microfibrils are supported by four longitudinal silk lines, two axial and two lateral. The axial lines lie next to each other and appear fused as a single, straight line whereas the lateral lines are well separated and are normally strongly crimped, forming a wave-like interlocking structure (Fig. 13). When the cribellate thread is stretched the lateral lines and the microfibril mass straighten (Fig. 14); these components may move as a unit which slides along the fused axial lines during stretching.

The cribellate silk structure of *Progradungula* differs slightly from that of *Hypochilus* Marx (Comstock, 1940; Shear, 1969). In *Hypochilus* the two straight 'axial' lines are well separated, rather than fused into a single line.

PREY CAPTURE

P. carraiensis adopts a head-down hunting position upon the lower surface of the sub-vertical catching ladder (Fig. 15). The third and fourth legs hold the spider onto the lateral support lines. The tarsi of the fourth legs are placed at or above the junctions of the latter with the upper bridge line. The tarsi of the third legs are placed near the middle of the cribellate platform. They push the lateral support lines away from the body so that the catching ladder is bent at an obtuse angle. This tenses the whole structure and creates a sizeable gap between the ladder and the spider's body. In this position the spider's chelicerae are approximately at the level of the lowest cribellate threads in the catching ladder. The first and second legs, with their enlarged prolateral tarsal claws, do not touch the web but are held poised in a partially outstretched position below and anterior to the ladder. However, the tarsi of the second legs sometimes rest near the junctions of the lower bridge and lateral support lines. The tarsal claws of the first legs are held just above ground level.

The two ground attachments of the catching ladder and the spider's outstretched first and second legs form a semi-circular prey capture zone some 10-15 cm^2 in area.

Prey moving just beyond the capture zone can be sensed by the spider. Air currents affecting the trichobothria or substrate vibrations transmitted via the ladder's

Fig. 15. Female *Progradungula carraiensis* in hunting position on catching ladder.

ground attachments may be the stimuli involved. In response the spider makes probing movements with its first legs toward the disturbance. At the same time the pliable catching ladder is flexed in the direction of probing. As soon as the first legs touch the prey the spider lunges forward and down, and uses the enlarged prolateral claws and ventrally-spined, concave tarsi of the first and second legs to scoop it up. These legs are flexed upwards so that the prey is thrust into the space between the catching ladder and the spider's body and so onto the cribellate silk of the ladder. At the same time the third legs are relaxed allowing the catching ladder to spring in towards the prey. The cribellate silk detaches readily from its supports and thoroughly enfolds the struggling prey. The spider then bites the enmeshed prey while maintaining a 'jack-knifed' embrace of it in its front legs for about ten seconds.

Once the prey is immobilized the spider moves to a head up position above it and begins prey wrapping, the tarsi of the fourth legs being used alternately to draw silk. This continues for several minutes. At this stage the prey is suspended from the tangled support lines of the upper platform; the lower cross bridge and the ground attachments of the lateral support lines remain undisturbed. The wrapped prey may be bitten again for a few seconds. The spider then climbs to the upper part of the web near the side wall holding the prey in its jaws and feeds upon it.

Only tineid moths (6-10 mm long), which are common on the floor of Carrai Bat Cave, have been observed as prey of *P. carraiensis.* Other potential prey includes small beetles, juvenile cave crickets, spiders and flies. Larger prey, such as carabid beetles, seems to be avoided, the spider possibly judging prey size during the probing movements. Avoidance behaviour involves retreat onto the support lines or into the upper web. If further disturbed here the spider will either move out of the web onto the rock wall; or it will drop from the web and lie motionless on the ground with the legs tightly flexed. The latter escape response is typical of that shown by many other araneomorph web builders.

In cave and equivalent epigean environments the invertebrate fauna is mainly substrate dwelling. The web, behaviour and morphology of *P. carraiensis* are well adapted for the capture of such prey. Very little energy has to be expended in web building, only the small cribellate platform requiring regular renewal. During prey capture the spider functions as an active extension of its web. It combines the ambushing tactics of the lie-in-wait hunter, aided in prey grasping by the modifications of the first and second tarsi, with the immobilizing effect of a cribellate snare which provides an 'instant prey wrapping' function. The simultaneous clasping and biting of the enmeshed prey upon the catching ladder precludes prey escape but probably limits the capture ability of *P. carraiensis* to prey of about its own body size or smaller. This contrasts with the net casting spiders (family Dinopidae) whose small cribellate snare represents another type of instant prey-enswathing/immobilization device. The first and second legs of these spiders hold the snare between the spider and its prey and direct its placement onto the latter. This snare is highly elastic and can be stretched to several times its original size, allowing quite large prey (e.g. male trapdoor spiders, crickets) to be successfully attacked.

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Lower Ordovician arthropod Trace Fossils from western New South Wales

B. D. WEBBY

WEBBY, B. D. Lower Ordovician arthropod trace fossils from western New South Wales. *Proc. Linn. Soc. N.S.W.* 107 (2), (1982) 1983: 61-76.

Eight trace fossil species attributed to the activity of arthropods are described and illustrated from the Lower Ordovician (Tremadoc-Arenig) clastic succession of western New South Wales. They include the new species *Cruziana warrisi, Diplichnites binatus* and *Rusophycus latus.* A number of different arthropods would seem to have been responsible, but not necessarily trilobites. The *Diplichnites* sp. A trackway is some 185 mm wide, suggesting a very large arthropod, larger than any known trilobite from accompanying beds of the N.S.W. Lower Ordovician succession. *R. latus* is the most common type of arthropod activity in the N.S.W. Lower Ordovician succession (Bynguano Quartzite and Scopes Range Beds). It closely resembles the *Rusophycus* found in central Australia — in the Pacoota Sandstone of the Amadeus Basin and the Tomahawk Beds of the Georgina Basin. The western N.S.W. arthropod traces are associated in shallow marine deposits with *Skolithos, Arthrophycus, Diplocraterion* and other unnamed trace fossils. A preliminary Lower-Middle Ordovician arthropod ichnostratigraphy is outlined based on these and other known Australian occurrences.

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manuscript received 8 February 1983, accepted for publication 20 April 1983.

INTRODUCTION

Of the many trace fossils preserved in Lower Palaeozoic clastic successions of Australia, those attributed to the activity of arthropods are among the most distinctive and common. They include such forms as *Cruziana, Dimorphichnus, Diplichnites, Merostomichnites, Monomorphichnus, Protichnites* and *Rusophycus.* The structure attributed by Woods (1862) to *Cruziana cucurbita* Salter appears to be the first record of a Lower Palaeozoic arthropod trail from Australia. It was not however until nearly one hundred years later that it became generally realized how widespread and abundant such occurrences were. Glaessner (1957) drew attention to the numerous occurrences of *Cruziana* in the Cambrian of South Australia and the Ordovician of central Australia, and many authors have since recorded such arthropod traces from these and other Lower Palaeozoic sequences. But few have yet carried out detailed studies of these trace fossils, or attempted to establish their stratigraphic or palaeoenvironmental potential.

In western New South Wales, Lower Ordovician arthropod traces were first noted from the Bynguano Range of the Mootwingee area by Wilson (1967) and Warris (1967, unpubl.), and from the Scopes Range by Rose and Brunker (1969). In the Bynguano Range, *Cruziana* was recorded from the Bynguano Quartzite (Warris, 1967, unpubl.; Shergold, 1971; in part the Lingula Beds of Wilson, 1967). However the morphological appearance of these most common arthropod traces in the Bynguano Quartzite are more properly identified as representatives of *Rusophycus,* as Pogson and Scheibner (1976) have already noted. Rose and Brunker (1969) and Webby (1974, unpubl.; 1977) reported the same variety of *Rusophycus* from the Scopes Range Beds at Scopes Range. The only trace fossil previously illustrated from the Ordovician of western New South Wales is a *Rusophycus* which was erroneously assigned a Cambrian age (Hill, 1972, fig. 10a).

STRATIGRAPHY

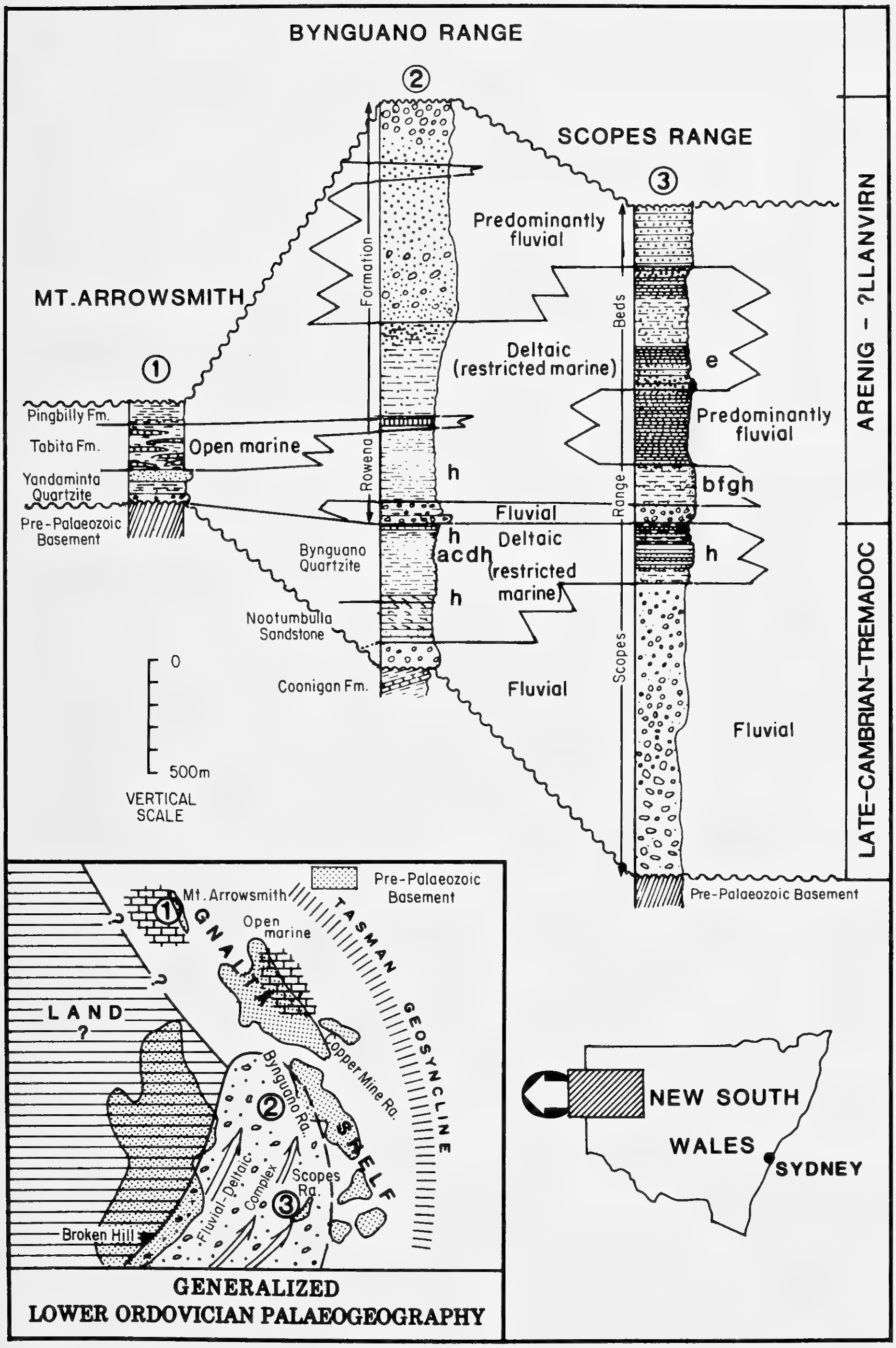
The stratigraphical terminology for the uppermost Cambrian-Lower Ordovician of western New South Wales is based on Warris (1967, unpubl.) and Rose (1968). In the Bynguano Range, the sequence comprises in ascending order, the Nootumbulla Sandstone, the Bynguano Quartzite and the Rowena Formation (Webby, *in* Shergold *et al.,* 1982, text-fig. 8). The Bynguano Quartzite is 305 m thick and the Rowena Formation, 1685 m thick. The Rowena Formation is a predominantly quartzitic sandstone succession but has some interbedded conglomerates and thin, impure limestones. In the Scopes Range, the sequence of Scopes Range Beds includes a lower, 1200 m thick 'non-marine' conglomerate unit overlain by a 1650 m thick alternating 'shallow marine' to 'non-marine' (fluvial) sandstone unit. Correlations between the successions of the two areas have been represented by Webby (1978, fig. 3; *in* Shergold *et al.,* 1982, text-fig. 9).

Rusophycus latus is common throughout the Bynguano Quartzite and occurs again in the lower part of the overlying Rowena Formation, up to the level of the thin, impure limestone beds. Other arthropod traces occur only rarely in the Bynguano Quartzite. They include *Cruziana warrisi, Cruziana* sp. B, and *Diplichnites binatus.* In Scopes Range, *R. latus* is mainly confined to the quartz-rich sandstones in the middle part of the Scopes Range Beds. It may be associated with rare occurrences of *Cruziana* sp. A, *Diplichnites* sp. B and *Monomorphichnus* sp. A stratigraphically higher unit of the Scopes Range Beds includes the isolated occurrence of *Diplichnites* sp. A. The *Rusophycus* occurrences in the Bynguano Quartzite are of broadly similar 'Tremadoc' age (Webby, *in* Shergold *et al.* 1982, pp. 220-21), while the occurrences in the lower part of the Rowena Formation are of slightly younger, possibly early Arenig age. The *Rusophycus* associations in the middle part of the Scopes Range Beds probably span a similar interval (Fig. 1).

The uppermost Cambrian-Lower Ordovician clastic successions in western New South Wales have been interpreted as having accumulated in a major delta complex (Webby, 1976; 1978). The deposits were spread in successive influxes across the Gnalta Shelf (a remnant of the former continental shelf) from uplifted land areas of Gondwanaland to the south and west (Fig. 1). The proportion of non-marine deposits (and coarse clastics) is greatest in the Scopes Range succession reflecting its more proximal position in the delta system. The most marine depositional conditions are of very shallow water type, recorded at three stratigraphic levels within the Scopes Range succession, and including representatives of the *Rusophycus, Skolithos* and *Arthrophycus*-dominated trace-fossil assemblages. Occasionally shells of inarticulate brachiopod *Trigonoglossa* and a gastropod may also be associated.

In the more markedly marine Bynguano Range succession, *Rusophycus, Skolithos* and *Arthrophycus* trace-fossil assemblages dominate the shallowest marine parts of the sequence but there is also a short-lived phase of more open marine conditions with a varied shelly fauna (Webby, *in* Shergold *et al.,* 1982, text-figs 8-9). This occurs in the middle part of the Rowena Formation. The fauna includes the trilobites *Carolinites, Asaphellus, Prosopiscus* and protopliomerids, the brachiopods *Obolus, Lingulella, Ectonoglossa,* gastropods and the conodonts *Microcoelodus, Chirognathus* and *Aphelognathus.* It closely resembles the fauna occurring in the Tabita Formation at Mount Arrowsmith (Fig. 1), and in the Horn Valley Siltstone of the Amadeus Basin, central Australia.

Fig. 1. Diagram to show location of arthropod traces in stratigraphic columns of the Upper Cambrian — Lower Ordovician succession in western New South Wales. Arthropod traces are typically represented in the 'deltaic facies' of the Bynguano Range and Scopes Range sections. Key to arthropod traces shown by letter symbols in stratigraphic columns, as follows: a, *Cruziana warrisi;* b, *Cruziana* sp. A; c, *Cruziana* sp. B; d, *Diplichnites binatus;* e, *Diplichnites* sp. A; f, *Diplichnites* sp. B; g, *Monomorphichnus* sp.; h, *Rusophycus latus.* Locality map and generalized palaeogeographic map for region during Lower Ordovician (Tremadoc-Arenig) time also shown.


BYNGUANO RANGE
②
SCOPES RANGE
③
MT.ARROWSMITH
①
Predominantly fluvial
Deltaic (restricted marine)
e
Predominantly fluvial
bfgh
Fluvial
Deltaic (restricted marine)
h
acdh
h
h
Fluvial
Fluvial
Open marine
Pingbilly Fm.
Tabita Fm.
Yandaminta Quartzite
Pre-Palaeozoic Basement
Rowena Formation
Bynguano Quartzite
Nootumbulla Sandstone
Coonigan Fm.
Scopes Range Beds
Pre-Palaeozoic Basement
0
500m
VERTICAL SCALE
ARENIG - ?LLANVIRN
LATE-CAMBRIAN-TREMADOC
Pre-Palaeozoic Basement
Mt. Arrowsmith
①
Open marine
TASMAN GEOSYNCLINE
GNALTA SHELF
LAND
?
Copper Mine Ra.
Bynguano Ra.
②
Scopes Ra.
③
Fluvial-Deltaic Complex
Broken Hill
NEW SOUTH WALES
SYDNEY
GENERALIZED LOWER ORDOVICIAN PALAEOGEOGRAPHY

Of the eight trace-fossil species described from the Lower Ordovician of western New South Wales, only one, the 'rest mark' *Rusophycus latus,* is commonly represented in the successions. There is frequently so much activity that entire bedding surfaces are covered with scratchings of the arthropod (Fig. 2A). Association of *Skolithos* in some beds directly below the surface of colonization raises the question of whether the activity was more concerned with digging for the soft-bodied *Skolithos* animal than with resting, sheltering or concealment from predators. The occasional association of desiccation cracks on undersurfaces with *Rusophycus* testifies to the shallowness of marine conditions, probably implying deposition in the intertidal zone. None of the eight arthropod trace-fossil species can be demonstrated to represent the activity of particular trilobites.

The *Rusophycus*-bearing Bynguano Quartzite and its equivalents in the Scopes Range may be regarded as correlatives of the Pacoota Sandstone of the Amadeus Basin (Wilson, 1967; Warris, 1967, unpubl.; Webby, 1978; Webby *et al.,* 1981), and probably also of the Tomahawk Beds of the Georgina Basin. The form illustrated by Ranford *et al.* (1965) and Wells *et al.* (1970) as *Cruziana* from the Pacoota Sandstone is more correctly referable to *Rusophycus.* Indeed it closely resembles the New South Wales ichnospecies described herein as *R. latus.* Similarly the 'rest mark' from the Tomahawk Beds referred to *Cruziana omanica* by Seilacher (1970) is erroneously assigned since it does not exhibit the 'procline furrows' of the holotype from Oman. Based on accepted modern taxonomic practices (Osgood, 1970; Birkenmajer and Bruton, 1971; Bergström, 1973; Crimes, 1975; Crimes *et al.*, 1977), the Tomahawk specimen should be grouped as a *Rusophycus.* A similar variety of *Rusophycus* is illustrated by Hill *et al.* (1969, pl. V, fig. 10) from the Ordovician (formation not stated) of the Toko Range, Georgina Basin. These Georgina and Amadeus Basin forms should perhaps be equated with *R. latus.*

TOWARDS AN AUSTRALIAN ORDOVICIAN ARTHROPOD TRACE-FOSSIL SUCCESSION

In the light of Seilacher's (1970) claims that arthropod traces of the *Cruziana* and *Rusophycus* type can be useful guide fossils, it is perhaps worth noting that a crude ichnostratigraphy is already recognizable in Australian Lower-Middle Ordovician clastic successions. First, in the Lower Ordovician (Tremadoc-Lower Arenig) sequences like the Bynguano Quartzite, Pacoota Sandstone and Tomahawk Beds, there is an abundance of occurrences of *Rusophycus latus* type — forms which may be assigned to Seilacher's *petraea* group.

Secondly, in Arenig-Lower Llanvirn successions such as the Nora Formation of the Georgina Basin and the Stairway Sandstone of the Amadeus Basin, there are representatives of Seilacher's *rugosa* group. A well preserved *Cruziana* illustrated by Hill *et al.* (1969, pl. V, fig. 9) from the Nora Formation is attributable to *C. rugosa,* and a *Cruziana* in the Stairway Sandstone (Ranford *et al.*, 1965; Conybeare and Crook, 1968) is, according to Ritchie and Tomlinson (1977), an occurrence of *C. furcifera.*

Thirdly, in the Middle Ordovician succession of the Georgina Basin, Draper (1977; 1980) has recorded two distinctly different assemblages. A variety of arthropod traces occurs in the lower part (sub unit A) of the Carlo Sandstone, including *Cruziana, Dimorphichnus, Diplichnites, Merostomichnites* and *Rusophycus.* The representatives of *Cruziana* and *Rusophycus* have the appearance of members of Seilacher's (1970) *imbricata* group. A markedly different species of *Rusophycus* occurs in the overlying Mithaka Formation. The large, oval, bilobate specimens may be in excess of 300 mm long, and are characteristically differentiated into an inner area with traces of segmentation (imprints of coxae) and broad outer paired lobes covered with scratchings. They exhibit a range of morphology, most commonly resembling *R. carleyi* but also including specimens with similarities to *R. dilatatus*. Seilacher's (1970) original description of this latter species is based in part on a photograph of a large specimen from the Toko Range of the Georgina Basin. Draper (1980) has regarded the Mithaka forms of *Rusophycus* as belonging to Seilacher's (1970) *carleyi* group, but they could just as appropriately be linked to the *almadenensis* group. For instance Ritchie and Tomlinson (1977) have referred to a *Cruziana* from a similar or slightly younger stratigraphical horizon, in the Carmichael Sandstone of the Amadeus Basin, as *C.* cf. *almadenensis*.

In very generalized terms the Australian Lower-Middle Ordovician succession of 'groups' (*petraea* → *rugosa* → *imbricata* → *carleyi* or *almadenensis*) is comparable with that depicted by Seilacher (1970) for European and North African sequences. However at the ichnospecies level few forms are common to both European/North African and Australian successions. None of the European 'Tremadoc' representatives of *Cruziana* (*C. semiplicata, C. furcifera, C. goldfussi, C. tortworthi, C. breadstoni*) or *Rusophycus* described or illustrated by Crimes (1970b; 1975) and Baldwin (1977) appears to be represented in the New South Wales 'Tremadoc' ichnofaunas.

SYSTEMATIC DESCRIPTIONS

Type specimens are housed in the palaeontological collection of the Department of Geology and Geophysics, University of Sydney, and have the prefix SUP. For grid references to fossil localities cited in the foregoing descriptions see 1:100,000 Orthophotomap Series — Topar 7334 (first edit., 1979), Nuchea 7335 (first edit., 1980) and Bunda 7434 (first edit., 1980).

Genus *Cruziana* d'Orbigny 1842

Type species: C. rugosa d'Orbigny 1842

Cruziana warrisi sp. nov.

Fig. 2**B**

Material: Holotype (SUP 16897) is from the Bynguano Quartzite just north-west of Bynguano Bore, Gnalta (grid ref. XL 2258). Another specimen (SUP 43900) from the Scopes Range Beds, 9 km south-east of Churinga (grid ref. XK 7284) may be tentatively assigned to the species.

Etymology: After B. J. Warris, the original collector of the holotype.

Description: Two large, moderately deep, bilobate trails intersecting one another almost at right angles, preserved in convex hyporelief; at least 140 mm long, up to 84 mm wide and 20 mm deep. Each lobe exhibits numerous fine, close-spaced ridges running inwards and slightly backwards to centre line. V-angle (angle subtended by adjacent ridges of each lobe) varies from 120° to 180°. Ridges may be continuous and parallel across the lobe, or discontinuous where they are intersected by more continuous ridges; sometimes a prominent criss-cross pattern of ridges exhibited with intersections mainly at angles of 25-40°; continuous ridges (latest-formed scratchings) are usually less markedly backwardly inclined, and may be paired; equally strongly impressed, and spaced from 1.5-1.8 mm apart; these paired ridges seem to define ?anterior side of sets each comprising five or more ridges. Much smaller trails and burrows of indeterminate type cut across holotype; one straight, faintly bilobated, narrow trail, 2 mm wide, extends along the flank of one of the *Cruziana* trackways, and has appearance of lateral ridge. However it is not continuous along length of trackway and is not duplicated on the other flank of trackway; nor is it seen in other trackway. From manner in which this small trail cuts some ridges and not others, it appears to postdate formation of *C. warrisi*.

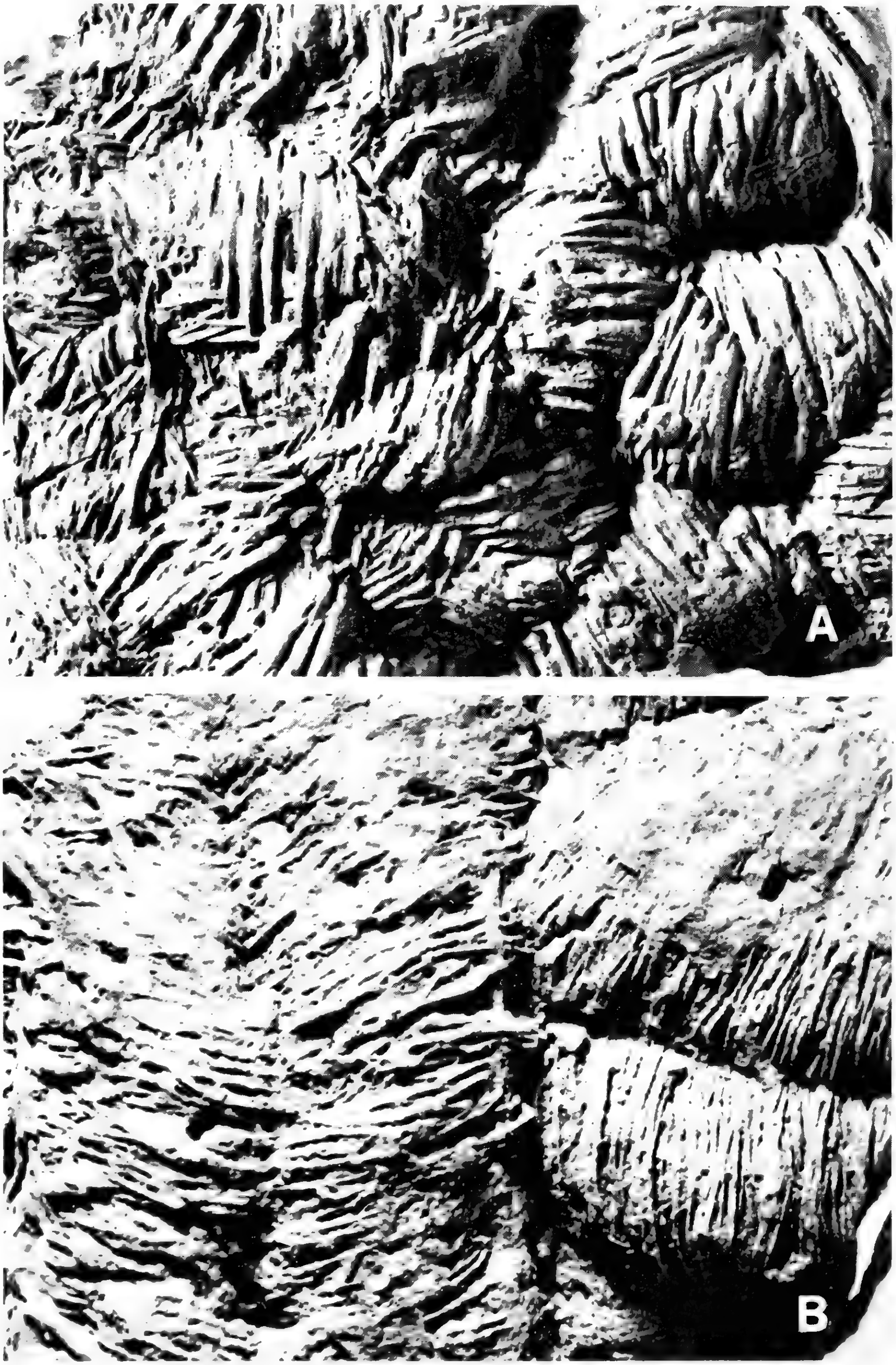


Fig. 2. **A**, undersurface of bedding plane (convex hyporelief) with activity of ***Rusophycus latus*** sp. nov.; from middle part of Scopes Range Beds west of Bilpa; SUP 42937, x0.75. **B**, *Cruziana warrisi* sp. nov., holotype, SUP 16897, x1.

Remarks: C. warrisi has a high V-angle, a narrow spacing between ridges and forms a relatively deep burrow, features consistent with the producer moving at relatively slow speed through the surface sediment. Crimes (1975, p.36) has noted that the forms of *Cruziana semiplicata* with higher V-angles were more deeply impressed, and usually do not show lateral ridges because in the burrowing technique its head was tipped downward. Consequently the 'general spines' did not make contact with the sediment. To what extent the very high V-angle is due to the ploughing activity of an head-down rather than tail-down arthropod (see Seilacher, 1970, fig. 4) is unknown. However no other large variety of *Cruziana* has such a high V-angle. The widely distributed Lower-Middle Ordovician species, *C. furcifera,* has a much lower V-angle, and coarser and more markedly anastomosing ridges (Crimes, 1968).

Cruziana sp. A
Figs 3**A** and 4**B**

Material: One well-preserved specimen (SUP 42927) is from middle part of Scopes Range Beds, south side of track, 6 km west of Bilpa (grid ref. XK 2774). A second incomplete and rather poorly-preserved specimen (SUP 42929) comes from the Scopes Range Beds, 9 km south-east of Churinga (grid ref. XK 7284).

Description: These shallow, bilobated trails are preserved as convex hyporeliefs. In well-preserved specimen, trail is slightly asymmetrical (Fig. 3**A**), 70 mm wide, 75 mm long and with a depth of up to 3 mm; V-angle from 80-100°; ornament of fine, paired, gently curved, obliquely (backwardly and inwardly) directed ridges; pairs spaced 2.5-3.5 mm apart; much closer spacing between anterior and posterior ridges of each pair, usually 1.0 mm apart; posterior ridge of pair usually more prominent. Only one lobe of second specimen is preserved (Fig. 4**B**); it is 160 mm long, and has a depth not exceeding 6 mm.

Remarks: The asymmetrical form of this shallowly-impressed variety of *Cruziana* may have been produced by an animal being swung slightly sideways by an obliquely-aligned current as it moved forward.

Cruziana sp B.
Fig. 4**A**

Material: One specimen (SUP 42930b) from the middle part of the Bynguano Quartzite, 1.5 km west of Bynguano Bore, Gnalta (grid ref. XL 2158).

Description: This small variety of *Cruziana* is preserved in convex hyporelief cutting across the anterior part of a large *Rusophycus,* and apparently post-dating its formation. The trail is strongly bilobated, 42 mm long, up to 16 mm wide and 4.5 mm deep. It exhibits very fine anastomosing ridges running obliquely across lobes and spaced 0.5-1.0 mm apart; V-angle is approximately 60-80°.

Remarks: Cruziana sp. B appears to be most closely comparable with the 'small variety of *Cruziana*' figured by Selley (1970, pl. 1b) from Lower Ordovician sandstones in Jordan. However lateral ridges seem to be present on the Jordanian specimens, not seen in the N.S.W. material.

Ichnogenus *Diplichnites* Dawson 1873

Type species: D. aenigma Dawson 1873

Diplichnites binatus sp. nov.
Fig. 3**B**

Material: Holotype (SUP 42926) is from the middle part of the Bynguano Quartzite in the Bynguano Range, near Mootwingee (grid ref. XL 2647).

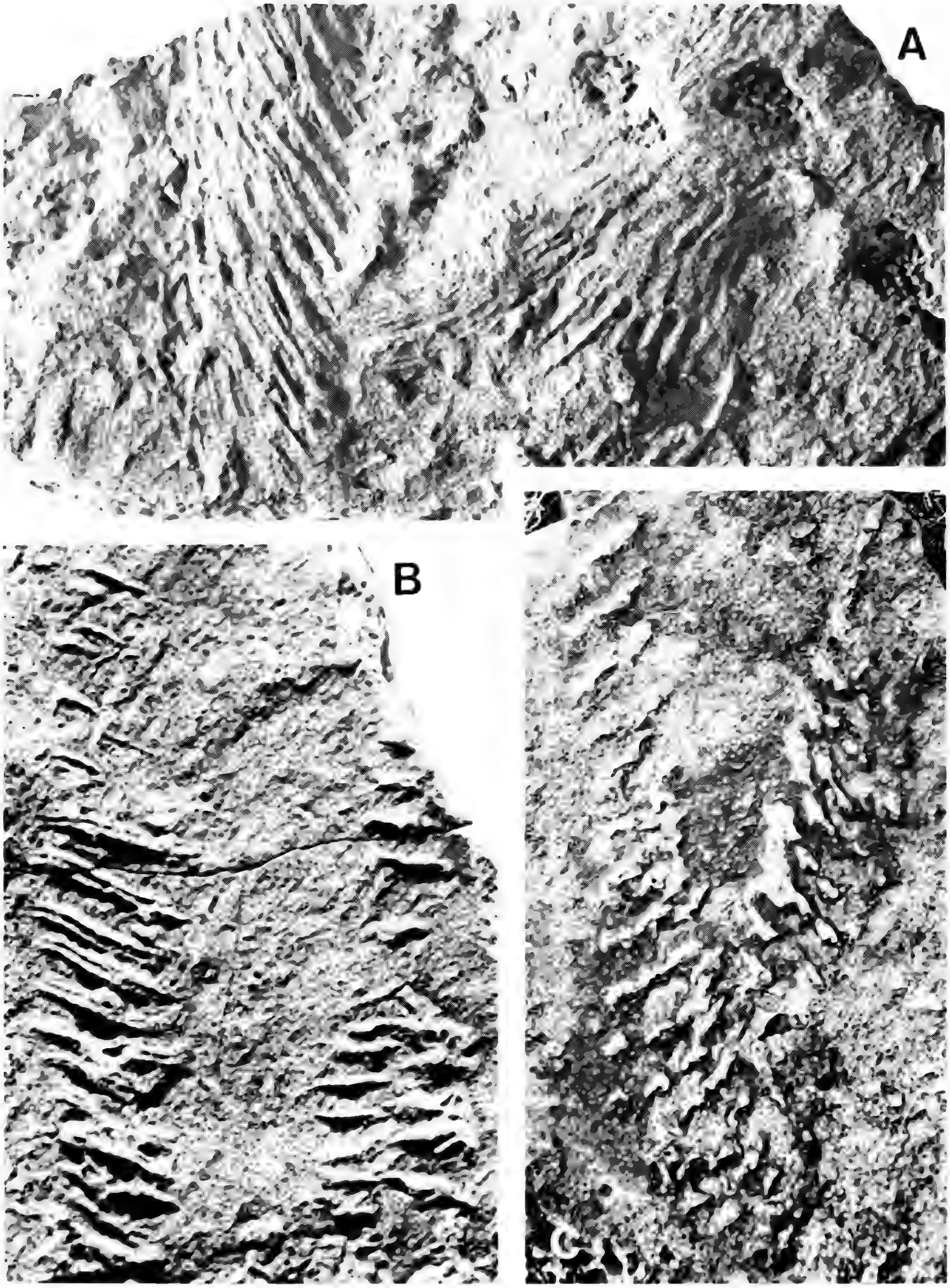


Fig. 3. **A**, *Cruziana* sp. A, SUP 42927, x1. **B**, *Diplichnites binatus* sp. nov., holotype SUP 42926, x0.75. **C**, *Diplichnites* sp. A, x0.25.

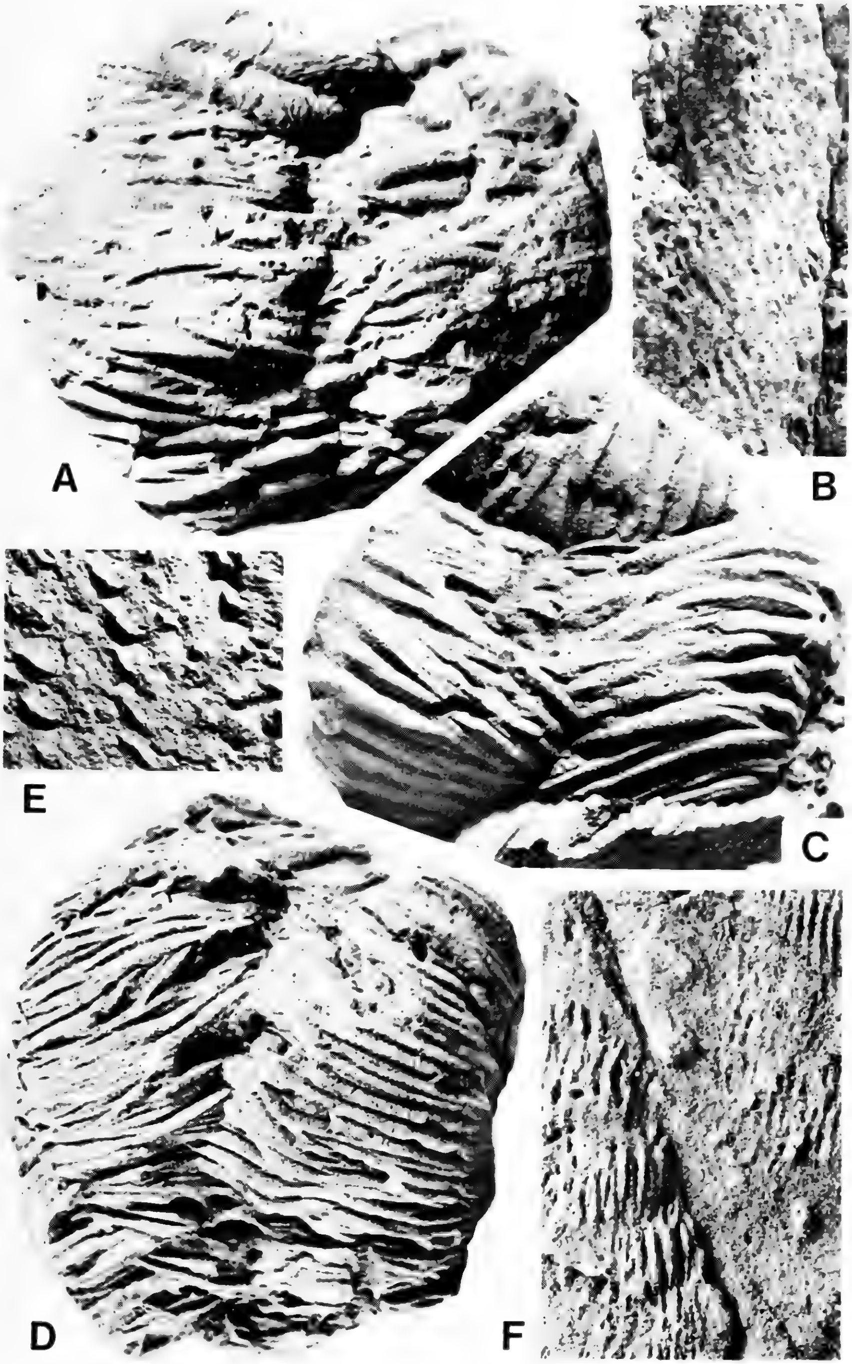


Fig. 4. **A**, specimen showing both *Cruziana* sp. B (top, SUP 42930b) and *Rusophycus latus* sp. nov. (SUP 42930a), x1. **B**, *Cruziana* sp. A, SUP 42929, x0.75. **C**, *Rusophycus latus* sp. nov., paratype SUP 42933, x1. **D**, *Rusophycus latus* sp. nov., holotype SUP 42932, x1. **E**, *Diplichnites* sp. B, SUP 42931, x0.75. **F**, *Monomorphichnus* sp., SUP 42928, x1.

Etymology: With reference to the bifid imprints probably representing two-clawed limbs.

Description: Trackway preserved in convex hyporelief; overall width 72 mm and 145 mm long; consists of two well-separated parallel rows of slightly diagonally-orientated imprints, some 23 mm apart. Regular, long, paired, equally prominent, straight to slightly sigmoidal ridges (or imprints) may extend completely across row, up to 27 mm long, or may be shorter, less regularly spaced and less uniformly raised, single linear markings; ridges of individual pairs spaced 1.5-2.5 mm apart; pairs of ridges from 2 to 5 mm apart. No apparent ordering of imprints into sets. V-angle is from 150° to 170°; presumably direction of gape is direction of movement (Crimes, 1970a).

Remarks: Although two-clawed limbs seem to have been responsible for producing the paired ridges, they lack continuity along the entire length of the trackway. Their change to single ridges may be explained by rotation of the limbs (Osgood and Drennan, 1975). The relatively great length of the paired claw markings and the relatively short distance between successive imprints (implying a short stride) may, following Crimes (1970a), suggest that the animal was moving relatively slowly across the sea floor. Possibly it was walking but with a fair component of drag of its two-clawed limbs. The high V-angle supports this view.

This trackway is distinguished from other described Ordovician representatives of *Diplichnites* by its large size and long, parallel, equally prominent bifid imprints. Only *Diplichnites* sp. A is larger (see below).

Diplichnites sp. A
Fig. 3**C**

Material: One specimen preserved in convex hyporelief from the upper part of the Scopes Range Beds near Bilpa (grid ref. XK 3175).

Description: This very large trackway narrows in width along its length; it has a maximum width of 185 mm and length of 400 mm. Two rows of diagonally orientated imprints well separated at one end, but gradually merge towards other end of trackway; alignment of imprints gives V-angle of 80-100°; number of imprints across width of row variable — may be just one elongate ridge up to 56 mm long, or up to three discrete irregular scratch marks. Individual ridges are from 16-24 mm apart along the row; no evidence of paired ridges.

Remarks: This large trackway may be interpreted as recording an arthropod moving from a walking or striding to a swimming mode of locomotion (Crimes, 1970a). The comparatively large spacing between individual ridges of each row, and the moderately low V-angle (as compared for instance with *D. binatus*) suggests that the animal was moving at a reasonable speed as it lifted off to assume a swimming mode. It does not however show a marked decrease in length of claw markings immediately prior to lift off as seems to have been suggested by Crimes (1970a, fig. 6).

From their respective dimensions and the nature of their imprints, the trackways of *D. binatus* and *D.* sp. A seem unlikely to have been produced by the same type of arthropod. It they were produced by trilobites they must have been remarkably large forms, significantly larger than any so far collected from Ordovician successions in western New South Wales. The *D.* sp. A animal must have been at least 185 mm wide and possibly of the order of one and a half times longer.

Diplichnites sp. B.
Fig. 4**E**

Material: One specimen (SUP 42931) from middle part of Scopes Range Beds, south side of track, 6 km west of Bilpa (grid ref. XK 2774).

Description: This specimen, preserved in convex hyporelief, shows short, oblique, crescent-shaped markings in three rows; a complementary fourth row is not preserved. Trackway attains maximum width of 48 mm and one row of imprints is traceable over bedding surface for a distance of 110 mm.
Remarks: In terms of the pattern shown by Seilacher (1955, Abb. 1f) for an arthropod trace from the Lower Silurian Nereiten-Schichten of Barrancos, Portugal, this incomplete trackway may be interpreted as being produced by an animal moving forward but, because of a cross current, with its body aligned slightly obliquely to the direction of movement. Consequently the sets of imprints on one side of the trackway, at least, markedly overlap one another.

Ichnogenus *Monomorphichnus* Crimes 1970a

Type species: M. bilinearis Crimes 1970a

Monomorphichnus sp.

Fig. 4**F**

Material: One specimen (SUP 42928) from the middle part of the Scopes Range Beds, south side of track, 6 km west of Bilpa (grid ref. XK 2774).
Description: Specimen preserved in convex hyporelief and shows separate sets of ridge-like impressions to either side of deep, obliquely-aligned groove; each set with seven or more parallel ridges but they are not continuous because ripple-like annulations intersect them almost at right angles; these latter are spaced at 10-13 mm apart. One of the sets exhibits clear differentiation into paired ridges, each pair with one more prominently impressed than the other; spacing between more prominent or paired ridges usually 2.5 mm apart. In the other set, the ridges are single and spaced from 1.5 to 2.0 mm apart.
Remarks: From the morphological similarities of *Cruziana* sp. A and *Monomorphichnus* sp., and their occurrences in the same horizon and locality in Scopes Range, it may be suggested that the two forms were produced by the same variety of animal. If *M.* sp. represents a structure formed by an arthropod being swept sideways in the current, as Crimes (1970a) has argued, then the number of pairs of ridges produced in a set may approximate the number of limbs of the animal. This would seem to suggest that the New South Wales *Monomorphichnus* animal had at least seven walking legs.

Morphological differences in spacing of ridges and the presence or absence of paired ridges may be explained by the orientation of the animal's appendages changing slightly as it was swept across the surface from one set to the other.

Ichnogenus *Rusophycus* Hall 1852

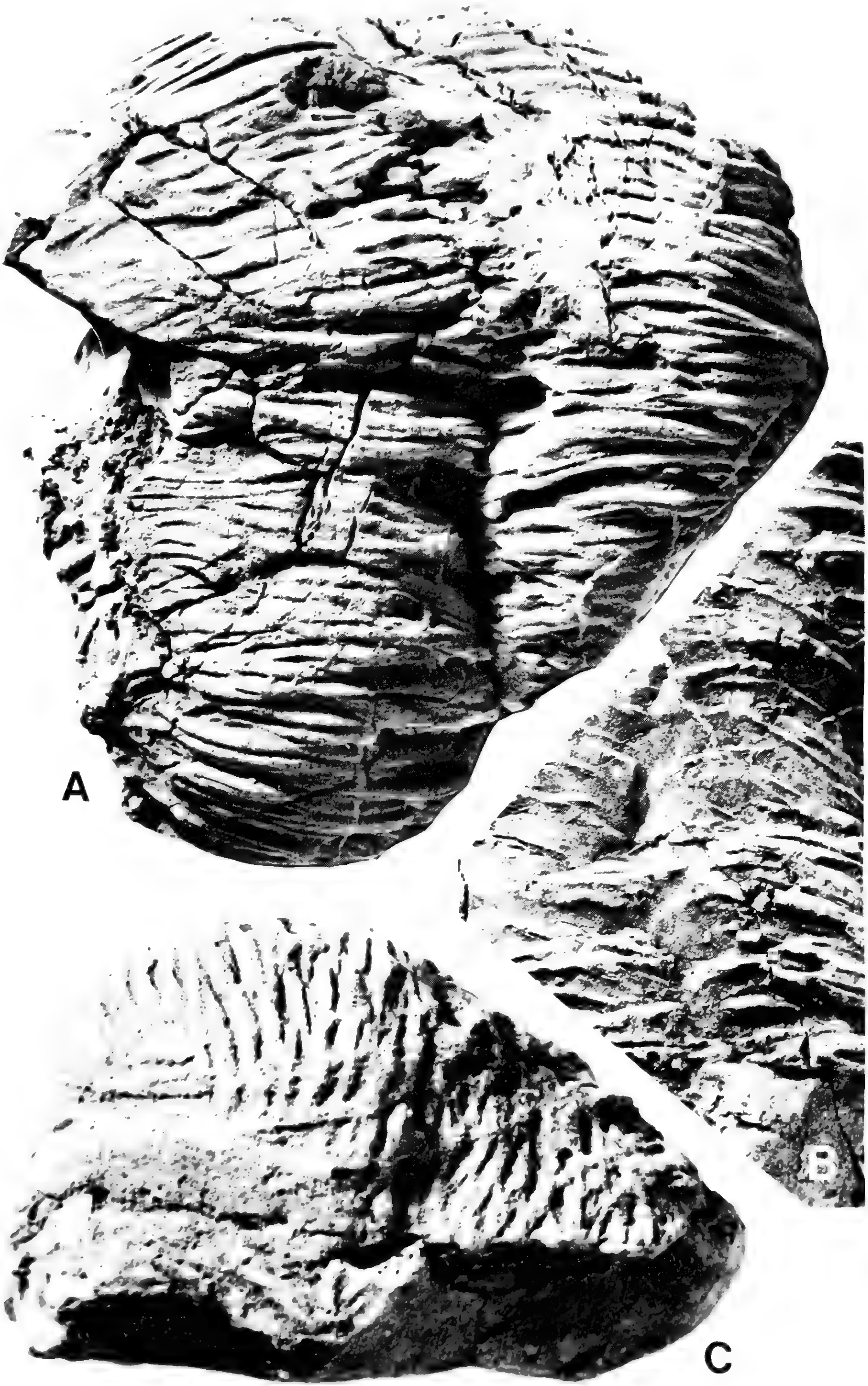
Type species: Fucoides biloba Vanuxem 1842.

Rusophycus latus sp. nov.

Figs 2**A**, 4**A**, 4**C-D**, 5**A**, & **C**, 6-7

?1970 *Cruziana omanica* Seilacher p.466 fig. 9b (*non* fig. 9a)
1972 'Trails of trilobites of Cambrian age' Hill, p.16, fig. 10a.

Material: Holotype (SUP 42932) from middle part of Scopes Range Beds, 5 km west of Bilpa (grid ref. XK 2874) and six paratypes (SUP 42930a; 42935-36; 42941; 42948; 43905) from middle part of Bynguano Quartzite 1.5 km west of Bynguano Bore, Gnalta (grid ref. XL 2158) and two paratypes (SUP 42933; 43903) from lower part of Bynguano Quartzite immediately west of Bynguano Bore (grid ref. XL 2257). SUP 42934 (collected by D. F. Branagan) and 43903 probably also come from this latter horizon and locality. Other specimens from same locality and horizon as holotype


A
B
C

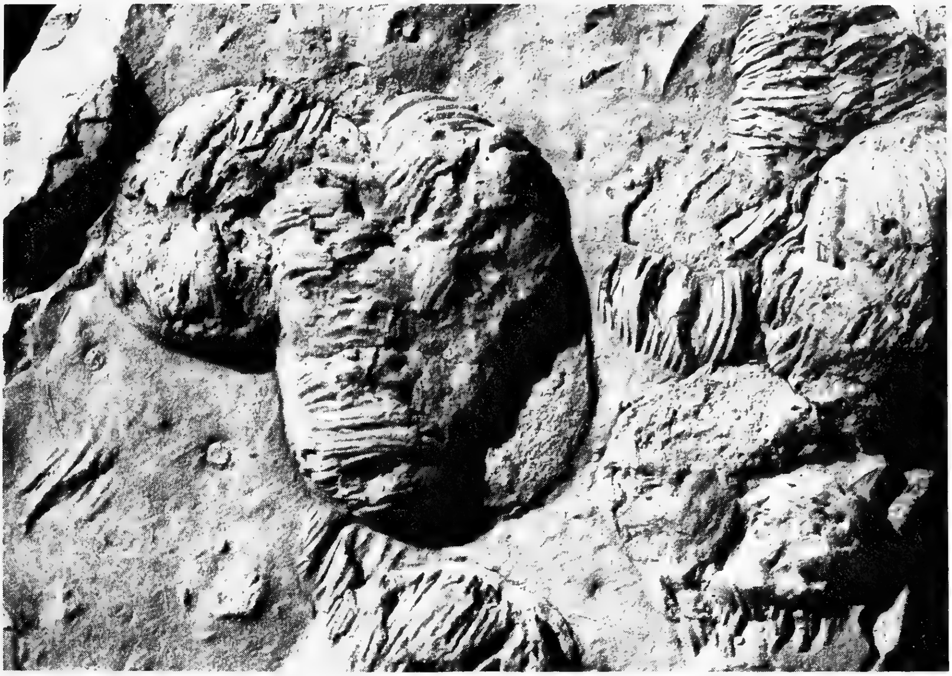


Fig. 6. Rusophycus latus sp. nov., SUP 42934, x0.5.

include SUP 42939-40, 42942, 42944, 42946, 43902, 43907-08, 43910. Three of these, SUP 42939, 42944 and 42946 also designated paratypes. At a slightly higher horizon in the middle part of the Scopes Range Beds, 6 km west of Bilpa (grid ref. XK 2774) specimens SUP 42943, 43901, 43904 and 43909 occur. SUP 42947 comes from middle part of the Bynguano Quartzite in the Bynguano Range (grid ref. XL 2647), and SUP 42945 and 43906 are from the Bynguano Quartzite cropping out on the old Broken Hill-White Cliffs coach road, Bynguano Range (grid ref. XL 2844).

Etymology: Alluding to its width characteristically being slightly greater than its length.

Description: Large bilobated traces preserved in convex hyporeliefs; varying from 36 to 120 mm in length, and from 43 to 115 mm in width; most commonly from 66 to 88 mm in width and from 55 to 84 mm in length (Fig. 7); following Crimes (1970b, p. 114), the shape factor (length divided by breadth) is 0.85. Depth varies from 8 to 38 mm, usually 9 to 27 mm (Fig. 7). Outline varies from transversely elliptical through subquadrate to heart shaped; widest and deepest part of trace usually in anterior half; in profile deeper burrows are markedly asymmetrical, and may show traces of lateral ridges (Fig. 5**C**). Convex lobes usually clearly differentiated by longitudinal median furrow; each lobe exhibits large number of predominantly transversely-directed coarse-textured ridges; but axially these ridges may deflect slightly forwards or backwards (Figs 4**C-D**). Ridges may be continuous or discontinuous across lobe; usually spaced 2.5 to 4 mm apart; frequently appear to be bifid or even trifid. Apart from a reduction in length consistent with narrowing of the lobes towards anterior and posterior

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Fig. 5. **A**, *Rusophycus latus* sp. nov., paratype SUP 42935, x1. **B**, coarse-textured, wide-spaced scratchings representing a type of moving trail probably made by same animal as produced *R. latus* markings; SUP 42938, x0.75. **C**, *Rusophycus latus* sp. nov., in side view; paratype SUP 42936, x1.

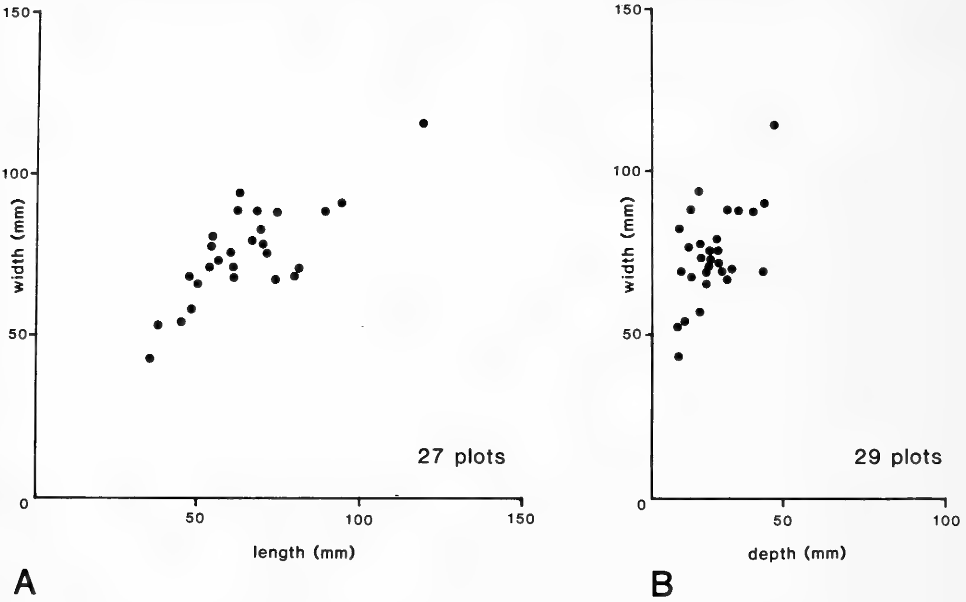

Fig. 7. Scatter diagrams of width against length (**A**) and width against depth (**B**) for specimens of *Rusophycus latus.*

margins, ridges show no apparent differentiation in spacing or form; usually about 20 to 35 ridges are represented; in the largest specimens up to 45 (Fig. 5**A**); occasionally ridges appear to be bundled into sets of three or four.

Remarks: This very common trace fossil in western New South Wales Lower Ordovician successions sometimes extends to entirely covering bedding surfaces with its activity (Fig. 2**A**). It exhibits a wide range of morphology, but no evidence of a gradation into a *Cruziana*-type furrow of the *C. omanica* type. The only markedly different type of trace which exhibits the same kind of coarse-textured scratchings is illustrated in Fig. 5**B**. This specimen comes from the same locality and horizon as the holotype. From the wide spacing of scatchings it probably represents some sort of moving trail, but not a typical *Cruziana.*

Crimes (1970b) has claimed that in ascending from the Upper Cambrian to the Arenig, British occurrences of *Rusophycus* show changes in form and gradual increases in mean width and mean 'shape factor' (length divided by breadth). They are therefore viewed as having biostratigraphic utility for distinguishing between Upper Cambrian, Tremadoc and Arenig strata in otherwise unfossiliferous successions. Crimes represented the 'shape factor' as rising from 1.5 in the Upper Cambrian to 2.0 in the Lower Ordovician. However, even Crimes's Upper Cambrian value is much higher than the 'shape factor' of 0.85 for the 'Tremadoc — lower Arenig' occurrences of *Rusophycus* from western New South Wales. It leads to the conclusion that Crimes's scheme is of localized rather than more wide-ranging biostratigraphical significance for correlating otherwise unfossiliferous Lower Palaeozoic sequences.

ACKNOWLEDGEMENTS

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Quaternary Kangaroos (Macropodidae: Marsupialia) from Nombe Rock Shelter, Papua New Guinea, with Comments on the Nature of Megafaunal Extinction in the New Guinea Highlands

T. FLANNERY, M-J. MOUNTAIN and K. APLIN

(Communicated by M. ARCHER)

FLANNERY, T., MOUNTAIN, M-J., & APLIN, K. Quaternary kangaroos (Macropodidae: Marsupialia) from Nombe rock shelter, Papua New Guinea, with comments on the nature of megafaunal extinction in the New Guinea highlands. *Proc. Linn. Soc. N.S.W.* 107 (2), (1982) 1983: 77-99.

Seven species of macropodids occur in the late Pleistocene-Holocene sediments of Nombe rock shelter, Simbu Province, Papua New Guinea. The four small species, *Dorcopsulus vanheurni, Thylogale brunii, Dendrolagus goodfellowi* and *Dendrolagus dorianus* are still extant. The three larger species, *Dendrolagus noibano* n. sp., *Protemnodon tumbuna* n. sp. and *Protemnodon nombe* n. sp. are extinct forms known only from Nombe. The two *Protemnodon* species are closest in morphology to Pliocene Australian and New Guinea representatives of the genus and differ markedly from Pleistocene Australian species. The faunal and associated cultural sequence at Nombe provides evidence of long temporal overlap between man and megafauna in montane New Guinea, but at present does not elucidate the causes of large mammal extinction.

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INTRODUCTION

The mountainous island of New Guinea contains a diverse and abundant mammalian fauna. However, the modern fauna is depauperate, especially in large animals, when compared with that present during the Pliocene and Pleistocene. Surprisingly, the Pleistocene fossil record of New Guinea has until now remained almost completely unknown. A single upper molar fragment of a large macropodid from Kafiavana (Plane, 1972) and unallocated diprotodontid, phalangerid and rodent remains from Pureni Swamp (Williams *et al.,* 1972; Hope and Hope, 1976) are the only Pleistocene mammal remains (apart from those from Nombe) thus far recorded. The Pliocene fauna of New Guinea is slightly better known, the rich Awe local fauna having been first noted by Anderson (1937) and described by Plane (1967a, b). The Awe local fauna includes three species of diprotodontids, (*Nototherium watutense, Kolopsis rotundus* and *Kolopsoides cultridens*), three macropodids, (*Protemnodon otibandus, Protemnodon buloloensis* and a large species of *Dorcopsis*), a dasyurid (*Myoictis* sp., Archer, 1982), a rodent, cassowary and crocodile. The location of these sites is shown in Fig. 1.

Nombe rock shelter is located in Simbu Province, at 6° 08′S, 145° 10′E, Map reference: Goroka Sheet 7985 (Ed. 1) BP957208, topographic survey, Papua New Guinea: series T601, 1:100,000. The rock shelter is developed in the mid-Eocene to lower Oligocene Chimbu Limestone, and is situated at an altitude of about 1720 metres on the northeast side of the Mt Elimbari ridge. Four main stratigraphic units

Fig. 1. Map showing fossil localities mentioned in the text.

have been discerned in the sediments of the rock shelter (Gillieson and Mountain, 1983, Mountain in press). Most of the specimens described herein were found in the lowest archaeological stratum of the deposits. This stratum (D) consists of a thick, red-brown clay, with little sign of internal stratigraphy. Radiocarbon dating of flowstones occurring in this clay places its accumulation at between 24,000 and 14,000 years B.P., at which time a stream ran through the cave system to feed a spring at the rock shelter. Human artefacts are present throughout this deposit; cultural activity can be documented at the site from 24,000 years B.P. to the present time, although it was not necessarily continuous, especially during the late Pleistocene.

Preliminary analysis of the faunal collection from Nombe by Mountain revealed the presence of a number of extinct marsupials, including a thylacine (*Thylacinus* sp. cf. *T. cynocephalus*), a taxonomically unallocated pig-sized diprotodontid, and several previously unknown species of macropodine kangaroo. These extinct kangaroo species and the four extant kangaroo species found at Nombe are the basis of the present study.

The specimens from Nombe rock shelter described here are to be lodged in the National Museum and Art Gallery of Papua New Guinea and bear the prefix PNG. The Museum catalogue number for the Nombe collection is 82/40; this is followed by an individual number for each specimen described. NCA was the National Antiquities File of Papua New Guinea code for the site at the time of excavation and marking. It has since been altered to PBG but due to lack of space and labour this has not been altered on the specimens. The site prefix is followed by square and level data which define the horizontal and vertical position of the specimen in the site. The name New Guinea is used in a geographic sense and refers to the whole island; Papua New Guinea is the political entity which encompasses the eastern part of the island. Dental terminology and homology follows Archer (1976, 1978). Species and subspecies level taxonomy of extant forms follows Laurie and Hill (1954).

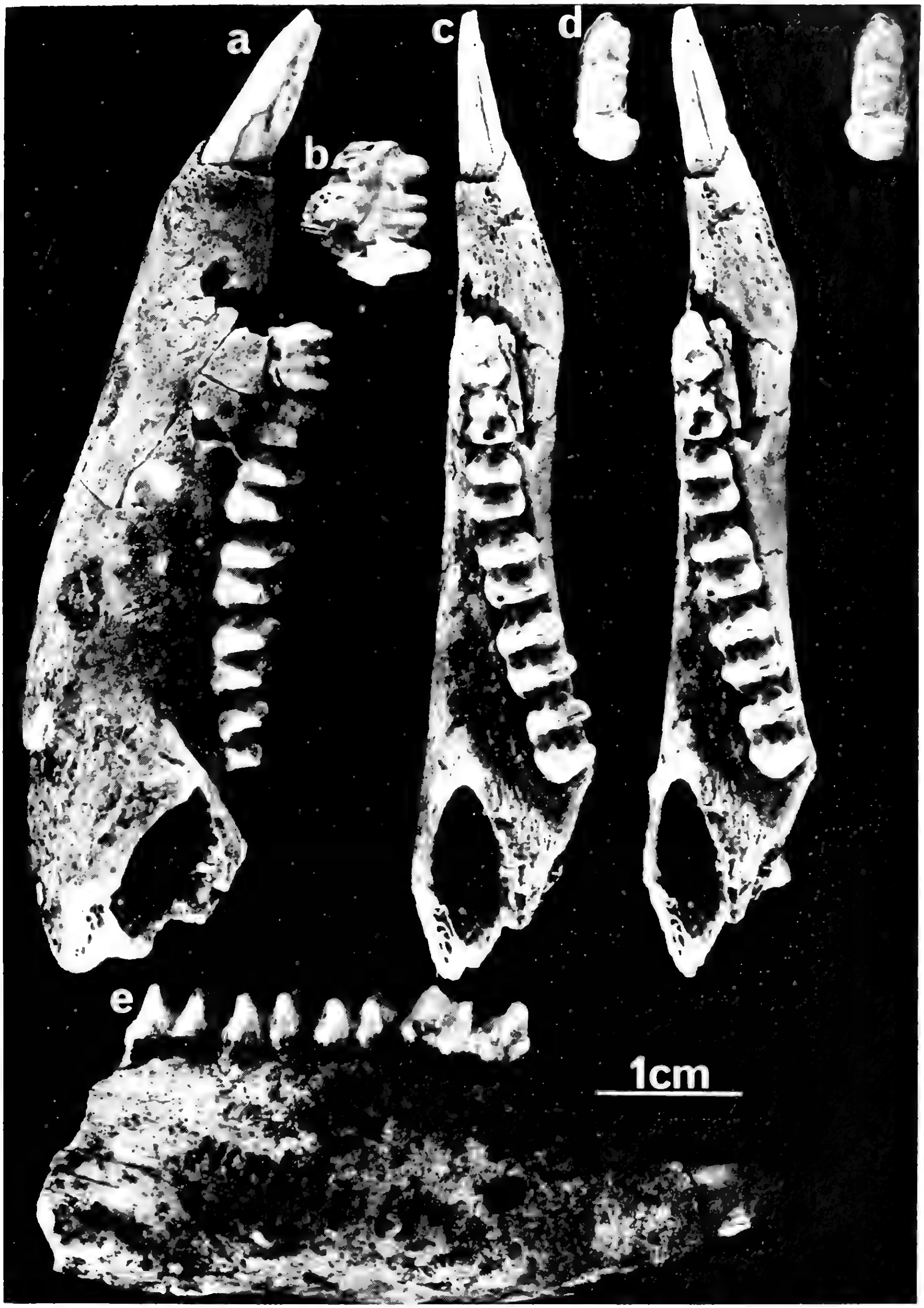

Fig. 2. **a**, buccal view and **b**, stereopair of occlusal view of holotype of *Dendrolagus noibano* (PNG/82/40/1), left dentary containing P/2, M/1-5. **c**, buccal view and **d**, stereopair of occlusal view of P/3 of holotype of *D. noibano* (removed from crypt). **e**, buccal view of left dentary of *D. noibano* (PNG/82/40/3) showing great depth of dentary attained with age.

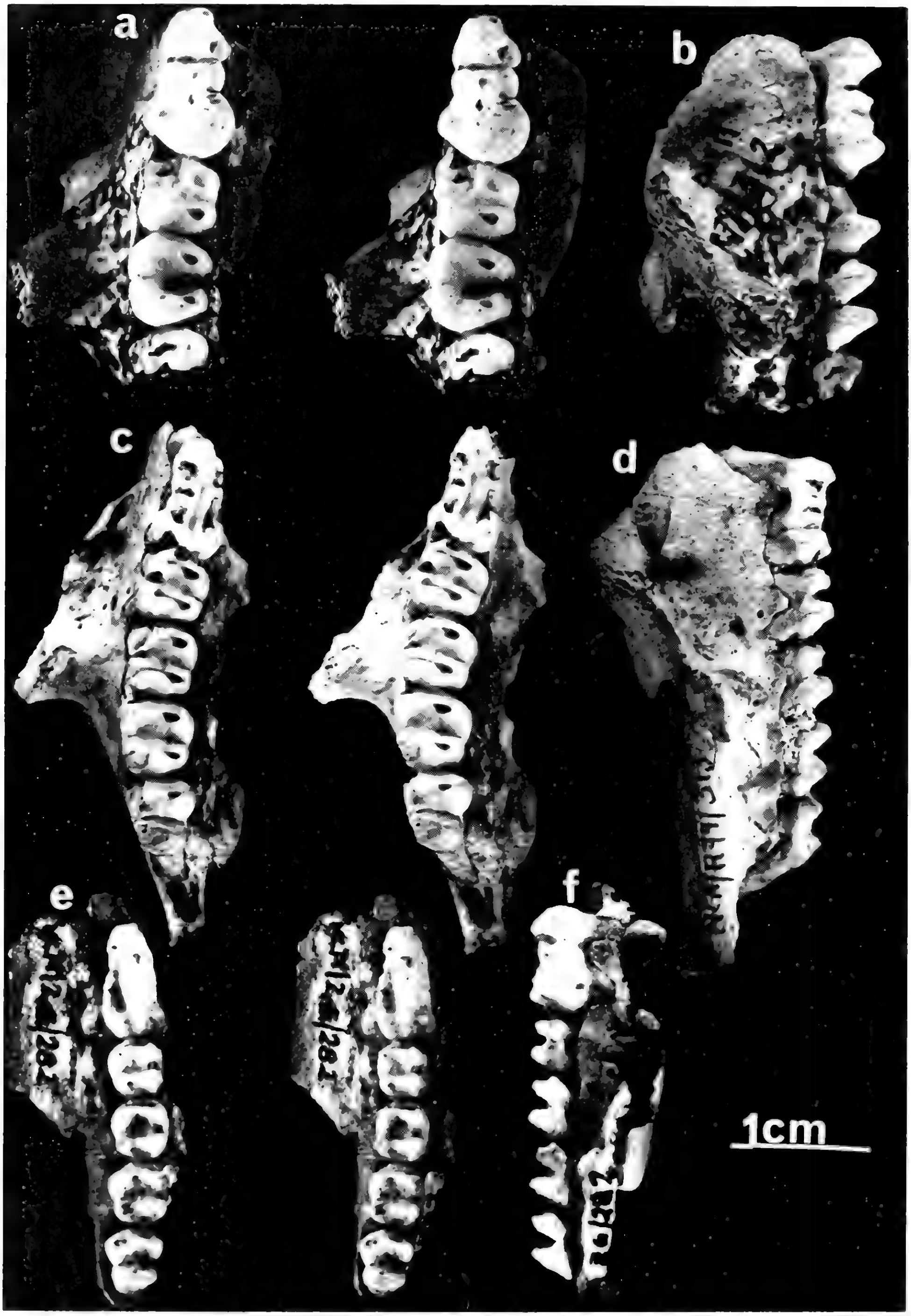

Fig. 3. **a**, buccal view and **b**, stereopair of occlusal view of maxilla containing P3/, M2-3/ of ***Dendrolagus noibano*** (PNG/82/40/4). **c**, buccal view and **d**, stereopair of occlusal view of maxilla fragment of ***Dendrolagus dorianus*** containing P3/, M2-5/ from Nombe rock shelter. **e**, buccal view and **f**, stereopair of occlusal view of maxilla fragment of ***Dendrolagus goodfellowi*** containing P3/, M2-5/ from Nombe rock shelter.

SYSTEMATICS

Superfamily MACROPODOIDEA

Family MACROPODIDAE

Subfamily MACROPODINAE

Dorcopsulus Matschie, 1916

Dorcopsulus vanheurni Thomas, 1922

The remains of *Dorcopsulus vanheurni* are abundant throughout the archaeological sediments of the Nombe rock shelter including the basal red-brown clay. They do not differ in size or morphology from those of the living species. *Dorcopsulus vanheurni* at present inhabits montane forests of the central ranges of New Guinea (Ziegler, 1977; George, 1973).

Thylogale Gray, 1837

Thylogale brunii Schreber, 1777

The remains of *Thylogale brunii* are common throughout the archaeological deposits including the red-brown clay. The fossil series is closely similar in size to specimens of the highland race *T. b. keysseri.,* and is smaller than the lowland forms *T. b. browni* and *T. b. brunii. Thylogale brunii* is widespread in Papua New Guinea, but has not been recorded from montane areas of Irian Jaya except as a subfossil (Hope, 1981). It is found in a variety of habitats, ranging from near sea level to the mountain tops. It makes extensive use of montane grassland, and may be the most abundant large mammal in these areas (Hope and Hope, 1976; George, 1973). The relationships of this endemic New Guinean species of *Thylogale* to the Australian representatives of this genus is at present unknown.

Dendrolagus Muller, 1839

Dendrolagus goodfellowi Thomas, 1908

Dendrolagus goodfellowi is the smallest of the three species of tree kangaroo found at Nombe. The remains of *D. goodfellowi* are found in all strata, including the red-brown clay, and are indistinguishable in size and morphology from the modern species. Today *D. goodfellowi* inhabits montane forests in eastern New Guinea. *Dendrolagus goodfellowi shawmayeri* (the only subspecies for which any detailed distributional data are available), is reported to occur between 1,200 and 2,750 m on the northern slopes of the central highlands (George, 1978). Groves (1982) has suggested that *D. goodfellowi* is a subspecies of *D. matschiei.* However, until biochemical and morphometric studies are completed these species will be regarded here as distinct, as on the basis of size and morphology at least the typical populations differ considerably.

Dendrolagus dorianus Ramsay, 1883

Dendrolagus dorianus is the largest of the living tree-kangaroos. Males can reach a weight of 18 kg (Ganslosser, 1980). Its remains are found in all layers at Nombe, including the red-brown clay. *Dendrolagus dorianus* is presently found throughout the central cordillera of eastern New Guinea (Groves, 1982). The western highlands form, *D. d. notatus,* is reported to occur only at altitudes above 2,400 m, but further east the typical subspecies is found at lower altitudes (George, 1978). *Dendrolagus dorianus* is thought to be more terrestrial in habit than other species of tree kangaroo (Ganslosser, 1980).

Dendrolagus noibano n. sp.

Figs 2-3, Table 1

Holotype: PNG/82/40/1 (NCA/M71/9), left dentary fragment containing I/1, P/2, P/3 (removed from crypt), M/1-5, but lacking condyle and coronoid process.

TABLE 1

Dental measurements of *Dendrolagus noibano* from Nombe Rock Shelter. L = length, AW = anterior width, PW = posterior width, in mm.

		L	AW	PW
PNG/82/40/4	P3/	11.9	5.6	
	M2/			6.4
	M3/	7.5	6.9	6.6
PNG/82/40/7	P3/	11.8	4.8	7.0
PNG/82/40/5	M4/	7.9	7.5	6.2
PNG/82/40/6	M3/	7.3	6.8	6.2
PNG/82/40/20	P/2	6.2	3.3	3.2
	M/2	7.0	4.8	5.0
	M/3	7.8	5.3	5.5
PNG/82/40/1	P/2	6.5	3.3	4.0
	P/3	12.5	4.4	5.3
	M/1	5.7	3.2	4.0
	M/2	7.4	4.8	5.1
	M/3	8.0	5.5	5.7
	M/4	8.4	6.1	6.2
	M/5	8.5	5.8	5.5
PNG/82/40/3	P/3	10.7	4.0	
	M/2	6.6	4.8	5.0
	M/3	7.6	5.4	5.5
	M/4	8.7	6.1	6.3

Referred specimens: PNG/82/40/2 (NCA/M71/9), left dentary with I/1, P/2, M/2-4 and possibly P/3 (unexcavated) in crypt. PNG/82/40/3 (NCA/M71/9), right dentary with P/3, M/2-4. PNG/82/40/4 (NCA/R79/312), right maxilla fragment containing P3/, M2-4/. PNG/82/40/5 (NCA/792.12/210), left M4/. PNG/82/40/6 (NCA/R79/320), right M3/. PNG/82/40/7 (NCA/792.12/203), right P3/.

Type locality and age: All specimens of *Dendrolagus noibano* are from Nombe rock shelter, Papua New Guinea. Six of the seven specimens were found in the red-brown clay (stratum D) and thus are dated to between 24,000 and 14,000 years B.P. PNG/82/40/7 was found in the mixed levels (stratum C) lying immediately over the top of stratum D and thus probably dates to between 14,000-10,000 BP. There is at present no evidence for the survival of *Dendrolagus noibano* into the Recent period.

Etymology: This species is named after Noibano, the traditional Siane owner of the Nombe rock shelter during the period of excavation by Mountain.

Diagnosis: Dendrolagus noibano can be distinguished from all other species of tree-kangaroo by possessing the following characteristics: it is larger than all other forms, and a deep transverse fissure divides the anterior portion of P3/ from the rest of the tooth. It differs from *Dendrolagus lumholtzi, D. bennettianus, D. goodfellowi, D. ursinus* and *D. inustus* in having a large, distinct posterobuccal cuspid developed on P/3. A similar, though less well-developed cuspid is often present in specimens of *D. dorianus* and *D. matschiei.*

Description: Maxilla. The maxilla is represented by a poorly-preserved fragment, with the zygomatic process broken away. The infraorbital canal opens just behind the anterior root of P3/.

P3/. The P3/ is represented by two specimens of which PNG/82/40/7 is the least worn. In both specimens the anterior cusp is strongly ridged, both buccally and lingually. The distinct anterior cusp and anterior-most tubercle of the lingual cingulum are separated from the rest of the tooth by a deep fissure. Between the anterior cusp and the bulbous posterior cusp are two smaller but prominent cuspules with associated buccal ridgelets. A well-developed posterobuccal crest is present on PNG/82/40/7, but is largely broken away on PNG/82/40/4. A discrete posterolingual cusp is present. Two tubercles and a crest which runs anteriorly from the posterolingual cusp make up an irregular lingual cingulum. Only an extremely tiny posterior fossette is present between the main crest and the posterolingual cusp.

Upper molars. The single known M2/ is badly damaged and in an advanced stage of wear. However, the tooth is clearly low-crowned and possesses a very poorly-developed midlink. A slight premetacrista and more clearly-discernible posthypocrista, which runs from the hypocone to the base of the metacone, are present.

The M3/ of PNG/82/40/4 is well-preserved, though worn, with both lophs breached by wear. The tooth is larger than M2/. The anterior cingulum is narrow, running from a point 1 mm linguad of the buccal side of the protoloph and ending approximately 2 mm short of the lingual end of the protoloph. A slight preparacrista connects the paracone to the buccal end of the anterior cingulum. The postparacrista and premetacrista are moderately well-developed and run linguad to converge at a point 2 mm from the buccal end of the median valley. The midlink is very poorly developed. The posthypocrista runs from the hypocone to the base of the metacone on the rear face of the hypoloph.

An isolated upper molar in an early stage of wear, PNG/82/40/5, probably represents the M4/ of *Dendrolagus noibano.* It is low-crowned and larger than M3/. The hypoloph is narrower than the protoloph. The anterior cingulum is relatively narrow, and ends approximately 3 mm short of the lingual end of the tooth. A short vertical preparacrista joins the paracone to the buccal end of the anterior cingulum. No forelink is present. The postparacrista and premetacrista are of similar morphology though better developed than on M3/. The midlink is weakly developed, consisting of a very low postprotocrista which meets a small posterior contribution from the anterior face of the hypoloph. A well-developed posthypocrista joins a weaker, near-vertical postmetacrista on the rear face of the hypoloph.

Dentary. The dentary is relatively shallow in the subadult specimens PNG/82/40/1 and 2, but is greatly deepened in PNG/82/40/3, an older individual. The mandibular symphysis extends to below the P/3 in PNG/82/40/3. The ventral margin of the dentary is nearly straight, but is interrupted by a prominent digastric sulcus and ventral flange. The mental foramen opens just anterior to P/2 or P/3 and the diastema is short. A buccinator groove is present between P/3 and M/3 on PNG/82/40/3. The opening of the masseteric canal is small in the holotype, but this may be due to the immaturity of the animal.

I/1. This tooth is closely comparable in morphology with the I/1 of other species of tree-kangaroo, but is larger. It exhibits dorsal and ventral enamel flanges and a small area of thin ventrolingual enamelling on the crown.

P/2. The P/2 is represented by two relatively unworn, almost identical teeth. They consist of a main blade made up of three evenly spaced, distinct cuspids which are subequal in size. Strong buccal and lingual ridges which enclose broad grooves originate from these cuspids. The P/2 of *D. noibano* is more similar in morphology to the P/2 of *D. goodfellowi* than it is to that of *D. dorianus,* where the anterior cuspid is usually more distinctly separated from the posterior two. However, extreme variants of P/2 of *D. dorianus* do approach the P/2 of *D. noibano* in morphology.

P/3. The P/3 is known from two specimens, one unerupted and one well-worn. The anterior cuspid is separated from the rest of the tooth by a deep cleft. This cuspid is sharply ridged both anteriorly and posteriorly, the former ending in a distinct, rounded cuspule at the anterior-most point of the tooth. The posterior cuspid of the main crest is offset lingually from the long axis of the tooth. In the holotype a distinct, buccally-directed crest links this cuspid to a larger posterobuccal cuspid. This ridge is absent in PNG/82/04/3, and although the posterobuccal cuspid was clearly present, it is now broken away. Between the posterior and anterior cuspids are two smaller though distinct cuspules. In the holotype these cuspules are isolated from the posterior cuspid by a relatively deep cleft but in PNG/82/40/3 they are united to it to form a continuous blade. The buccal side of the P/3 of the holotype is ornamented by a series of ridgelets and bulges of enamel. These are not as evident on the referred specimen, where they may have been reduced by wear.

Lower molars. The hypolophid of the only known M/1 (the holotype), is breached by wear, and a small portion of the lingual side of the protolophid is missing. The trigonid of M/1 consists of a well-developed longitudinally oriented paracristid and a barely-developed lophid, the latter oriented with its long axis rotated at approximately 30 degrees clockwise relative to the hypolophid. The hypolophid is well-formed. The cristid obliqua is barely visible, running between the hypoconid and the posterior surface of the protoconid. The preentocristid is strongly-developed. In general, the trigonid morphology of *D. noibano* is most similar to that of *D. goodfellowi,* and differs from that of *D. dorianus,* which displays a better-formed, more nearly transverse protolophid.

The M/2 of the holotype is virtually unworn. It is a low-crowned and rather bulbous tooth, with the protolophid slightly narrower than the hypolophid. The anterior cingulum is narrow and anteroposteriorly short. The paracristid and cristid obliqua are very poorly-developed, the latter running just linguad of the protoconid. Distinct though small premeta- and preentocristae are present, running perpendicular to the molar lophids. The rear face of the hypolophid is swollen but no posterior cingulum is present.

The M/3 differs from M/4 in being larger and having the protolophid and hypolophid subequal in width. The paracristid and cristid obliqua are better-developed.

The M/4 is larger than the M/3 and has a slightly better-developed cristid obliqua and paracristid. The anterior cingulum is broader.

The M/5 differs from M/4 in being narrower, in having a more poorly-developed preentocristid and an anterior cingulum that is slightly less extensive buccally.

Discussion: On the basis of dental morphology, *Dendrolagus noibano* appears to be most closely related to *D. dorianus* and *D. goodfellowi.* Along with *D. matschiei* and *D. ursinus,* these four extant species form a derived group of tree kangaroos which are definable on the basis of hindlimb morphology (Flannery and Szalay, 1982). *D. noibano* clearly belongs within this group, which is endemic to New Guinea, and not within the more plesiomorphic grouping of Flannery and Szalay, which contains the remaining New Guinean and both Australian species of *Dendrolagus.*

Similarities between *D. noibano* and *D. goodfellowi* include features such as the compressed trigonid on M/1 and the evenly-spaced cuspids on P/2. These are probably primitive retained characteristics, as they are seen in primitive tree-kangaroos and/or other macropodines, and thus do not indicate a close phylogenetic relationship. However, features shared with *D. dorianus,* such as the presence of large buccal cusps on P3/ and P/3 are derived states, and appear to indicate a close relationship between these forms.

On the basis of P3/3, M3/ and M/4 measurements, *D. noibano* is 13% larger on average than *D. dorianus* (see Table 2). While *D. noibano* and *D. dorianus* are closely related it is thought unlikely that they represent components of a dwarfing lineage, in the sense of Marshall and Corruccini (1978), for several reasons. First, the remains of

TABLE 2

Measurements of P3/, P/3, M3/ and M/4 for a modern sample of *Dendrolagus dorianus* held in the Australian Museum, and *Dendrolagus noibano*. Based on mean measurements, the *D. noibano* material is 13% larger in average than that of *D. dorianus*. L = length, AW = anterior width, PW = posterior width, $\bar{x}$ = mean, R = range, N = sample size, STD = standard deviation.

			D. dorianus	*D. noibano*
P3/	L	$\bar{x}$	10.8	11.9
		R	10.3–11.5	11.8–11.9
		N	12	2
		STD	.40	
	AW	$\bar{x}$	5.1	5.2
		R	4.5–5.7	4.8–5.6
		N	12	2
		STD	.41	
	PW	$\bar{x}$	6.5	7.0
		R	6.0–7.1	
		N	12	1
		STD	.31	
P/3	L	$\bar{x}$	9.7	11.6
		R	8.8–10.4	10.7–12.5
		N	12	2
		STD	.47	
	AW	$\bar{x}$	3.8	4.2
		R	3.4–4.7	4.0–4.4
		N	12	2
		STD	.41	
	PW	$\bar{x}$	4.2	5.3
		R	3.6–5.0	5.3
		N	12	
		STD	4 1	
M3/	L	$\bar{x}$	6.7	7.4
		R	6.2–7.3	7.3–7.5
		N	12	2
		STD	3 3	
	AW	$\bar{x}$	6.7	6.9
		R	6.2–7.3	6.8–6.9
		N	12	2
		STD	.34	
	PW	$\bar{x}$	6.1	6.4
		R	5.7–6.5	6.2–6.6
		N	12	2
		STD	.26	
M/4	L	$\bar{x}$	6.8	8.6
		R	6.3–7.2	8.4–8.7
		N	12	2
		STD	.29	
	AW	$\bar{x}$	5.5	5.8
		R	5.0–5.8	5.4–6.1
		N	12	2
		STD	.23	
	PW	$\bar{x}$	5.4	6.3
		R	5.0–5.6	6.2–6.3
		N	12	2
		STD	2 3	

both species are present in strata D and C at Nombe, and thus the species were contemporaneous if they were not actually sympatric and, second, considerable morphological differences in P3/, P/2, P/3, and M/1 exist between these species.

Dendrolagus noibano is a relatively rare element in the fauna of the Nombe rock shelter compared with the other tree-kangaroos, being represented by a minimum number of 3 individuals. It is also the smallest extinct macropodid at Nombe. Given the sharp cut-off of living and extinct species at this point, the relatively small size difference between *D. noibano* and *D. dorianus* may have been a crucial one in terms of survival or extinction in late Pleistocene New Guinea. Unfortunately, post-cranial remains referable to *D. noibano* have yet to be isolated in the collections, and thus its degree of arboreal adaptation cannot be established. Large size alone may not have barred it from an arboreal existence, as Flannery and Szalay (1982) have described a gigantic and apparently at least partly arboreal tree kangaroo from New South Wales.

Protemnodon Owen, 1874
Protemnodon tumbuna n. sp.
Figs 4-5, Table 3

Holotype: PNG/83/40/8 (NCA/792.11/177), right maxillary fragment containing P2/ M1-2/, P3/ removed from crypt. The premaxillary and nasal sutures are partly preserved.

Referred specimens: PNG/82/40/18 (NCA/Z6/324), left I1/. PNG/82/40/9 (NCA/H71/9), right dentary fragment containing P/2, P/3 (in crypt), M/1-3, M/4 (in crypt). PNG/82/40/10 (NCA/Z6/311, R79/312, R79/313), left dentary containing I/1, P/3, M/2-5. PNG/82/40/11 (NCA/D79/90), left dentary fragment with roots of P/3, M/2. PNG/82/40/12 (NCA/TT/39), right M4/. PNG/82/40/13 (NCA/A5/336), left M/1. PNG/82/40/14 (NCA/A4/3), right I/1. PNG/82/40/15 (NCA/H71/9), right I/1. PNG/82/40/16 (NCA/D79/338), right I/1. PNG/82/40/17 (NCA/D79/73), left I/1.

Type locality and age: All specimens are from Nombe rock shelter, Papua New Guinea. Nine specimens were found in the red-brown clay (stratum D), which was deposited during the late Pleistocene, between 24,000 and 14,000 years BP. The holotype was found in the mixed levels (stratum C) that overlie the clay and which are dated at between 14,000 and 10,000 BP. Specimen PNG/82/40/11 was found in the bone level (stratum B) which overlies the mixed levels. The bone level dates to a period after 10,000 years BP. Unlike most of the pieces found in the lower levels, the specimen is burnt. There are very few specimens of extinct macropodids present in the stratum B levels, and there is some reason to believe that those found there have been redeposited from the red-brown clay. At the back of the shelter is a trench, dug during the accumulation of stratum B which extends into the clay of stratum D (the layer containing most of the specimens discussed in this paper). A few specimens may have been dug up from their original context and become part of the refuse at stratum B, becoming thoroughly burnt in the process. It may be possible to test this hypothesis by chemical analysis in the future.

Etymology: The species name *tumbuna* means ancestor or of the ancestors in Neo Melanesian Pidgin. It is used in double allusion, first in reference to the primitive morphology of some aspects of the dentition the species, and, second, to its association with the Pleistocene human inhabitants of highland Papua New Guinea.

Diagnosis: Protemnodon tumbuna can be distinguished from other species of *Protemnodon* by possessing the following characteristics. The main crest of the P3/ is strongly concave buccally and bears a sharp, raised lingual cingulum which lacks tubercles. This type of morphology is otherwise only approached in some variants of *P. otibandus,* e.g. CPC69857. In other species of *Protemnodon,* the main crest is shorter and the lingual

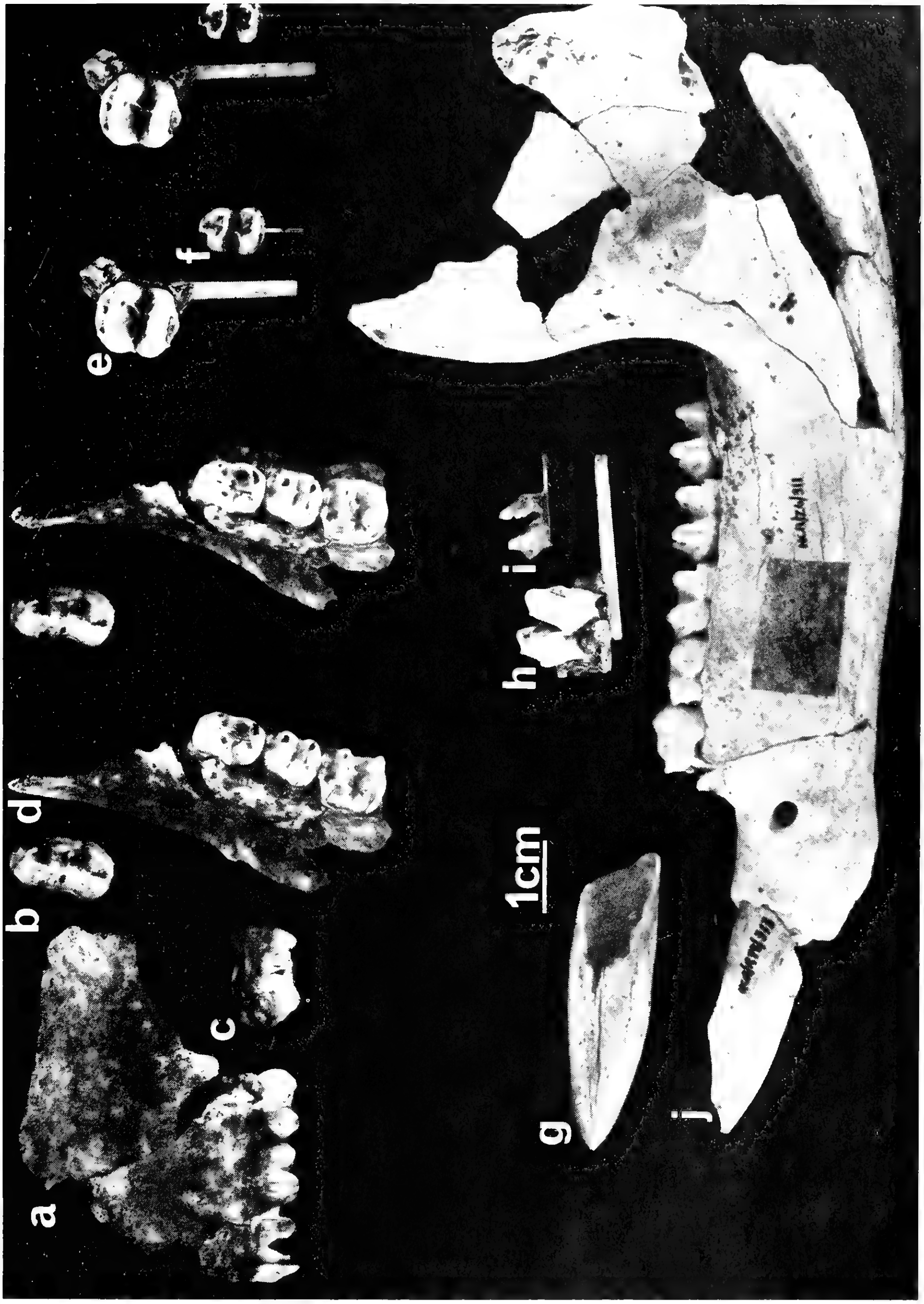

Fig. 4. **a**, buccal view and **d**, stereopair of occlusal view of holotype (PNG/82/40/8) of *Protemnodon tumbuna* containing P2/, M1-2/. **b**, stereopair of occlusal view and **c**, buccal view of P3/ of holotype of *P. tumbuna* (removed from crypt). **e**, stereopair of occlusal view and **h**, buccal view of M4/ (PNG/82/40/12) of *P. tumbuna*. **f**, stereopair of occlusal view and **i**, buccal view of M/1 (PNG/82/40/13) of *P. tumbuna*. **g**, lingual view of PNG/82/40/14, right I/1 of *P. tumbuna*. **j**, buccal view of left dentary (PNG/82/40/10) of *P. tumbuna*, containing P/3, M/2-5.

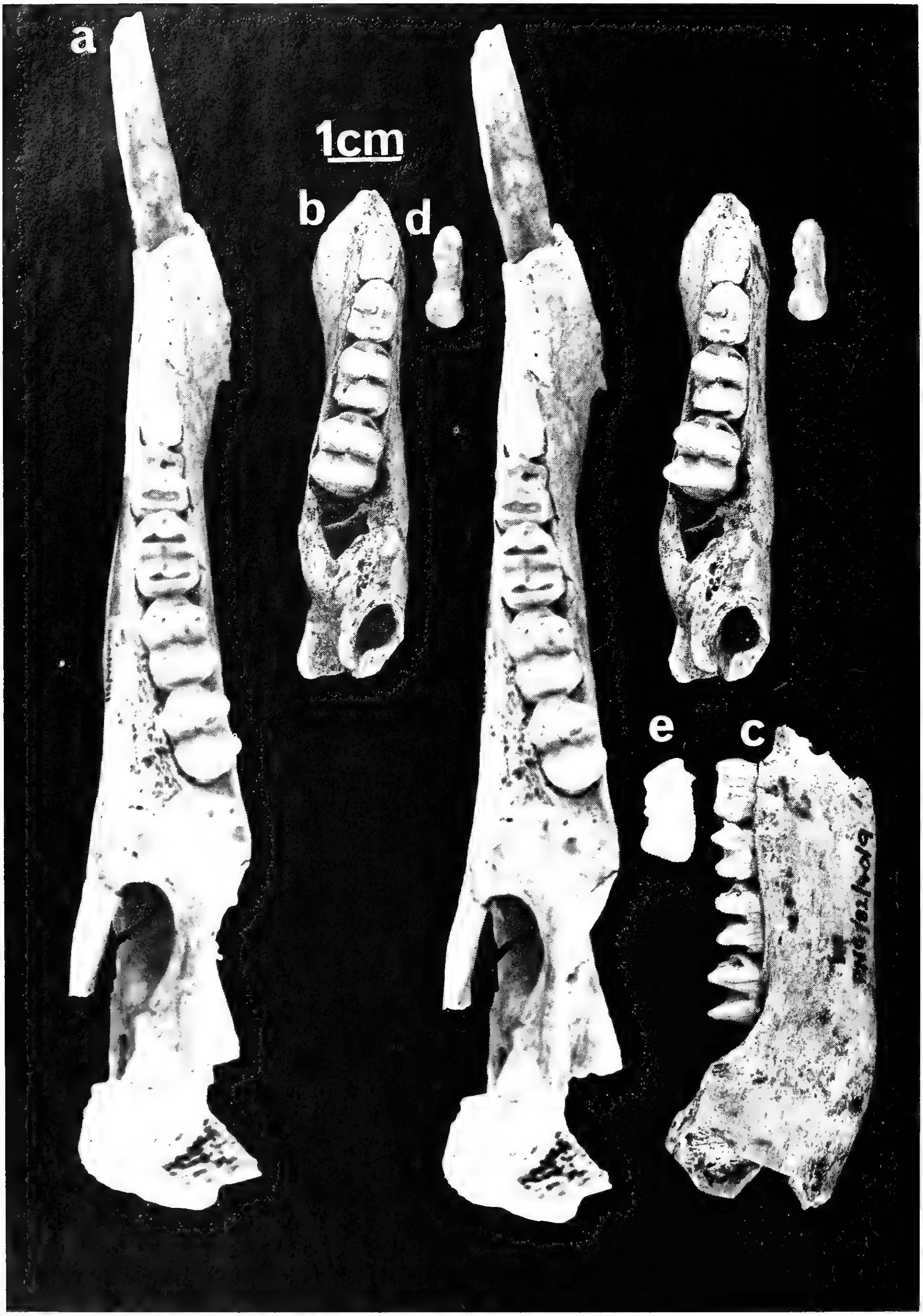

Fig. 5. **a**, stereopair of occlusal view of left dentary (PNG/82/40/10) of *P. tumbuna,* containing P/3, M/2-5. **b**, stereopair of occlusal view and **c**, buccal view of PNG/82/40/9, right dentary fragment of *P. tumbuna* containing P/2, M/1-4 (M/4 in crypt). **d**, stereopair of occlusal view and **e**, lingual view of P/3 (removed from crypt of PNG/82/40/9).

TABLE 3

Dental measurements of the species of *Protemnodon* from Nombe rock shelter. L = length, AW = anterior width, PW = posterior width, JD = diastema length, in mm.

		L	AW	PW
Protemnodon tumbuna				
PNG/82/40/8	P2/	10.0	6.0	7.3
	P3/	15.1	8.0	8.9
	M1/	8.7	7.2	8.0
	M2/	10.4	9.6	9.8
PNG/82/40/12	M4/	11.9	10.4	10.0
PNG/82/40/9	P/2	8.9	4.5	4.8
	P/3	14.4	3.7	5.6
	M/1	8.2	5.8	6.3
	M/2	9.8	7.4	
	M/3	12.1	8.7	9.0
PNG/82/40/13	M/1	9.5	6.5	7.0
PNG/82/40/10	P/3			5.3
	M/2	9.9		8.0
	M/3	11.8	8.6	8.7
	M/4	12.4	9.4	9.8
	M/5	13.2	9.4	8.6
Protemnodon nombe				
PNG/82/40/23	JD	21.0		
	P/3	12.2	4.5	5.3
	M/2	8.0		6.6
	M/3	9.8	7.6	8.0
	M/4	11.2	8.8	8.8
	M/5	11.4	8.9	8.3
PNG/82/40/19	JD	24.0		
	P/3	11.7	4.0	5.0
	M/2	7.7		
	M/3	9.5	7.0	7.1
	M/4	10.8	8.0	7.9
	M/5	11.5	8.2	7.2

cingulum is blunter and composed to some extent of low tubercles. On P2/ of *P. tumbuna,* the lingual cingulum extends far anteriad and is united to the main crest by an accessory cingular crest. In other species the lingual cingulum joins the main crest more posteriorly and there is no accessory cresting. The anterior upper molars of *P. tumbuna* have a weak postlink present on the rear face of the hypoloph, a feature otherwise seen only in *P. otibandus.* The preparacrista is virtually absent on upper molars of *P. tumbuna,* being better developed in other forms. In common with *P. roechus* and to a lesser extent *P. otibandus,* the I/1 lacks a sharp ventral enamel flange in its posterior portion. The coronoid process of the dentary ascends at a steeper angle than in other *Protemnodon* species where this structure is preserved.

Description: Maxilla. The maxillary fragment of the holotype preserves a portion of both the nasal and premaxillary suture. The premaxillary suture is nearly vertically oriented with respect to the tooth row, and the nasal suture is straight and horizontally oriented. The infraorbital canal opens above the midpoint of P2/. A shallow fossa is present between the anterior rim of the orbit and the infraorbital foramen.

I1/. The single, left I1/ known is heavily worn. The root is laterally compressed and oval in cross section. The wear facet slopes gently dorsally and posteriorly from the anterior margin. Enamel is restricted to the anterior face of the tooth.

P2/. The P2/ is short but broad, being subequal in length to the M2/. The main crest is composed of distinct anterior and posterior cusps and a single medial cuspule with associated buccal and lingual ridgelets. The buccal surface of the tooth is further ornamented by strong cresting from the principal cusps. A broad posterolingual blade joins the main crest to form the posterior portion of a continuous high lingual cingulum. The lingual cingulum joins the main crest anteriorly by two cristae, one joins the main crest in the centre of the anterior cusp, and is clearly the analogue of the structure that joins the lingual cingulum to the main crest in other *Protemnodon* species, while another weaker crest connects the lingual cingulum to the main crest at the anteriormost point of the tooth. This crest is unique to *P. tumbuna* amongst near relatives and is probably a neomorphic structure.

P3/. The P3/ is relatively short and slightly broader posteriorly than anteriorly. The main crest is strongly concave buccally. Distinct anterior and posterior cuspids are present, the former with strong buccal and anterior and weaker lingual cresting. Between these cusps the main crest is somewhat irregular and crenulate. Two weak ridgelets are present on the buccal and lingual faces, the buccal pair enclosing a small fossette. The obliquely oriented posterolingual blade is slightly lower than the main crest. Two ridges run between these structures to enclose a small posterior fossette.

Upper molars. The M1/ of the holotype is slightly worn, both lophs being breached by wear. It is extremely low-crowned. The lingual margin of the tooth is more gently inclined towards the tooth base than is normally seen in macropodoids, resulting in a marked constriction of the loph apices. The protoloph is slightly narrower than the hypoloph. A weak preparacrista joins the protoloph to the buccal end of the lingually restricted anterior cingulum. A very weak forelink is present. The midlink is worn but was evidently poorly-developed. A well-developed postparacrista and premetacrista converge in the median valley, approximately 3 mm linguad of the buccal margin of the tooth. The postmetacrista is extremely weakly-developed, running almost vertically down the rear face of the hypoloph. The posthypocrista is well-developed; it swings buccally to disappear midway across the rear of the molar.

The M2/ is similar to the M1/ in being low-crowned and in displaying a gently-inclined lingual side. However, it is larger, and differs from that tooth in the following ways. The preparacrista is barely indicated and does not contact the anterior cingulum. The anterior cingulum is slightly more extensive though no forelink is present. The midlink and all accessory cresting are better-developed, with the exception of the premetacrista, which is distinctly weaker than the postparacrista. A low crest descends the anterior face of the hypoloph to join the midlink. A distinct but small postlink is present near the apex of the hypoloph midway along its length.

The M4/, PNG/82/40/12, differs from the M2/ in being larger, having a more steeply-inclined lingual margin and in being subequal in anterior and posterior width. The tooth is also slightly higher-crowned (which may be due in part to its being unworn). The anterior cingulum extends further lingually than on M2/. The postparacrista appears to be stronger although this may also be a reflection of wear. The premetacrista is weaker. The postlink is reduced to a slight fold of enamel on the rear face of the hypoloph. The posthypocrista and postmetacrista are more strongly developed, the latter forming a broad shelf at the base of the posterior fossette.

Dentary. In the adult specimens the mandibular symphysis is extensive and rugose, and extends to below the anterior end of P/3 on the holotype. The ventral border of the dentary is almost straight and bears a poorly-developed digastric sulcus and ventral ridge. The opening of the masseteric canal is moderately large. The anterior border of the coronoid process rises sharply, leaning forward at an angle of less than 90 degrees to the molar row. The large mental foramen lies just below and anterior to P/3. The diastema is short. A poorly-defined buccinator groove extends below the cheektooth row from P/3 to the midpoint of M/4.

I/1. Five specimens of I/1 are known, one of which (PNG/82/40/10) is retained within a dentary. These teeth are relatively narrow and lanceolate in form, being similar to those of *Protemnodon otibandus,* and do not display the spatulate morphology seen in *P. roechus.* On unworn examples, it can be seen that the tooth is thickly enamelled buccally and ventrolingually. The crown possesses a dorsal and ventral enamel flange. On the posteroventral portion of the tooth, enamel continues posterior to the flange as a rounded hump.

P/2. The single known P/2 (PNG/82/40/9) is only slightly worn. The tooth is short and bulbous relative to that of *Protemnodon otibandus.* The anterior cuspid forms the highest point on the crest, and is slightly buccally offset from the main crest. This cuspid bears a strong buccal crest which terminates before reaching the crown base. Shallow grooving on the buccal and lingual faces of the tooth suggest that two faint cuspules may have been present between the anterior and posterior cuspids. The posterior cuspid is blade-like, and is flexed lingually out of alignment with the main crest. A distinct but narrow groove demarcates the posterior cuspid on its lingual side.

P/3. The unerupted P/3 of PNG/82/40/9 is almost complete and is unworn. It is a relatively elongate tooth consisting of a straight longitudinal crest and prominent anterior and posterior cuspids. The anterior cuspid is slightly offset buccally from the main crest, and bears three ridges, one on each of its buccal, lingual and anterior sides. Between the main cusps are two distinct cuspules with associated buccal and lingual ridgelets. These are subequal in height to the anterior cuspid, but lie somewhat below the high posterior cuspid. A low cingulum in the form of a basal enamel bulge is present on the buccal side of the tooth. The base of the crown on the lingual side is broken away. The P/3 fragment of PNG/82/40/10 differs from that described above in that the two cuspules are more sharply defined and larger, the tooth overall is more bulbous, and the base of the lingual side of the crown is preserved, showing that the basal cingulum is barely distinguishable on that side.

Lower molars. The M/1, known from two specimens, is low-crowned and is quite bulbous basally, particularly on the buccal margins of the lophids. The protolophid is slightly narrower than the hypolophid. The anterior cingulum is very short and low but extends to the lingual side of the tooth. The paracristid runs from the apex of the protoconid to intersect the anterior cingulum at a point just buccal of the midline of the tooth. The premetacristid is well-developed and runs from the apex of the metaconid to the lingual end of the anterior cingulum. A poorly-defined fossette is present between the paracristid and the buccal extension of the anterior cingulum. The cristid obliqua is rather poorly-developed and runs to a point well buccal to the midline of the tooth. A well-developed preentocristid and a posterior cingulum are present, the latter being confined to the buccal half of the tooth.

The M/2 of PNG/82/40/9 is only lightly worn, but the entoconid is broken away. It is similar to the M/1 in overall form but differs in the following details. The protolophid and hypolophid are more nearly subequal in width. The paracristid and cristid obliqua are better-defined, the latter crest originating well below the apex of the hypoconid. Both crests swing further linguad, and the anterobuccal fossette is correspondingly better-defined. The protolophid contribution to the cristid obliqua is also better-defined. The premetacristid is less extensive anteriorly, just failing to contact the anterior cingulum; a faint accessory cristid curves buccally for a short distance below the metaconid apex. A weak postmetacristid runs buccally to a point just linguad of the cristid obliqua. The posterior cingulum is well-developed, but is restricted to the buccal two thirds of the tooth.

The M/3 of PNG/82/40/9 is unworn and complete. It differs from M/2 in the following ways. The anterior cingulum is short and less extensive lingually. The protoconid is rotated anteriad relative to the metaconid. The paracristid is strongly sinuous in form, swinging lingually and then anteriorly to contact the anterior cingulum just buccal to the midline of the tooth. The cristid obliqua is slightly better-developed, originating about 3 mm below the apex of the hypoconid and ending midway across the rear face of the protolophid. The hypoconid is noticeably taller than the entoconid, and is positioned lingually relative to the protoconid. A distinct although weakly-developed preentocristid is present, originating from the apex of the entoconid it runs anteriorly, then turns sharply buccally to terminate just linguad of the anterior end of the cristid obliqua; the anterobuccal portion of a similar crest is just preserved in M/3 of PNG/82/40/10. The posterior cingulum of PNG/82/40/9 is well developed but restricted to the buccal two thirds of the tooth. In the M/3 of PNG/82/40/10 it is both broader and more extensive lingually.

The M/4 and M/5 are known only from PNG/82/40/10. The M/4 differs from M/3 in the following ways. It is larger. The paracristid forms a straight crest between the protoconid and the anterior cingulum at the midline of the tooth. The anterior cingulum is lower and less extensive lingually. The cristid obliqua runs to a point on the midline of the tooth as in M/3. The buccally-directed preentocristid may be slightly better developed. The posterior cingulum is similar to that of M/3 of the same specimen (PNG/82/40/10). The degree of protoconid and hypoconid rotation cannot be established as the specimen is worn.

The M/5 differs from M/4 in the following ways. The anterior cingulum is anteroposteriorly lengthened but is less extensive lingually. The cristid obliqua is less well-developed, forming a low, rounded enamel hump. The hypolophid is narrower than the protolophid. The premetacristid and preentocristid are marginally better-developed, the latter running more nearly vertically down the lingual margin of the hypolophid. The posterior cingulum is less extensive buccally but more extensive and broader lingually.

Discussion: Protemnodon tumbuna most closely resembles Pliocene New Guinean and (more distantly) Pliocene Australian species of *Protemnodon*. The similarity between these forms is due primarily to a retention of many plesiomorphic states such as low-crowned molars, the presence of a weak postlink on upper molars and the lanceolate form of I/1. However, the high continuous lingual cingulum of P3/ in *P. tumbuna* and some specimens of the Pliocene New Guinean *P. otibandus* may be a derived characteristic linking these forms, as may be the unusual ventral enamel distribution of I/1. Many features of *P. tumbuna* are, however, unique or apomorphic within *Protemnodon*. Included here are the short, buccally-concave main crest of P3/, the anterior linking of the lingual cingulum and the bulbous nature of P2/, the short, bulbous P/2 and the steep angle of ascent of the coronoid process of the dentary. Thus if, as appears likely, *P. tumbuna* is descended from a *P. otibandus*-like ancestor, the lineage has undergone substantial morphological change during the late Pliocene-Pleistocene.

Protemnodon tumbuna, represented by a minimum number of four individuals, is the largest macropodid and the second largest marsupial (the largest being a diprotodontid) in the fauna of the Nombe rock shelter. *P. tumbuna,* however, is small compared with extinct Australian Pleistocene macropodids, and was probably smaller than several living Australian macropodids (the species of *Macropus* and some *Osphranter*). It seems most likely that *P. tumbuna* inhabited rainforest areas, as its molars are very low-crowned, as are those of living rainforest-inhabiting macropodids (e.g. the species of *Dorcopsis, Dorcopsulus* and *Dendrolagus*). *Thylogale brunii,* which may be locally very abundant in montane grassland habitats in New Guinea has considerably higher-crowned molars than any of these forms including *P. tumbuna.*

Protemnodon nombe n. sp.

Figs 6-7, Table 3

Holotype: PNG/82/40/23 (NCA/M71/9), right dentary containing root of I/1, P/3, M/2-5 but lacking most of the dentary posterior to M/5.

Referred specimen: PNG/82/40/19 (NCA/R79/313, NCA/R79/314, NCA/R79/297, NCA/R79/312), left dentary containing broken I/1, P/3, M/2-5 but lacking much of ascending ramus.

Locality and age: Both specimens of *Protemnodon nombe* were recovered from the red-brown clay (stratum D) of Nombe rock shelter, which is dated to between 24,000 and 14,000 years BP.

Etymology: The species is named for the type and only known locality of *Protemnodon nombe,* the Nombe rock shelter.

Diagnosis: Protemnodon nombe is the smallest species of *Protemnodon* known. It is closest in size to *P. buloloensis* of the Pliocene Awe local fauna of New Guinea, but differs from that form in having a proportionately much shorter P/3, less elongate molars and a longer dentary diastema. Its molars are lower crowned than those of *P. anak, P. devisi* and *P. snewini.* It differs from *P. tumbuna* by possessing a narrow I/1 which has a distinct ventral enamel flange which extends to the posterior end of the crown, by a much less strongly-ridged P/3, a relatively narrower anterior cingulum on lower molars, a proportionately broader angle of the dentary, and a more swollen masseteric canal.

Description: Dentary. Much of the description of the dentary is based on the referred specimen (PNG/82/40/19), as it is more complete. The dentary is relatively narrow and slender below the cheektooth row, but is nonetheless quite large relative to tooth size. The diastema is relatively short, but less so than in *P. buloloensis.* The mental foramen is positioned well forward of the anterior root of P/3. The mandibular symphysis appears to have been less extensive than in *P. tumbuna.* The ventral margin of the horizontal ramus is gently concave below the posterior molars. The buccinator groove is quite shallow. In contrast to the horizontal ramus, the posterior main muscle-bearing structures are surprisingly robust. In particular both the masseteric canal and pterygoid fossa are very large and swollen. The mandibular foramen in the pterygoid fossa is also of large size. Although broken off at its base, enough of the ascending ramus survives to indicate the presence of a steeply inclined coronoid process.

I/1. The I/1, although known only from its posterior portion on the referred specimen, was clearly small and slender relative to that of *Protemnodon tumbuna.* It also retains a well-defined ventral enamel flange that extends posteriorly to the base of the crown. The tooth is heavily worn but the remnants of a distinct dorsal enamel flange can be seen.

P/3. The P/3 of the holotype of *Protemnodon nombe* is almost complete and only slightly worn. Only a sliver of enamel from the anterior-most portion of the tooth is missing. The occlusal edge is straight and of even height. The anterior cuspid forms a distinct prominence and is flanked by a sharp ridge lingually and a blunter one buccally. On the referred specimen a sharp ridge can be seen to descend anteriorly also. Three ill-defined buccal and lingual ridgelets are present on the crest posterior to the anterior cuspid. The posterior cuspid is ill-defined and is the broadest part of the tooth. It is slightly swollen buccally. A slight crest runs down the posterolingual portion of the tooth.

Lower molars. The M/2 of the holotype is heavily worn and enamel is broken away

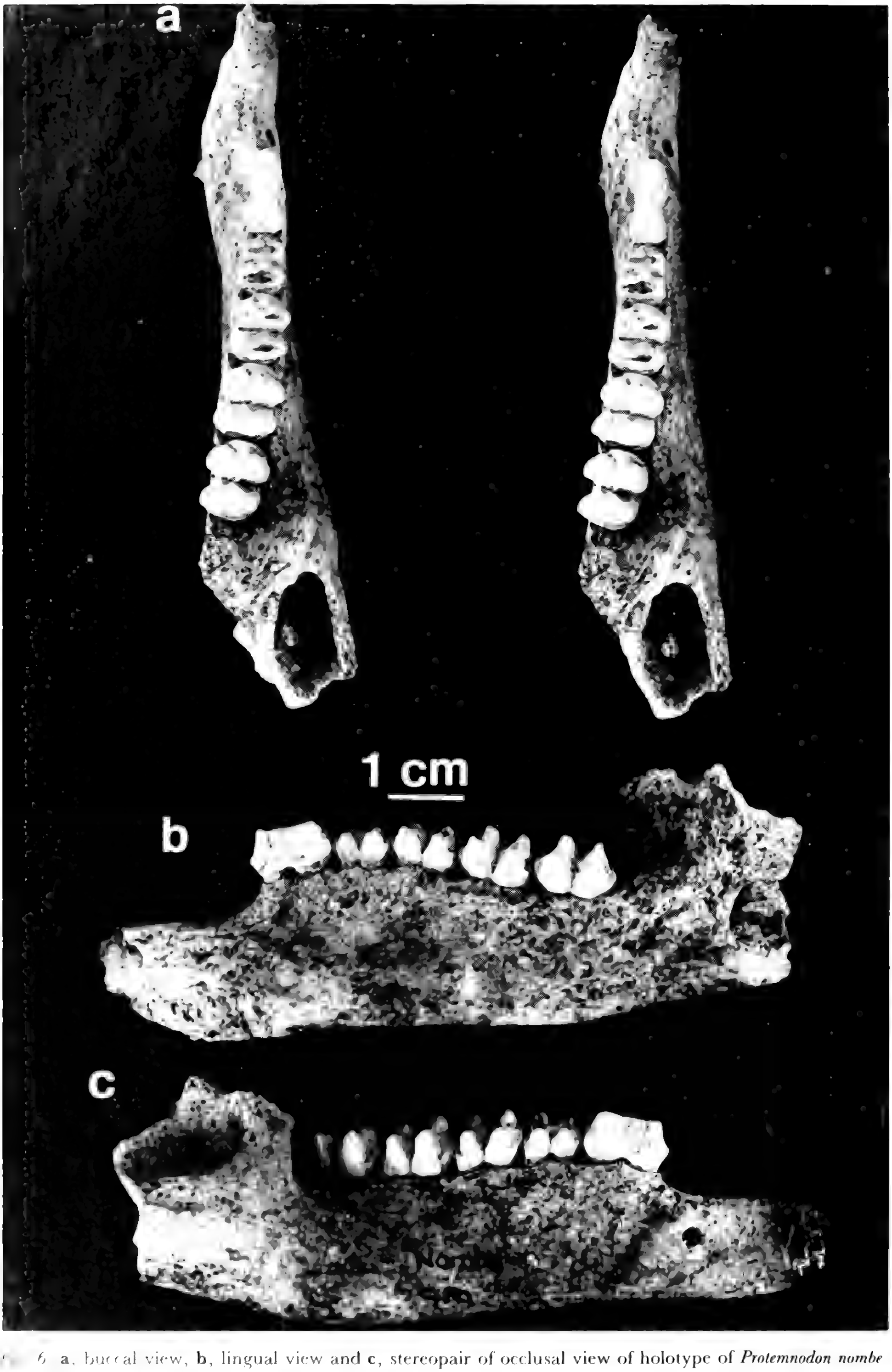

Fig. 6. **a**, buccal view, **b**, lingual view and **c**, stereopair of occlusal view of holotype of *Protemnodon nombe* (PNG/82/40/23), right dentary containing P/3, M/2-5.

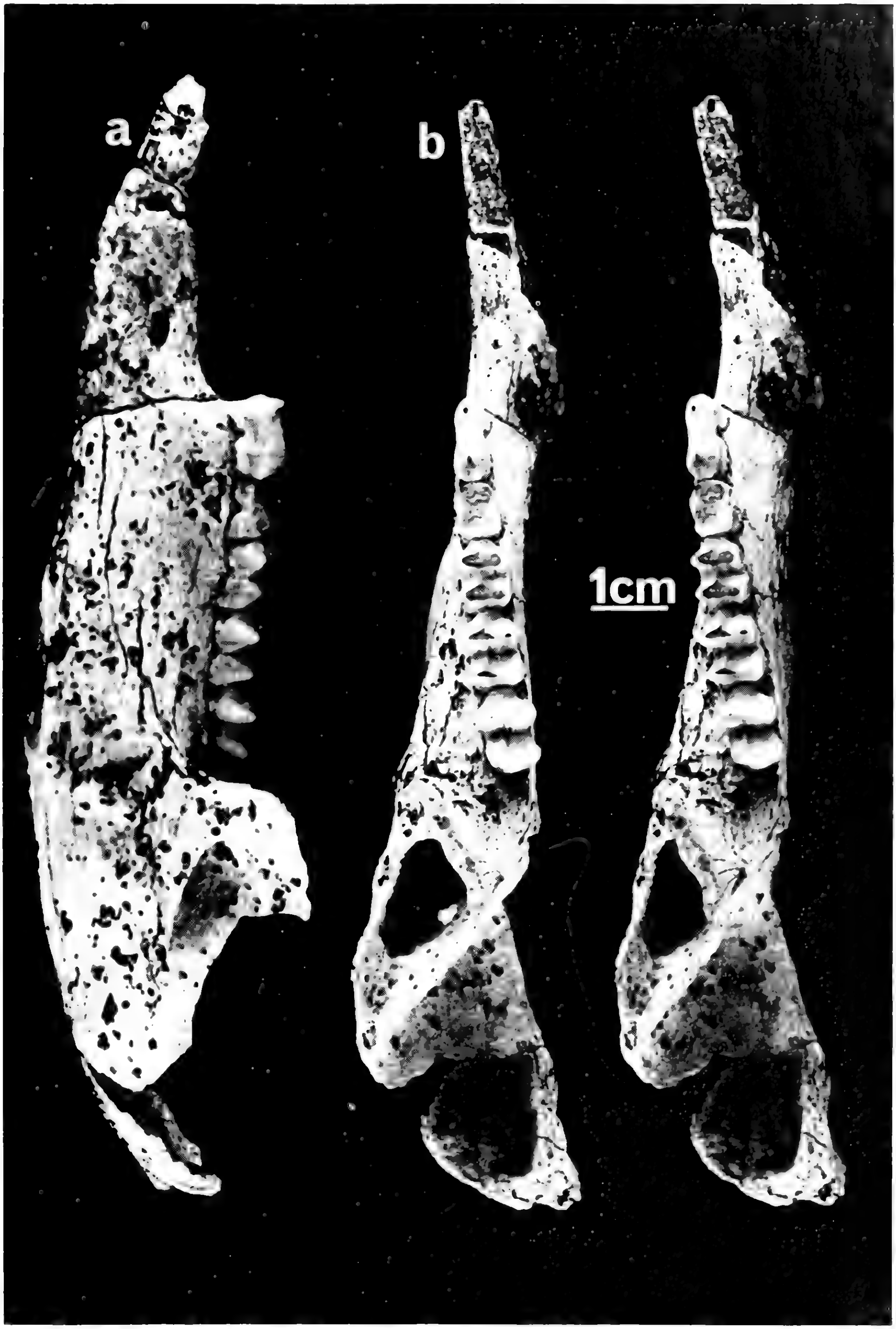

Fig. 7. **a**, buccal view and **b**, stereopair of occlusal view of referred specimen of *Protemnodon nombe* (PNG/82/40/19), left dentary containing I/1, P/3, M/2-5.

from the metaconid. An ill-defined straight paracristid and cristid obliqua can be discerned. A well-defined posterior cingulum is the best-preserved structure on the tooth. Buccally it reaches the tooth margin, but lingually it terminates about 1.5 mm buccal of it.

The M/3 of the holotype is in a more moderate stage of wear. However, the enamel of both lophids is breached. M/3 is larger than M/2 and the protolophid and hypolophid are subequal in width. It is much broader in the holotype than in the referred specimen. The anterior cingulum is low and anteroposteriorly short. Lingually it runs to near the tooth margin while buccally it terminates about 2 mm from the tooth edge. The paracristid is low, running from just buccal of the tooth midline (its exact relationships are obscured by wear) to the anterior cingulum. Its relationship to the protoconid is obscured by wear. The cristid obliqua is low and worn. It originates just buccal of the tooth midline but its exact relationships are obscured by wear also. A well-developed posterior cingulum is present on the rear face of the hypolophid. It terminates before reaching the buccal edge of the tooth.

M/4 differs from M/3 in the holotype in the following ways. It is larger and less worn. The lingual margins of the lophids are distinctly bowed while the buccal margins are vertical. A distinct fissure frustrates contact of the lingual end of the protolophid with the anterior cingulum (this detail is obscured by wear on M/3). A well-developed premetacristid runs directly anterior from the lingual margin of the protolophid. The M/4 of the holotype is broader than that of the referred specimen.

The M/5 of the holotype is virtually unworn. It differs from M/4 in the following ways. The protolophid is broader than the hypolophid. The protolophid is of an unusual morphology. Buccal to the paracristid the protolophid apex runs along the midline of the loph. Lingual to the paracristid, however, it is shifted posteriorly, giving the anterior face of the protolophid a convex surface in this region. This may have been the case on M/4 also, but this region is obscured by wear. A strong premetacristid runs anteriorly from the lingual end of the protolophid at a 90 degree angle. A preentocristid runs anteriorly from the entoconid, then swings sharply buccally to end against the posterior surface of the protolophid 2 mm from the lingual margin of the tooth. The posterior cingulum is more weakly developed than on M/4. The M/5 of the holotype is broader than that of the referred specimen, and the posterior cingulum is more strongly developed.

Discussion: Protemnodon nombe is the rarest macropodid in the fauna of the Nombe rock shelter, being known from two specimens representing two individuals. The species is interesting in that it displays an unusual combination of very primitive dental characteristics and a specialized mandibular morphology. Among the species of *Protemnodon,* the combination of very low-crowned and weakly ridged molars, only moderately elongate premolar and non-specialized lower incisor probably represent the basic dental groundplan. Within the limits of our present knowledge of its dental morphology, *P. nombe* could be considered the most primitive member of the genus. The dentary of *P. nombe,* however is highly unusual and probably derived in morphology. It is large relative to molar size and thus the species could be described as being microdont in the sense that Wells and Murray (1979) describe *Simosthenurus maddocki.* Also striking are the greatly enlarged muscular fossae of the posterior ramus. The functional implications of this peculiar morphological complex are not immediately apparent, and clearly warrant further investigation. However, such features are seen among the species of *Simosthenurus,* a group which, as far as is known, failed to reach New Guinea, and for which *P. nombe* may be an ecological vicar. As with *P. tumbuna,* the low-crowned molars of *P. nombe* suggest a browsing diet and probable rainforest habitat.

DISCUSSION

The macropodids of the Nombe rock shelter shed light on several areas of kangaroo zoogeography and evolution. The New Guinean mammal fauna appears to be a relict one, similar assemblages, at least at the generic level, being found in late Tertiary fossil deposits in Australia (e.g. Turnbull and Lundelius, 1970). The extinct Pleistocene *Protemnodon* species from Nombe support this hypothesis, as they are closest in morphology to Pliocene New Guinean and (more distantly) to Pliocene Australian forms.

Filters obviously existed between New Guinean and Australian montane rainforest areas, as many forms, including potoroids, present in montane rainforests in Australia are not known from New Guinea. Indeed, the New Guinean macropodid assemblage is remarkably limited at higher taxonomic levels, all living and extinct forms belonging to the subfamily Macropodinae. A much richer source of material from which the New Guinean assemblage was derived existed in late Tertiary Australia, where four subfamilies are known. Apart from *Prionotemnus agilis* and *Thylogale stigmatica,* which are found in lowland southern New Guinea, and are probably recent immigrants from Australia, the macropodid fauna of New Guinea is endemic. The living and extinct endemic New Guinean macropodids consist of the species of five genera (*Thylogale, Dorcopsulus, Dorcopsis, Dendrolagus* and *Protemnodon*). The last two have undergone minor radiations within New Guinea. The species of *Dorcopsis* and *Dorcopsulus* together are probably monophyletic, and thus the entire montane macropodid fauna of New Guinea can be accounted for by the initial presence of only four original kinds of kangaroos. All are similar in that they represent primitive kinds of macropodines.

The fossils of the Nombe rock shelter allow a comparison of late Pleistocene extinction in New Guinea and Australia. Of the mammals from Nombe, the four largest species of herbivore are extinct. These include a species of pig-sized diprotodontid, two species of *Protemnodon* (grey kangaroo sized and smaller) and a tree kangaroo slightly larger than *Dendrolagus dorianus.* Of these species, at least the macropodids are inferred on the basis of dental morphology to have lived in rainforest, and not 'shrub-rich treefern grassland', as has been previously postulated (Hope and Hope, 1976). Interestingly, there is no evidence for post Pleistocene dwarfing in New Guinean macropodids, a phenomenon so prevalent in larger Australian macropodid lineages (Marshall and Corruccini, 1978). There is also no evidence of size overlap between living forms and those which became extinct in the late Pleistocene, the converse of which is true in Australia. In New Guinea, the cut off size between living and extinct forms is sharp. Those with an adult bodyweight of over 18 kg became extinct, whilst smaller forms survived. The very association of man and megafauna at Nombe is unusual in the Australian context at present, and may denote a real difference in the causes of extinction in the two areas. Finally, there is some evidence that some megafaunal species at Nombe survived to 14,000 years BP or later. In Australia, although megafaunal elements may have survived until as recently as 16,000 BP (Hope *et al.,* 1977), most sites containing megafaunal elements are older, (e.g. Lancefield, about 25,000 BP, Gillespie *et al.,* 1978).

The terminal Pleistocene period was one of quite dramatic climatic change in the New Guinea highlands. Glaciation was probably extensive throughout the period of deposition of the red-brown clay (stratum D), and the treeline may have been depressed to just above the altitude of the Nombe rock shelter. On nearby Mt Wilhelm deglaciation was underway by 14,000 years BP and virtually complete by 10,000 years BP. However, it may have taken a further 5,000 years before vegetation stabilized into modern communities (Hope and Hope, 1976). The terminal Pleistocene also saw initial agricultural experiments at mid-montane altitudes, possibly causing further vegetational disruption at this time. However, the effect of both human disturbance and changing climate on vegetational parameters is as yet poorly known, and it would be premature to attempt to assess the impact of such factors on the mammalian fauna.

CONCLUSIONS

1, The three larger species of nacropodid from Nombe rock shelter are newly-described extinct forms (*Dendrolagus noibano, Protemnodon tumbuna* and *P. nombe*); the four smaller species represented in the site are extant and previously known.

2, *Protemnodon tumbuna* and *P. nombe* are both primitive species of *Protemnodon,* but they display some unique specializations.

3, Megafaunal species in New Guinea appear not to have undergone post-Pleistocene dwarfing and may have persisted longer than their counterparts in Australia.

4, While man and megafauna apparently co-existed for an extended time in the Nombe area, the extent and nature of their interaction is still unclear.

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The taxonomic Status of small Fossil Wombats (Vombatidae: Marsupialia) from Quaternary Deposits, and of related modern Wombats

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DAWSON, L. The taxonomic status of small fossil wombats (Vombatidae: Marsupialia) from Quaternary deposits, and of related modern wombats. *Proc. Linn. Soc. N.S.W.* 107 (2), (1982) 1983: 101-123.

The taxonomic value of characters of the upper and lower incisors and premolars, of the anterior region of the palate, and of the nasals and frontals has been verified for modern species of *Vombatus* and *Lasiorhinus*. However, characters of the lower dentition and the mandible reliably distinguish between *Vombatus* and *Lasiorhinus* at the generic level only, and are inadequate for identification of species within these genera.

Three modern subspecies of *Vombatus ursinus* are recognized; *V. u. ursinus* (Shaw, 1800), *V. u. tasmaniensis* (Spencer & Kershaw, 1910), and *V. u. platyrhinus* (Owen, 1853). *Vombatus ursinus mitchellii* (Owen, 1838) is recognized as a fossil subspecies from Pleistocene deposits of Wellington Caves, New South Wales. *Phascolomys parvus* Owen, 1872, *Phascolomys pliocenus* McCoy, 1866, and *Phascolomys thomsoni* Owen, 1872 have been placed in the synonymy of *Vombatus ursinus* (Shaw, 1800). *Vombatus hacketti* Glauert, 1910 is recognized as a fossil species from Pleistocene deposits of Mammoth Cave, Western Australia. *Phascolomys gillespiei* De Vis, 1900 and *Lasiorhinus latifrons barnardi* Longman, 1939 have been placed in the synonymy of *Lasiorhinus krefftii* (Owen, 1872). *Lasiorhinus angustidens* (De Vis, 1891) is recognized for a fossil species from the eastern Darling Downs, Queensland. The relationships of the plesiomorphic species *Warendja wakefieldi* Hope & Wilkinson, 1982 have not yet been established.

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INTRODUCTION

Classification of living and fossil wombats has long been the source of considerable confusion. Kirsch and Calaby (1977: 23), who listed three species of two genera of living wombats, stated that '. . . the nomenclature of wombats has an arbitrary element.' The confusion is partly due to the complex historical background of the nomenclature, and partly due to poor understanding generally of the taxonomic value of skeletal and dental characters of wombats.

Modern wombats were first known from Flinders Island in Bass Strait, and from Tasmania, and given a variety of names by early workers (see Thomas, 1888). The earliest name for the southern island form is *Didelphis ursina* Shaw, 1800. Although the name *Opossum hirsutum* Perry, 1811 probably applied to the mainland Common Wombat (see Troughton, 1941), a mainland form was not known to the British palaeontologist, Richard Owen, when he named a wombat fossil from Pleistocene deposits at Wellington Caves, New South Wales as *Phascolomys mitchellii* (Owen in Mitchell, 1838). The island form was known to Owen as *Phascolomys vombatus* Leach, 1815. Owen (1845) was the first to recognize the modern Southern Hairy-nosed Wombat as a distinct species, *Phascolomys latifrons* Owen, 1845. Owen later had access to skulls of the modern mainland Common Wombat and his study of cranial bones led him to describe this form as a fourth species, *Phascolomys platyrhinus* Owen, 1853. He considered this modern species to be very similar to, but distinct from, the fossil species

P. mitchellii. In both papers (Owen, 1845, 1853) Owen defines characters of the skull bones to distinguish between these 'species', which he assigned to two groups — the 'platyrhine' (= common or forest wombats) and 'latifront' (= hairy-nosed) wombats. Murie (1865) placed Owen's species *latifrons* in *Lasiorhinus.* The generic distinction of *latifrons* was never recognized by Owen, nor by other 19th century writers who referred all wombats (except the giant *Phascolonus gigas*) to the genus *Phascolomys.*

In 1872 Owen produced two large treatises on fossil wombats, the first (Owen, 1872a) bearing on species similar in size to existing wombats, and the second (Owen, 1872b) being confined to species exceeding the present in size. Owen (1872a) described three more fossil species very similar to living forms: *Phascolomys krefftii,* from Wellington Caves, and *Phascolomys thomsoni* and *Phascolomys parvus* from Pleistocene deposits of the eastern Darling Downs, Queensland.

Since then three other small fossil species have been described in the genus *Phascolomys: Phascolomys pliocenus* McCoy, 1866 from Dunolly, Victoria; *Phascolomys angustidens* De Vis, 1891 from the eastern Darling Downs; and *Phascolomys hacketti* Glauert, 1910 from Mammoth Cave, Western Australia. Another unique small wombat, *Warendja wakefieldi* Hope & Wilkinson, 1982 has been described for jaw fragments from Pleistocene deposits in McEacherns Cave in southwestern Victoria.

It is necessary to review current opinion on the taxonomy of modern wombats before discussion of the status of fossil species. In the most recent review of living and fossil wombats Tate (1951) recognized three geographically separate forms of the living Common Wombat as subspecies of *Vombatus ursinus:* a Tasmanian form, *V. u. tasmaniensis* (Spencer & Kershaw, 1910); a continental form, *V. u. platyrhinus* (Owen, 1853); and the Flinders Island form, *V. u. ursinus* (Shaw, 1800). He also considered the fossil form *V. u. mitchellii* from Wellington Caves, to be a subspecies most similar to *V. u. platyrhinus.* Ride (1970) and Kirsch and Calaby (1977) did not recognize these subspecies and included all living forms in a single species *Vombatus ursinus.* Tate (1951) considered *Phascolomys hacketti* from Western Australia to be a synonym of *V. u. platyrhinus,* and listed *thomsoni, parvus* and *pliocenus* as fossil species of *Vombatus* without further comment.

Classification of the geographically separate forms of the modern hairy-nosed wombats has also been uncertain. Tate (1951) listed three modern subspecies of *Lasiorhinus latifrons: L. l. latifrons* (Owen, 1845) from South Australia, *L. l. gillespiei* (De Vis, 1900) from Moonie River, Queensland, and *L. l. barnardi* Longman, 1939 from Clermont, Queensland. He considered the fossil forms, *L. krefftii* and *L. angustidens,* to be distinct species. Ride (1970) listed each of the three modern forms of hairy-nosed wombat as full species. Kirsch and Calaby (1977) recognized *L. latifrons* from South Australia at the specific level, but followed Wilkinson (quoted in Merrilees, 1973), in placing *L. barnardi* and *L. gillespiei* in the synonymy of *L. krefftii* although no data were given by Wilkinson to support this suggestion.

In this study dental nomenclature follows Archer (1978). Accordingly, the dental formula of wombats is I^{1}_{1}, P^{3}_{3}, M^{2-5}_{2-5}. All measurements are in millimetres.

Taxonomic Characters of the Skull and Teeth of Wombats

Until 1967 there had been no reassessment of the taxonomic value of characters used by Owen and others to distinguish between the various species of fossil wombat, nor had any study been made of inter- and intraspecific variation in living wombats. Two studies published in that year (Merrilees, 1967; Crowcroft, 1967) represent the first important steps in the clarification of vomatid taxonomy.

Merrilees (1967) reassessed the taxonomic value of many characters of the skull and teeth described by Owen between 1846 and 1872 to distinguish between

TABLE 1

Non-metric character states diagnostic at the generic level for modern wombats

No.	Description of Character	*Vombatus*	*Lasiorhinus*
1.	Proportions of nasals	Narrow relative to length	Wide relative to length
2.	Shape of upper incisors	Wider than deep	Deeper than wide
3.	Wear angle on upper incisors	Near transverse	Near vertical
4.	Upper premolars	Anterolingual groove	No anterolingual groove
5.	Palate width between posterior lobe of $_M2\text{-}2$	Narrow	Wider
6.	Depth of 'ectalveolar plate' of maxilla*	Shallow	Deep
7.	Shape of anterior palate	Narrow, less concave	Flares anteriorly
8.	Premaxillary/nasal suture	Much longer than maxillary/nasal suture	Shorter than maxillary/ nasal suture
9.	Cross-sectional shape lower incisor	Triangular	Spatulate
10.	Upper symphyseal surface between $P_{3\text{-}3}$	Flat base	Concave base
11.	Shape of lower premolars	Oval in T.S.	Subrectangular in T.S.
12.	Foreward extent of 'ectalveolar groove'**	To anterior edge M_5	To anterior edge M_4
13.	Upper surface mandibular diastema	Convex	Flat
14.	Maximum depth ramus	Below M_4	Below M_3
15.	Masseteric fossa	Deep, large masseteric canal	Shallow, masseteric canal absent or small

* Term introduced by Owen (1872a) for the portion of the maxilla directly below the anterior origin of the zygomatic arch.

** Name introduced by Owen (1872a) for the labial valley between the posterior molars and the base of the ascending ramus of the coronoid process of the dentary.

'platyrhine' and 'latifront' wombats (i.e. between species of *Vombatus* and *Lasiorhinus*). He noted high variability in most of Owen's characters in modern populations of *Lasiorhinus latifrons* and *Vombatus ursinus* (= *V. hirsutus*). This variability occurred even within a single population of one species. Merrilees (1967) concluded, particularly, that non-metric morphological characters of the molar teeth do not suffice to distinguish modern taxa, even at the generic level. He also confirmed that absolute tooth size is unreliable as a taxonomic character in wombats due to the open-rooted continuously growing nature of the teeth. Characters of the incisor and premolar teeth and of the palate, cranial bones and mandible were found by Merrilees (1967) to be adequate to identify specimens from the modern fauna at the generic level only. He made no attempt to distinguish between taxa within *Lasiorhinus* using these characters.

A study by Crowcroft (1967) of variation in some cranial characters of geographically separate populations of *Lasiorhinus latifrons* from South Australia also indicated great intraspecific variability. However, he demonstrated some consistent differences between these populations on the basis of the configuration of the naso-frontal sutures and other skull features. He also considered these characters and some other cranial features as adequate to distinguish between *L. latifrons* and the Queensland hairy-nosed wombats, probably at the specific level.

Further assessment of intergeneric and intraspecific variation of cranial and dental characters of wombats has been undertaken in this study. Table 1 presents a summary of the non-metric characters used in this study for the assignment to genera

TABLE 2

Metric characters of the skull and teeth of wombats

NUMBER	
1.	Basicranial length
4.	Maximum length nasals
5.	Maximum length frontals
6.	Maximum posterior width nasals
7.	Width nasals at anterior edge of premaxilla
8.	Mid-line length of anterior nasal projection
9.	Depth of premaxillary suture between incisors
10.	Length of premaxillary/nasal suture
12.	Maxilla depth below origin of zygomatic arch (= ectalveolar plate of Owen 1872).
14.	Length upper cheek tooth row at level of alveolus
16.	Width of palate between posterior lobes M^2
17.	Maximum diameter of P^3
18.	Minimum diameter of P^3
19.	Width of enamel on upper incisor
20.	Depth of upper incisor
21.	Width of enamel of lower incisor
22.	Vertical depth of lower incisor
23.	Minimum diameter of P_3
24.	Maximum diameter of P_3
25.	Length of lower cheek tooth row at level of alveolus

TABLE 3

Cranial and dental dimensions (mm) of modern Vombatus ursinus. *Numbered characters are described in Table 2. Specimens are from the collections of the Australian Museum*

CHARACTER	M2258	S 799	M7485	M3378	M3709	M3360	M3044	M2958	M2339
1	131.0	140.0	135.0	160.0	162.0	162.0	150.0	140.0	161.0
4	57.5	66.0	58.0	67.0	73.5	71.5	69.5	65.0	73.0
5	54.0	56.0	53.0	64.0	—	69.0	65.0	61.0	—
6	36.5	41.5	46.0	51.0	47.0	51.0	48.0	47.0	53.0
7	11.0	14.5	12.0	17.0	17.5	17.0	17.0	20.0	19.0
8	6.5	8.0	9.0	11.0	10.0	10.0	8.0	12.0	10.0
9	7.0	7.0	6.0	7.0	8.0	8.0	10.0	7.0	8.0
10	33.5	40.5	36.5	43.0	50.0	48.5	44.0	37.0	47.5
12	12.0	12.0	11.0	12.5	12.5	13.0	12.5	13.5	12.0
14	44.0	45.5	43.0	51.5	50.0	52.0	48.0	46.0	53.0
16	5.5	4.5	5.5	7.0	7.0	7.0	6.0	5.0	5.0
17	7.5	6.0	5.5	7.0	7.5	7.5	7.5	6.2	7.0
18	5.3	4.8	4.8	6.5	6.2	6.0	6.0	4.6	6.5
19	9.3	10.0	8.6	11.5	10.7	11.0	10.0	10.2	11.3
20	4.7	5.3	5.2	6.5	6.2	6.5	5.8	5.8	6.1
21	7.0	7.2	6.5	8.8	8.1	8.5	7.0	8.3	8.3
22	5.5	6.2	6.0	8.0	7.3	6.6	6.8	7.0	7.0
23	5.5	5.5	5.5	6.5	6.7	6.5	6.5	6.0	6.4
24	4.0	4.0	3.9	5.0	5.0	5.0	4.5	4.5	4.8
25	45.5	45.5	—	52.0	53.3	53.0	49.0	47.5	54.5
	Flinders Is., SA 1919	Tasmania	Flinders Is., SA 1929	Oberon, NSW	Oberon, NSW	Mittagong, NSW	Mt Darrah, Cooma, NSW	Mt Darrah, Cooma, NSW	Batlow, NSW

TABLE 4

Cranial and dental dimensions (mm) of modern Lasiorhinus latifrons *from South Australia*
Specimens are from the collections of the Australian Museum. Numbered characters are described in Table 2

CHARACTER	M8024	M8026	M8027	M8028	M8029	S 801	S 787
1	148.0	157.0	156.0	149.0	136.0a	—	158.0
4	54.0	60.0	61.0	55.0	52.0a	60.0	60.0
5	69.0	—	67.0	65.0	58.0a	66.0	63.0
6	59.0	59.0	59.0	51.0	57.0	63.0	58.0
7	30.0	25.0	24.0	26.0	28.0	25.0	26.0
8	15.5	16.3	14.5	14.8	11.5	15.0	18.0
9	16.0	16.0	16.0	16.0	14.0	15.5	16.0
10	26.0	26.0	24.0	22.0	20.0	23.5	21.0
12	18.5	20.0	20.0	20.0	15.0	18.5	18.5
14	45.0	49.0	51.0	49.0	43.0	50.0	52.5
16	12.0	11.0	12.0	11.0	8.0	10.0	9.0
17	8.0	7.0	7.8	7.0	7.0	8.0	—
18	5.5	6.0	5.7	6.0	5.0	6.1	—
19	9.0	9.8	9.7	9.8	8.5	—	10.0
20	7.0	7.2	7.2	7.5	6.5	—	7.5
21	5.7	6.0	5.9	5.9	4.7	6.1	5.8
22	6.8	7.6	7.2	7.4	5.8	7.1	8.0
23	5.1	5.9	5.5	5.0	5.5	5.7	5.8
24	5.5	6.0	6.0	5.1	4.8	5.5	6.2
25	45.0	—	52.0	49.0	43.0	48.0	50.0
	Portee, SA	Portee, SA	Portee, SA	Portee, SA	Portee, SA	No location	South Australia

of incomplete fossil fragments. These have been selected from those used by Owen (1846, 1872a), Merrilees (1967) and Crowcroft (1967). In addition, 19 metric characters have been defined in Table 2.

Tables 3 and 4 present data for these characters for modern *V. ursinus* and *L. latifrons*. Measurements were made on skulls in the collection of the Australian Museum. These data are summarized with the sample mean ($\overline{X}$), standard deviation(s), and coefficient of variation (CV) for each character in Table 5. The relatively high values obtained for CV of *V. ursinus* reflect the geographic heterogeneity of the sample, as well as the high degree of intraspecific variability noted by Merrilees (1967). Skulls of modern Queensland wombats in the collections of the Queensland Museum were also measured. These include the type of *Lasiorhinus barnardi* from Clermont (QM 6239) and three syntypes of *L. gillespiei* from Moonie River (QM J13145, J13144, J13143). Three wombat skulls from Deniliquin, New South Wales, were measured from the collections of the National Museum of Victoria. These data are presented in Table 6.

The diagnostic value, at the species level, of some of these characters is suggested by the separation of the species of modern wombats into clusters in bivariate scattergrams, some examples of which are shown in Fig. 1. The data indicate that several of the characters measured here distinguish between at least two modern species of *Lasiorhinus*. Thus, the wombats from Clermont, Moonie River, and Deniliquin can be distinguished from *L. latifrons* from South Australia by having the nasals longer relative

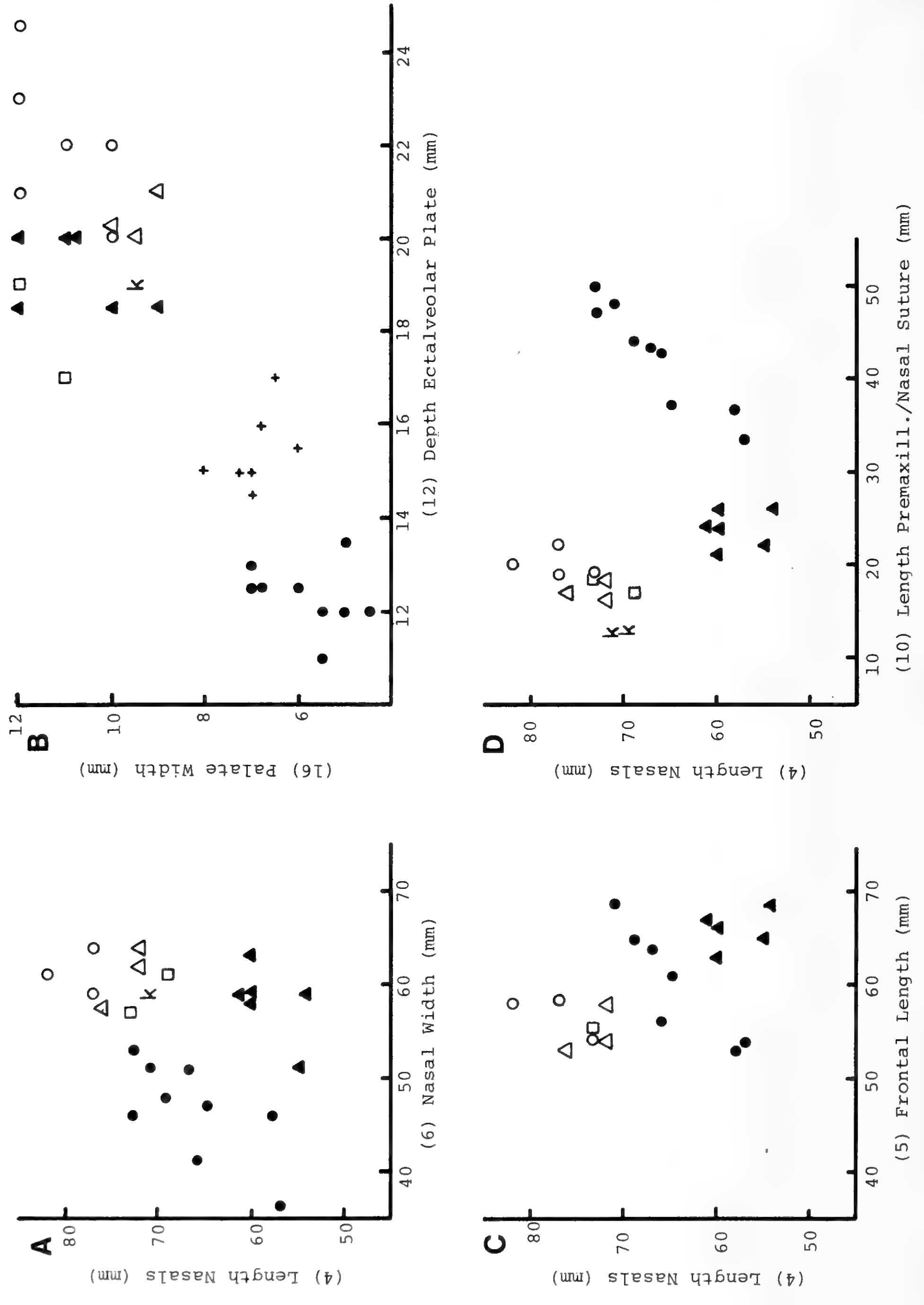

Fig. 1. Bivariate scattergrams illustrating clustering of three species of modern wombats, and some fossil specimens, using selected skull characters. The species are indicated as follows: • *Vombatus ursinus,* + *V. ursinus mitchellii* (Wellington Caves), ▲ *Lasiorhinus latifrons* (South Australia), △ *L. krefftii* (Moonie R.), ○ *L. krefftii* (Clermont), □ *L. krefftii* (Deniliquin), 'k' *L. krefftii* (Wellington Caves). Data from Tables 3, 4, 5, 6.

TABLE 5

Statistical summary of cranial and dental dimensions (mm) of modern Lasiorhinus latifrons *and* Vombatus ursinus
Data are from Tables 3 and 4. Numbered characters are described in Table 2

	Vombatus ursinus					*Lasiorhinus latifrons*				
CHARACTER	N	$\overline{X}$	O.R.	S	C.V.	N	$\overline{X}$	O.R.	S	C.V.
1	9	149.0	131.0–162.0	12.7	8.8	6	150.7	136.0–158.0	8.3	5.8
4	9	66.8	57.5–73.5	5.9	9.1	7	57.4	52.0–61.0	3.6	6.7
5	7	60.3	53.0–69.0	6.1	10.4	6	64.7	58.0–69.0	3.8	6.1
6	9	46.8	36.5–53.0	5.1	11.3	7	58.0	51.0–63.0	3.6	6.5
7	9	16.1	11.0–20.0	3.0	19.4	7	26.3	24.0–30.0	7.8	8.1
8	9	9.4	6.5–12.0	1.7	18.1	7	15.1	11.5–18.0	2.0	13.6
9	9	7.6	6.0–10.0	1.1	15.3	7	15.6	14.0–16.0	0.8	5.0
10	9	42.3	33.5–50.0	5.8	14.2	7	23.2	21.0–26.0	2.3	10.5
12	9	12.3	11.0–13.5	0.7	6.0	7	18.6	15.0–20.0	1.8	9.9
14	9	48.1	43.0–50.0	3.7	7.9	7	48.5	43.0–52.5	3.4	7.2
16	9	5.8	4.5–7.6	1.0	17.2	7	10.4	8.0–12.0	1.5	15.1
17	9	6.9	5.5–7.5	0.8	11.1	6	7.5	7.0–8.0	0.5	7.2
18	9	5.6	4.8–6.5	0.8	13.9	6	5.7	5.5–6.1	0.4	7.7
19	9	10.3	8.6–11.5	0.9	9.4	6	9.5	8.5–10.0	0.6	6.4
20	9	5.8	4.7–6.5	0.6	10.9	6	7.2	6.5–7.5	0.4	5.4
21	9	7.7	6.5–8.8	0.8	10.7	7	5.7	4.7–6.1	0.5	8.6
22	9	6.7	5.5–8.0	0.7	11.1	7	7.1	5.8–8.0	0.7	10.2
23	9	4.5	3.9–5.0	0.5	10.5	7	5.6	4.8–6.2	0.5	9.6
24	9	6.1	5.5–6.7	0.5	8.5	7	5.5	5.0–5.9	0.3	6.5
25	8	50.3	45.5–54.5			6	47.8	43.0–52.0		

to their width (characters 4, 6) and relative to the length of the frontals (character 5); by the longer anterior projection of the nasals (character 8); by the shorter premaxillary/nasal suture (character 10); and by the wider I^1 (character 19). The Moonie River and Deniliquin wombats agree with each other and differ from *L. latifrons* in consistently having a backward projection of the nasals at their median suture with the frontals, although the form of this suture differs considerably in detail between individuals (e.g. QM J13143 and QM J13144). A median backward projection of the nasals into the frontals was not observed in any specimen of *L. latifrons* in either the Australian Museum or the South Australian Museum.

Skulls of the Clermont wombats are slightly larger than those from Moonie River and Deniliquin, but cluster close to those populations in the bivariate scattergrams. However, they differ consistently from the other two populations in all having a forward projection of the frontals into the nasals at their median suture. All Clermont specimens also possess a narrow posterior extension of the maxillae to form a short suture with the frontals. However, this character is not diagnostic for the Clermont wombats, having been observed as a rare variant in *L. latifrons* (e.g. SAM M8029) and in the Deniliquin wombats (e.g. NMV C6228).

Very few characters of the mandible could be shown to have taxonomic value at the species level. Merrilees (1967) has pointed out the great variability within *L. latifrons* in the depth of the masseteric fossa and presence or absence of a masseteric canal, as well as the level of origin of the coronoid process. These are all characters used by Owen. Although these characters are diagnostic at the generic level in modern wombats, the degree of intraspecific variability is insufficiently understood at the species level. No clear distinguishing features could be found between the mandibles of *L. latifrons* from South Australia and the Queensland and Deniliquin wombats. For example, depth of the masseteric fossa was variable in the specimens from Moonie

TABLE 6

Cranial and dental dimensions (mm) of modern Lasiorhinus krefftii *from New South Wales and Queensland Specimens are from the collections of the Queensland Museum and the National Museum of Victoria. Numbered characters are described in Table 2*

CHARACTER	QM J6239	QM J14051	QM J20354	QM J6283	QM J6284	QM J6240	QM J13143	QM J13145	QM J13144	NMV C6230	NMV C6228	NMV
1	169.0	171.0	172.0	—	171.0	162.0	156.0	160.0	158.0	155.0	155.0	155.0
4	77.0	77.0	82.0	73.5	—	—	76.0	72.5	72.0	—	73.0	69.0a
5	58.0	58.0	58.0	54.5	55.5	60.0	53.0	54.0	58.0	55.0	55.0	—
6	64.0	59.0	61.0	—	52.0a	52.0	57.5	62.0	64.0	60.0	57.5	61.0a
7	43.5	35.6	37.0	—	34.0	34.0	31.0	35.0	34.0	30.0	28.0	30.0
8	27.0	25.0	25.0	25.0	—	—	23.0	23.0	24.0	—	22.0	23.0
10	19.2	22.2	20.0	19.0	23.5	17.0a	17.5	18.0	16.0	18.0	19.0	17.5
12	24.8	21.0	22.0	23.0	22.5	20.0	20.0	21.0	20.0	19.0	17.0	18.0
14	58.0	54.5	57.0	—	56.5	56.0	47.0	51.0	50.0	48.5	53.0	52.0
16	12.0	12.0	11.0	12.3	10.0	10.0	10.0	9.0	9.5	12.0	11.0	14.0
17	7.5	7.2	—	—	—	—	—	—	6.8	7.5	—	7.0
19	10.3	11.0	11.5	10.5	11.0	10.0	9.5	10.0	9.5	10.5	—	11.4
20	8.5	7.3	7.5	8.8	8.0	9.0	7.7	8.5	7.8	7.3	—	8.0
21	7.7	7.4	7.7	7.5	—	—	—	—	6.3	6.5	—	7.0
22	9.1	9.0	9.2	8.2	—	—	—	—	7.2	7.4	—	8.5
23	5.8	5.9	5.8	5.5	—	—	—	—	5.3	4.8	5.3	5.1
	Clermont, Qld	Clermont, Qld	Clermont, Qld	Clermont, Qld	Clermont, Qld	Clermont, Qld	Moonie R., SE Q.	Moonie R., SE Q.	Moonie R., SE Q.	Deniliquin, NSW	Deniliquin, NSW	Deniliquin, NSW

River, being very shallow and non-perforate in QM J13145, but deeper and possessing a small masseteric canal in QM J13144. The ectalveolar groove extended as far forward as the posterior lobe of M_4 in the Queensland wombats studied here, agreeing with the majority of specimens of *L. latifrons* from South Australia (Merrilees, 1967). It extended slightly further forward, to the anterior lobe of M_4, in the three specimens examined from Deniliquin. It is concluded that it is not possible to use these mandibular characters to distinguish species within either genus of living wombats.

It must be assumed that the difficulties encountered in using characters of the teeth and jaws of modern wombats for taxonomic purposes also apply to fossil genera and species especially those most closely related to modern forms. With few exceptions, fossil taxa have been described from incomplete and unassociated jaw fragments only, however some cranial bones are known. Postcranial bones have not been studied. At present, fossil wombat taxonomy is heavily dependent on morphological features of the incisor and premolar teeth, the shape and proportions of the palate, and the morphology and proportions of the most anterior bones of the cranium.

In this study the status is reviewed of fossil vombatid species similar to living wombats in size. For two of these, *Phascolomys mitchellii* Owen and *Phascolomys krefftii* Owen, relatively large samples are available from their type locality, Wellington Caves, New South Wales. These samples have permitted detailed study of variability in the fossil taxa under review.

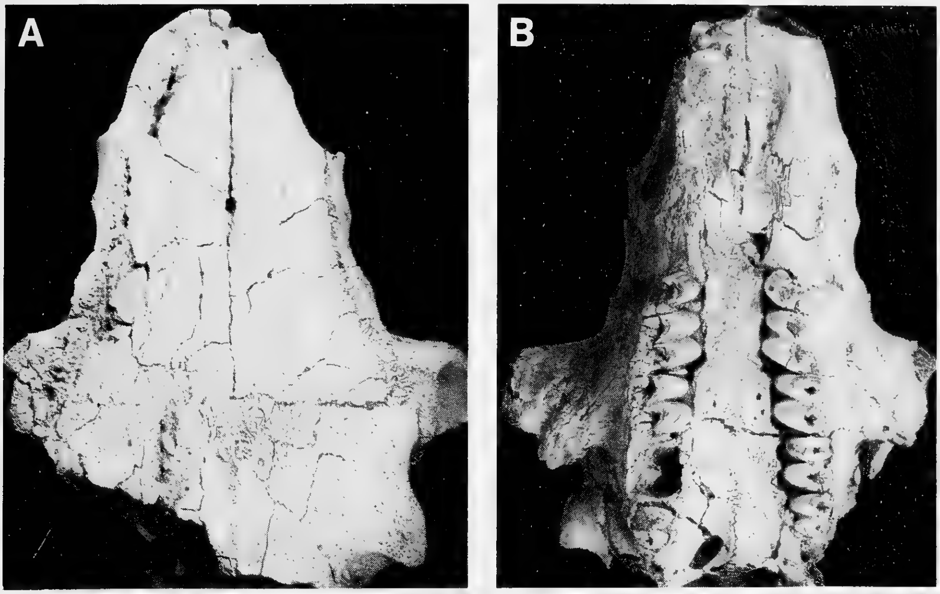

Fig. 2. Skull, AM F58703 of *Vombatus ursinus mitchellii* (Owen, 1838) from Wellington Caves. **A**. Dorsal view. **B**. Palatal view, with alveoli for left and right P^3, M^{2-5}.

SYSTEMATICS

Genus *VOMBATUS* Geoffroy, 1803

Vombatus ursinus (Shaw, 1800)

Synonymy: Fossil taxa in the synonymy of *Vombatus ursinus* Shaw are *Phascolomys mitchellii* Owen, 1838, *Phascolomys parvus* Owen, 1872, *Phascolomys pliocenus* McCoy, 1866 and *Phascolomys thomsoni* Owen, 1872.

i) *Phascolomys mitchellii* Owen, 1838

The type locality of *Phascolomys mitchellii* is given as 'Wellington Valley', New South Wales (Owen in Mitchell, 1838). However, Owen (1872a) is more specific, listing the origin of the syntypes as the Breccia-cavern, Wellington Valley. The four syntypes of *Phascolomys mitchellii* are present in the Sir Thomas Mitchell Collection of the British Museum (Natural History). Mahoney and Ride (1975) have discussed at length the problem of the exact origin of specimens in this collection, and have concluded that the possibility that some of them originated from Buree (or Boree), also in the Wellington Valley, cannot be discounted. One syntype, BM M10791, a mutilated cranium (figured Mitchell, 1838, pl. 30, fig. 4) has been selected here as the lectotype of *Phascolomys mitchellii* Owen. Paralectotypes are BM M10792, a partial right mandibular ramus (ibid. fig. 5); BM M10793, a right maxillary tooth row (ibid. fig. 6); and BM M10794, a right mandibular fragment with I_1 broken off, P_3-M_5 (ibid. fig. 7). Three other specimens from Wellington jcaves referable to this subspecies were noted by Owen (1872a). These are BM 42598, a mutilated cranium (ibid. pl. 17, figs 1, 3, 4, 5); BM 42612, an edentulous right maxillary fragment (ibid. pl. 17, figs 7, 8); and BM 42604, a left mandibular fragment (ibid. pl. 19, fig. 5; pl. 21, figs 5, 6). The Australian Museum collection from Wellington Caves includes six fragments of the skull and upper jaws: AM F58703 (Fig. 2**A-B**), F5372, F5398, F5380, F5378, MF730; and

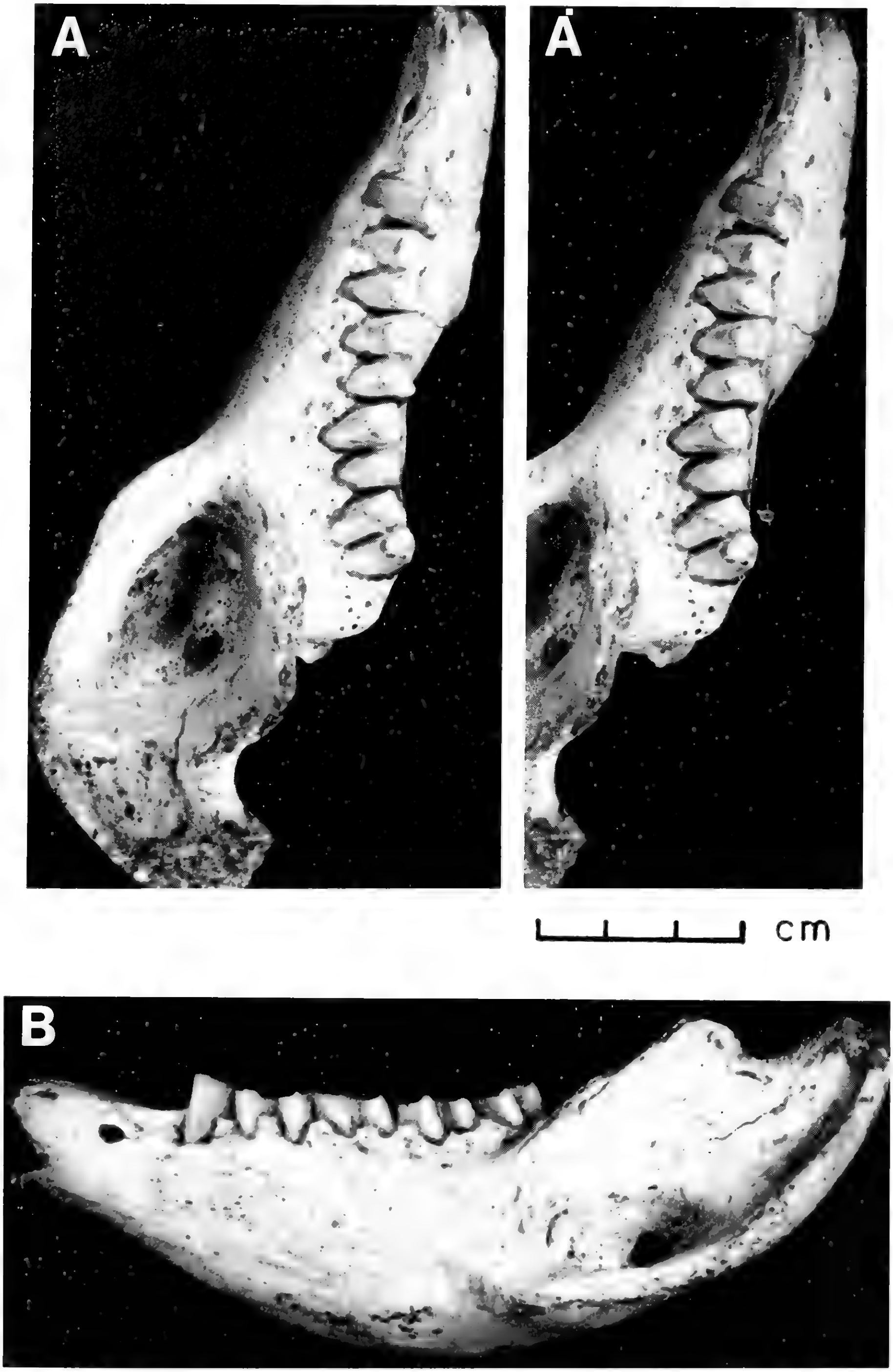

Fig. 3. A left mandibular ramus, AM F31055 of *Vombatus ursinus mitchellii* (Owen, 1838) from Wellington Caves. **A, A'**. Stereopair of occlusal view with P_3, $M_{2\text{-}5}$. **B**. Labial view.

TABLE 7

List of specimens of Vombatus ursinus mitchelli *from Wellington Caves in the Australian Museum (AM numbers) The Table indicates the characters which are present in each specimen in the state diagnostic for the genus* Vombatus. *These characters are described in Table 1*

SPECIMEN NUMBER	DESCRIPTION	CHARACTERS DIAGNOSTIC FOR *VOMBATUS*
F58703	Crushed cranium, I^1 broken, edentulous	1, 5, 7
F5372	Partial skull, with left and right P^3-M^5	4, 5, 7
F5398	Partial palate, with left P^3-M^5	4, 5
F5380	Partial palate, edentulous	5
F5378	Palate fragment, edentulous	4, 5, 6
F5383	Right maxillary fragment $M^{2\text{-}5}$	5
MF730	Right maxillary fragment M^2	6
F35406	Left mandibular ramus, I_1, P_3-M_5	9, 11, 12, 13, 15p
F58707	Right mandibular ramus, I_1	9, 10, 12, 13, 15p
F18866	Left and right mandibular rami, $I_{1\text{-}1}$	9, 10, 12, 13
F31055	Left mandibular ramus, I_1, P_3-M_5	9, 10, 12, 15p
MF720	Right mandibular ramus, P_3-M_5	11, 12, 13, 15np
F58705	Left mandibular ramus, I_1, $M_{2\text{-}5}$	9, 12, 15np
F5390	Right mandibular ramus, P_3-M_5	11, 12, 14, 15p
MF721	Right mandibular ramus P_3-M_5	11, 12, 15p
MF723	Right mandibular ramus, $M_{2\text{-}5}$	12, 15p
F35404	Left mandibular ramus $M_{2\text{-}5}$	12, 15p
F5386	Right mandibular ramus, M_4	12, 15p
F5381	Right mandibular ramus, $M_{4\text{-}5}$	12, 15np
F5373	Left mandibular ramus, edentulous	12, 15np
MF105	Left mandibular ramus I_1	9, 11, 13, 14, 15np
F5382	Left mandibular ramus, $M_{2\text{-}4}$	12, 15np
F58706	Right mandibular ramus, edentulous	9, 10, 12, 15np
F5401	Left mandibular ramus, I_1,$M_{3\text{-}5}$	9, 12, 14, 15np
F5387	Right mandibular ramus, edentulous	12, 15p
F53719	Left mandibular fragment, P_3-M_4	11, 12, 15p
F5377	Left mandibular ramus I_1, $M_{3\text{-}5}$	9, 12, 15p
F5332	Right mandibular fragment, P_3-M_5	11, 12, 14, 15p

p = perforate, np = non-perforate.

twenty two mandibular fragments: AM F35406, F58707, F18866, F31055 (Fig. 3**A-B**), MF720, F58705, F5390, MF723, MF721, F35404, F5386, F5381, F5373, MF105, F5382, F58706, F5401, F5387, F5315, F5332, F53719, F5377, which are referable to a species of *Vombatus*. These specimens are described in Table 7, in which the characters enabling each to be referred to a species of *Vombatus* are noted.

Measurements and Comparisons. Fossil material from Wellington Caves has been compared with a sample of 9 skulls of modern *jvombatus ursinus* from New South Wales, Tasmania, and South Australia (Table 3), and with observations of that species by Merrilees (19673. Metric data of taxonomic importance for the modern species are summarized in Table 5. The corresponding data for the fossil sample are presented in Table 8 and 9.

Data for the fossil sample generally fall within, or close to, the observed ranges for the same characters in modern *V. ursinus* with the exception of the values for character 12, the depth of the ectalveolar plate of the maxilla. This is deeper in all of the fossil specimens (see Fig. 1**B**). Thus fossil specimens form a discrete cluster in all bivariate

TABLE 8

Dimensions (mm) of the upper dentition, palate and cranial bones of Vombatus ursinus mitchelli *from Wellington Caves Numbered characters are described in Table 2. Specimen numbers refer to the Australian Museum collection (AM)*

CHARACTER	MF730	F58703	F5372	F5398	F5380	F5378	F5383
6	—	50.0	—	—	—	—	—
10	—	47.0	—	—	—	—	—
12	14.5	17.0	15.3	16.0	15.5	15.0	15.0
14	49.0	50.0	44.5	47.3	—	54.5	49.0
16	7.0a	6.5	7.3	5.8	6.0	8.0	7.0a
19	—	9.0	—	—	—	—	—
20	—	6.5	—	—	—	—	—

(a) approximate measurement.

comparisons involving character 12. The fossil specimens cluster with *V. ursinus* in all other bivariate comparisons. Only two cranial specimens, F58703 (Fig. 2**A-B**) and BM 42598 Owen 1872a, pl. 17, figs 1, 3, 4, 5), exhibit the taxonomically important maxillae, frontals and premaxillae. In both these specimens the form and estimated length of the nasals and the proportional lengths of the premaxillary/nasal and maxillary/nasal sutures agree closely with the condition in modern *V. ursinus.* The extremely short maxillary/frontal suture, which was noted by Owen (1872a), appears to be more characteristic of modern mainland *V. ursinus* than the Tasmanian or Flinders Island races, although the full range of possible variation in these characters has not been studied here. The dentition and palate of the fossil specimens are indistinguishable morphologically from modern *V. ursinus.*

While the mandibular fragments from Wellington Caves have been referred to the genus *Vombatus* on the basis of the character states listed in Table 7, they are extremely fragmentary and exhibit no characters that indicate significant variation from modern *V. ursinus.* All measurements (Table 9) fall within, or close to the observed ranges of values for modern *V. ursinus.*

Discussion. Owen (1872a) recognized close similarity between the extinct *Phascolomys mitchellii* and the 'platyrhine' wombats (i.e. the mainland Common Wombat and the Tasmanian Wombat) in most features of the dentition and anterior cranial bones. However, he considered them to be specifically distinct on the basis of possession of certain character states typical of 'latifront' (i.e. *Lasiorhinus* sp.) wombats. These include a supposed shorter maxillary/nasal suture, the more deeply concave anterior palate, and the greater vertical depth of the maxilla beneath the anterior root of the zygomatic arch (the 'ectalveolar plate'). Similarly, he considered that the mandibular fragments exhibited a slightly more anterior origin for the coronoid process, and more forward posterior termination of the symphysis relative to the molar teeth, features that he considered to be more characteristic of 'latifront' wombats. However, the present study and the work of Merrilees (1967) have indicated that such variability is characteristically found both within and between modern populations of *V. ursinus,* with the exception of character 12, the depth of the ectalveolar plate of the maxilla, which is consistently greater in the fossils than in any modern specimens.

In view of the high degree of variability found in this study for a geographically heterogeneous sample of modern *V. ursinus* (Table 5) Tate's (1951) decision to recognize the following subspecies may be justified: *Vombatus ursinus ursinus* (Shaw, 1880) from Flinders Island; *V. u. tasmaniensis* (Spencer & Kershaw, 1910) from

TABLE 9

Dimensions (mm) of the mandible and lower teeth of Vombatus ursinus mitchelli *from Wellington Caves Numbered characters are described in Table 2. Specimen numbers refer to the Australian Museum collection (AM)*

SPECIMEN	CHARACTER 21	22	23	24	25
F35406	9.0	8.0	4.5	6.7	51.0
F58707	7.9	7.2	—	—	47.5
F18866	8.5	8.0	—	—	—
F31055	—	—	4.7	6.8	53.5
MF721	—	—	4.3	5.7	47.0
F5373	—	—	—	—	56.5
MF720	—	—	4.5	—	52.0
F5390	—	—	3.7	—	47.0
F5401	—	—	—	—	53.0
F35404	—	—	—	—	44.0
F332	—	—	—	—	51.0
F58706	—	—	4.5	6.7	51.0
F58705	—	—	—	—	46.0
MF105	—	—	4.3	6.7	54.0
F5379	—	—	4.5	—	47.5

Tasmania, and *V. u. platyrhinus* (Owen, 1853) from eastern mainland Australia. jhowever, a more comprehensive study, possidly considering serological, isozyme or chromosomal characters, is needed to clarify the taxonomic satus of modern wombat populations. The present study has demonstrated at least one distinctive morphological character (depth of the ectalveolar plate of the maxilla) in the Wellington Caves fossils. Thus it is considered here that recognition of the fossil population from Wellington Caves as a subspecies, *V. ursinus mitchellii* (Owen, 1838), is warranted on the basis of present knowledge.

Although the mandibular fragments from Wellington Caves are indistinguishable from modern *V. ursinus* they have also been referred here to *V. u. mitchellii* as part of the topotypical sample, since the sparse data do not justify the recognition of more than one subspecies of *V. ursinus* in this fauna.

Specimens referable to species of *Vombatus,* and similar in size to modern *V. ursinus* have been reported from many other Pleistocene deposits in mainland Australia and from Tasmania. Since it has not been possible to include them in this study their specific or subspecific status is unknown.

ii) *Phascolomys parvus* Owen, 1872

Merrilees (1967) selected BM No. 32893, a partial left mandibular ramus from the eastern Darling Downs, Queensland, as a lectotype of *P. parvus* from four mandibular syntypes described and figured by Owen (1872). While Owen (1872) regarded these as specifically distinct because of their small size, Merrilees (1967) has shown that they represent juvenile specimens, and as such has demonstrated that *P. parvus* Owen is a junior synonym of *Vombatus ursinus* (as *V. hirsutus*). That BM 32893 is referable to a species of *Vombatus* is confirmed by the anterior extent of the 'ectalveolar groove' and deep masseteric fossa (characters 12 and 15, respectively in Table 1). The fossil material exhibits no taxonomic characters sufficient for further identification. It is concluded that *P. parvus* Owen is a junior synonym of *Vombatus ursinus* (Shaw).

iii) *Phascolomys pliocenus* McCoy, 1866

The holotype of *P. pliocenus* McCoy is a mandibular ramus, NMV P7422 from Dunolly, Victoria (see Mahoney and Ride, 1975). This specimen has been redescribed and refigured by Wilkinson (1978) who has presented evidence supporting the correct reference of this specimen, and others referred to *P. pliocenus* by McCoy (1874) to *Vombatus ursinus* (as *V. hirsutus*). According to criteria described in the present study NMV P7422 agrees with *V. ursinus* in size, and with a species of *Vombatus* according to characteristics of the masseteric fossa (characters 12, 14, 15 of Table 1). Other diagnostic characters are obscured by adhering matrix in this specimen. Two other specimens were referred to *P. pliocenus* by McCoy (1874), these being two partial mandibles, NMV P7441 and NMV P7442 from Lake Bullenmerrie, Victoria. Wilkinson (1978) has refigured these specimens, but they are mislabelled in plate 17 of that paper. The correct labelling should show pl. 17, figs 1 and 2 to represent NMV P7441, while pl. 17, figs 3 and 4 represent NMV P7442. These specimens have been examined by me. Both exhibit character states of the masseteric fossa and premolar and incisor teeth diagnostic for a species of *Vombatus* (characters 10-15, Table 1), probably *V. ursinus,* as suggested by Wilkinson (1978). The lower incisors of NMV P7442 vary slightly from *V. ursinus* as described here and by Merrilees (1967) in that they are somewhat more spatulate in cross section, and in that the enamel does not entirely cover the outer face of the tooth. Dimensions of I_1 of NMV P7442 are width = 0.8 mm, depth = 7.5 mm. Reference to Table 5 indicates these are within the range of *Vombatus ursinus*.

The name *Phascolomys pliocenus* McCoy is therefore considered to be a junior synonym of *Vombatus ursinus* Shaw. However, the holotype and other mandibular fragments described by McCoy (1874) cannot be referred to any subspecies of *V. ursinus* on the basis of present understanding of the characters they exhibit.

iv) *Phascolomys thomsoni* Owen, 1872

The holotype of *P. thomsoni* is a partial right mandibular ramus, probably from the eastern Darling Downs, Queensland (Mahoney and Ride, 1975), figured by Owen (1872, pl. 18, figs 8, 9; pl. 21, fig. 7). Owen (1872) recognized the similarity of this specimen to the modern 'platyrhine' wombat, but diagnosed the species solely on its possession of narrower molars than *P. mitchellii* and *P. platyrhinus*. Merrilees (1967) has demonstrated that this character does not distinguish between modern wombat species, even at the generic level. It cannot, therefore, suffice to describe a species of *Vombatus*. It is concluded, therefore, that *P. thomsoni* Owen is a junior synonym of *Vombatus ursinus* Shaw, supporting De Vis (1891) who had suggested its synonymy with *P. mitchellii*.

Vombatus hacketti Glauert, 1910

The holotype of *Phascolomys hacketti* Glauert is an incomplete skeleton including a cranium and mandible, no. 60.10.3 in the Western Australian Museum. The specimen is from the Pleistocene 'Le Soeuf deposit' of Mammoth Cave, Western Australia (Archer *et al.*, 1980). The skull, mandible and postcranial elements have been described in Glauert's original diagnosis of the species (Glauert, 1910). It was only possible to examine the edentulous skull (Fig. **4A-C**) during the present study. The dimensions of the skull for numbered characters described in Table 1 are as follows: 1) Basicranial length = 163.0 mm; 4) Maximum length nasals = 80.0 mm; 5) Maximum length frontals = 56.0 mm; 6) Maximum posterior width nasals = 48.0 mm; 7) Anterior width nasals = 11.0 mm; 8) Length anterior nasal projection = 10.5 mm; 10) Length premaxillary/nasal suture = 39.0 mm; 12) Depth ectalveolar plate of

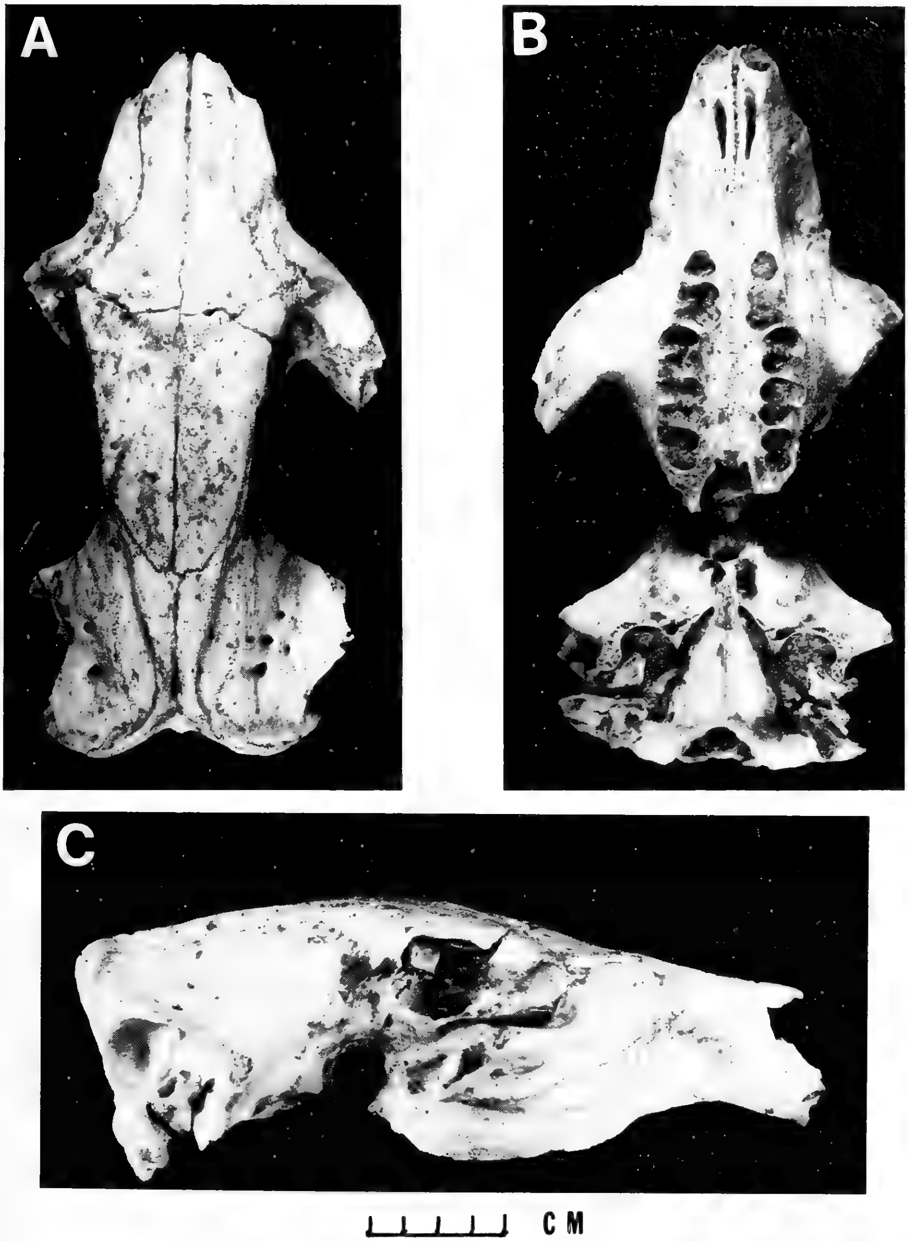

Fig. 4. Holotype skull of *Vombatus hacketti* (Glauert, 1910), Western Australian Museum No. 0.10.3 from Mammoth Cave, Western Australia. **A**, Dorsal view. **B**, Ventral view. **C**, Right lateral view.

maxilla = 17.5 mm; 14) Length upper cheek tooth row = 54.5 mm; 16) Width palate between posterior lobes of M_2 = 6.0 mm.

That this skull is referable to a species of *Vombatus* is supported by the following characters, as described in Table 1: 1) long narrow nasals; 4) grooved P^3; 5) narrow

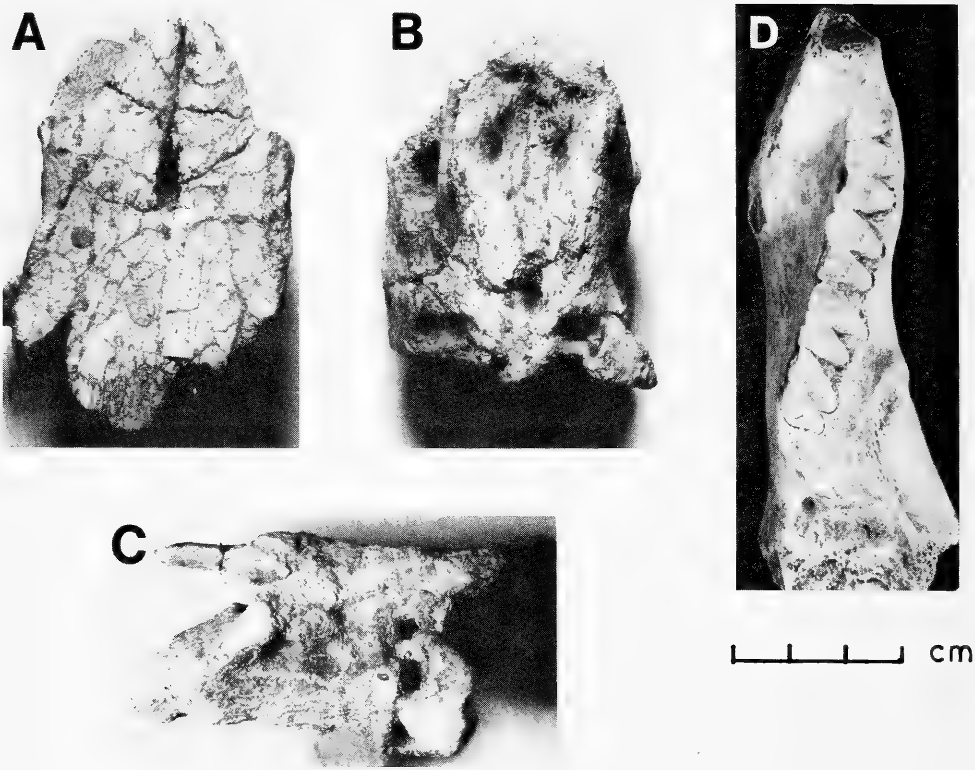

Fig. 5. Lasiorhinus krefftii (Owen, 1872) from Wellington Caves. **A**, holotype of *L. krefftii,* BM 42601, nasal and premaxillary region of the skull, dorsal view. **B**, BM 42601, ventral view. **C**, BM 42601, left labial view. **D**, right mandibular ramus, AM F35405, with P_3, $M_{2\text{-}5}$, occlusal view.

palate between $M^{2\text{-}2}$; 7) narrow flat anterior palate; 8) proportionately long premaxillary/nasal suture. The Mammoth Cave skull shows general agreement in size with modern *Vombatus ursinus* in most characters measured here (see Table 5). However, three characters distinguish it from modern *V. ursinus.* The nasals are absolutely and relatively longer than in any modern or fossil *V. ursinus* measured in this study (character 4, Tables 2 and 3); postorbital processes of the frontals are absent in *V. hacketti;* and the depth of the ectalveolar plate of the maxilla is greater than in modern *V. ursinus* (character 12, Tables 2 and 3). In this latter character *V. hacketti* resembles specimens from Wellington Caves, here ascribed to *V. ursinus mitchellii* (see Table 8). Further comparison between the two fossil forms is difficult, since in all specimens from Wellington Caves the bones of the nasal region are badly crushed and broken, and frontal bones are missing. Although the nasals of specimens from Wellington Caves cannot be measured, their estimated length is not greater proportionately than nasals of modern *V. ursinus.* Thus it appears that the Mammoth Cave skull is unique in having nasals which are much longer, both absolutely and relative to their width and to the length of the frontals. Glauert (1910) also noted that the skull of *V. hacketti* was characterized by greater intertemporal constriction than modern *V. ursinus.* There are no teeth in the holotype skull. The alveoli for I^1 suggest that these teeth are less triangular in cross-section than I^1 of modern *V. ursinus* or of *V. u. mitchellii* from Wellington Caves. Glauert (1910: 18) has described loose incisor teeth from

TABLE 10

List of specimens of Lasiorhinus krefftii *(Owen) from Wellington Caves in the Australian Museum (AM numbers) The table indicates the characters present in each specimen in the state diagnostic for the genus* Lasiorhinus. *These characters are described in Table 1*

SPECIMEN NUMBER	DESCRIPTION	CHARACTERS DIAGNOSTIC FOR *LASIORHINUS*
F35405	Right mandibular ramus, P_3, $M_{2\text{-}5}$	10, 11, 12, 14, 15p
F51851	Left and right mandibular rami, I_1 (broken), right P_3, $M_{2\text{-}5}$	10, 11, 14
F58704	Right mandibular ramus, I_1 (broken), P_3, $M_{2\text{-}5}$	9, 10, 12, 14
F5400	Anterior symphysis of mandibile, edentulous	10, 13
F5389	Right mandibular fragment, edentulous	12
F5393	Right mandibular fragment, $M_{3\text{-}5}$	12, 15p
F5394	Right mandibular fragment, P_3, $M_{2\text{-}4}$	11, 12
F5385	Right mandibular fragment, $M_{4\text{-}5}$	12, 15np
F5392	Right mandibular fragment, edentulous	12
F5388	Left mandibalar fragment, P_3, $M_{2\text{-}5}$	11, 12
F5391	Right mandibular fragment, edentulous	12, 15np
F51853/4	Left and right rami, right P_3, $M_{2\text{-}4}$	11, 12, 14, 15np
F5331	Right mandibalar fragment, P_3, $M_{2\text{-}5}$	11, 12, 15np
F5323/97	Left mandibular ramus, $M_{2\text{-}5}$	12
F5309	Right mandibular fragment $M_{3\text{-}5}$	12, 15p
F5320	Right mandibular fragment, P_3, $M_{2\text{-}5}$	11, 12, 15np
MF719	Crushed rostral region of skull with right I^1, left and right P^3, $M^{2\text{-}5}$	1, 2, 4, 5, 6, 8
F5403/4	Palate with left P^3, $M^{2\text{-}5}$, right P^3, $M^{2\text{-}3}$	4, 5, 6
F58702	Palate fragment, right P^3, $M^{2\text{-}5}$, left $M^{2\text{-}4}$	4, 5, 6

(p) perforate.
(np) non-perforate.

Mammoth Cave that '. . . have no sharp anterior edge, . . . their section, too, being broad and oval', supporting the suggestion from the holotype that I^1 of *V. hacketti* differs from that tooth in *V. ursinus.* Glauert (1910) has noted features of the sacrum and scapula which he considers to be uniquely characteristic of *V. hacketti.* These characters have not as yet been studied sufficiently to support their taxonomic value.

It is considered that the differences noted here between the Mammoth Cave skull and skulls of modern *V. ursinus* and the Wellington Caves fossil subspecies are sufficient for its recognition as a distinct species, *Vombatus hacketti* Glauert. The geographic and stratigraphic range of this species is yet to be investigated.

Genus *LASIORHINUS* Gray, 1863

Lasiorhinus krefftii (Owen, 1872)

Synonymy: *Phascolomys gillespiei* De Vis, 1900, *Lasiorhinus latifrons barnardi* Longman, 1939, *Phascolomys krefftii* Owen, 1872.

The holotype of *Phascolomys krefftii* Owen is a partial cranium with broken upper incisors, from the 'Breccia Cave', Wellington Caves, New South Wales, BM 42601 (Fig. 5**A-C**) (Mahoney and Ride, 1975). Paratypes are three mandibular fragments,

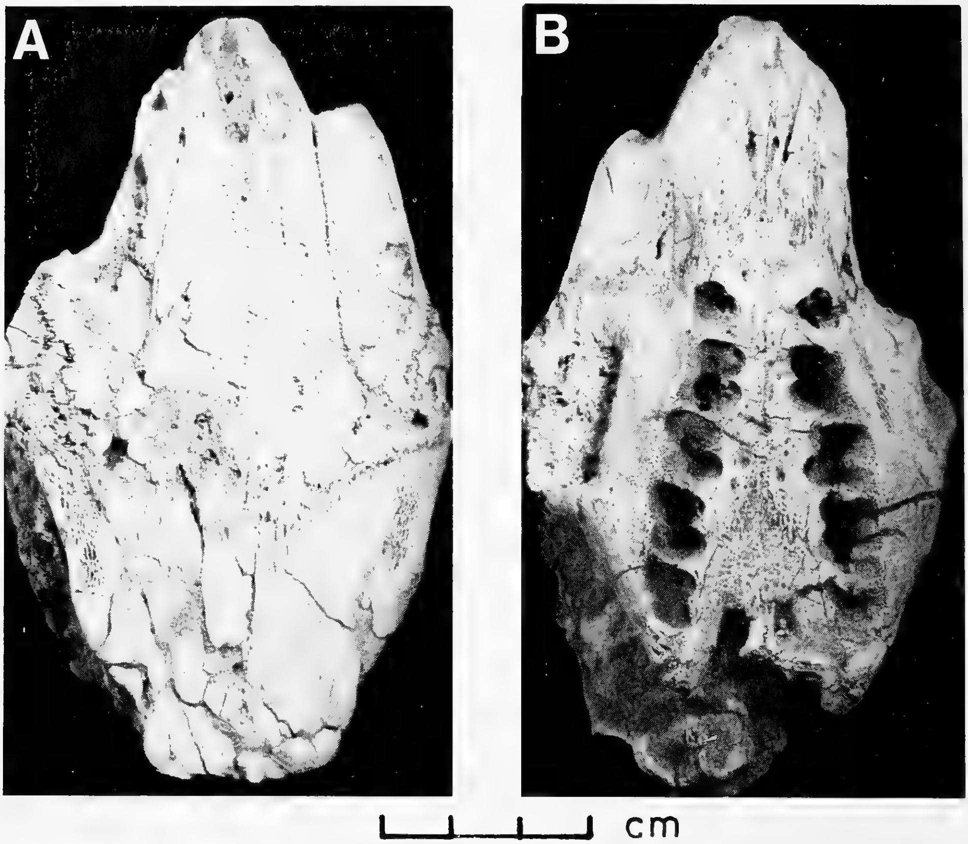

Fig. 6. The skull, AM MF719, of *Lasiorhinus krefftii* (Owen, 1872) from Wellington Caves. **A**, dorsal view. **B**, palatal view, with left and right $P_{3,}$, M_{2-3}, left M_4, and left and right M_5.

BM 42609 Owen 1872a pl. 19, fig. 4; pl. 21, fig. 4; pl. 22, fig. 4), BM 42610 ibid. pl. 19, fig. 3; pl. 22, fig. 6; pl. 23, fig. 5), and BM 42602 (ibid. pl. 20, fig. 2; pl. 23, fig. 4; pl. 22, fig. 7). The Australian Museum collection from Wellington Caves contains a further three fragments of the skull and maxilla: AM MF719 (Fig. 6**A-B**), F5403/4 and F58702; and sixteen mandibular fragments: AM F35405 (Fig. 5**D**), F51851, F58704, F5400, F5389, F5393, F5394, F5385, F5392, F5388, F5391, F51853/4, F5331, F5323/F5397, F5309, F5320, which have been referred to *L. krefftii*. These specimens are described in Table 10 which also lists the characters by which each has been identified as belonging to a species of *Lasiorhinus*.

Measurement and comparisons. Fossil material referable to *Lasiorhinus krefftii* (Owen) from Wellington Caves has been compared with skulls of modern hairy-nosed wombats from Clermont and Moonie River in Queensland and from Deniliquin in New South Wales (see Table 5) and with a sample of seven skulls of modern *L. latifrons* from South Australia (Table 4). Measurements for all metric characters of taxonomic importance evident in the fossil sample are given in Tables 11 and 12.

The fossil specimens, BM 42601 and AM MF 719, exhibit the taxonomically important nasal, maxillary and premaxillary bones, and the naso-frontal suture (Figs 5

TABLE 11

Dimensions (mm) of the cranium and upper dentition of Lasiorhinus krefftii *(Owen) from Wellington Caves*
Numbered characters are described in Table 2

CHARACTER	AM MF719	BM 42601	AM F58702	AM F5403/4
4	71.5	70.0a	—	—
6	59.0	—	—	—
7	38.5	36.0a	—	—
8	23.0	21.0	—	—
10	13.0	13.0a	—	—
12	16.0	—	19.0	21.0
14	52.5	—	48.0	48.5
16	10.5	—	9.5	8.5
17	—	—	7.5	8.0
18	5.6	—	5.0	5.0
19	10.8	—	—	—

(a) approximate measurement.

and 6). Both agree with specimens from Clermont, Moonie River, and Deniliquin and are distinct from *L. latifrons* from South Australia in the greater length, relative to the width, of the nasals (characters 4 and 6, Table 2); in the longer anterior projection of the nasals (character 8, Table 2); and the greater enamel width of I^1 (character 19, Table 2). In both fossil skulls the naso-frontal suture runs perpendicular to the long axis of the skull laterally, but is directed posteriorly toward the midline (i.e. there is a median backward projection of the nasals into the frontals) and is extremely convoluted toward the midline. AM MF719 shows the maxilla to have a narrow posterior extension which forms a short, convoluted suture with the frontal, as is found in one specimen from Deniliquin (NMV C6228), in all skulls from Clermont, and as occasionally found in *L. latifrons* from South Australia (e.g. AM M8092). The anterior projection of the nasals (character 8, Table 2) is relatively longer in the fossils than in *L. latifrons,* within the observed range of values for specimens from Moonie River and Deniliquin, but shorter than in specimens from Clermont. Neither specimen from Wellington Caves exhibits any downward deflection of the anterior nasal projection, a character state found in the skulls from Queensland and Deniliquin.

Of the fragmentary fossil mandibular specimens here referred to *L. krefftii* (see Table 10) few possess taxonomically useful metric characters. All available data are presented in Table 12. One specimen, F58704, has I_1 deeper and wider (characters 21 and 22, Table 2) than observed in modern *L. latifrons,* but within the observed range of Clermont wombats. Other data fall within the observed range of *L. latifrons* from South

TABLE 12

Dimensions (mm) of the lower teeth of Lasiorhinus krefftii *(Owen) from Wellington Caves*
Numbered characters are described in Table 2

CHARACTER	AM F35405	AM F51851	AM F58704	AM F5331	AM F5320
21	—	—	7.5a	—	—
22	—	—	9.0a	—	—
23	5.3	5.7	—	5.1	4.6
25	52.0	50.0	54.0	47.5	47.1

(a) approximate measurement.

Australia. The ectalveolar groove of the fossil specimens extends forward to the anterior lobe of M_4 (as observed in the Deniliquin wombats) except in F51853/4, where it only reaches the posterior lobe of that tooth. The masseteric fossa is relatively shallow in the fossils and non-perforate, except in AM F35405, F5393, and F5309, in which a small masseteric foramen is present.

Discussion. Owen (1872a) named the species *Phascolomys krefftii* on the basis of a single crushed cranium (the holotype), and several mandibular fragments from the Wellington Caves. He recognized the close similarity of the holotype to the modern species, *Lasiorhinus latifrons* and noted, as the sole distinguishing feature of this cranium, the posteriorly-directed projection of the nasals at their median suture with the frontals (Owen, 1872a: 178). He distinguished the referred mandibular fragments from *L. latifrons* by the more backward extent of the symphysis, by the slightly longer and deeper ectalveolar groove, by some slight variations in the shape of the ridges bounding the non-perforate masseteric fossa, and on his assessment that the molar teeth were narrower than in *L. latifrons.* In the same publication he stated that other mandibular fragments from Wellington Caves were indistinguishable from modern *L. latifrons.* The larger sample available in the present study supports the distinction of the Wellington Caves fossils from modern South Australian *L. latifrons,* the only living species of *Lasiorhinus* known to Owen.

Wilkinson (in Merrilees, 1973) proposed the synonymy of *Lasiorhinus krefftii* and the modern Queensland species, *L. barnardi* and *L. gillespiei,* but presented no supporting data. While some differences in size and anatomical detail have been recorded here between the skulls of the hairy-nosed wombats from Clermont, Moonie River, and Deniliquin, this is comparable in degree to differences found by Crowcroft (1967) between geographic races of *L. latifrons* from South Australia and to the differences indicated here, and by Merrilees (1967) between sub-species of *Vombatus ursinus.* Therefore the modern hairy-nosed wombats from Queensland and from Deniliquin are considered conspecific. The synonymy of this modern species with *L. krefftii* from Wellington Caves, and its distinction from *L. latifrons* is supported by the following characteristics comparable in fossil and modern skulls: length of nasals relative to their width, greater anterior width of nasals, the longer anterior projection of the nasals, and the greater enamel width of I^1. Fossils of *L. krefftii* share a tendency with modern *L. krefftii* to have a shorter premaxillary/nasal suture than *L. latifrons.* However, this suture is absolutely shorter in the Wellington Caves specimens than in any modern wombat. A median backward projection of the nasals at their suture with the frontals, not observed in *L. latifrons,* was found in *L. krefftii* from Wellington Caves, Moonie River and Deniliquin, but not in specimens from Clermont, all of which have a median forward projection of the frontals into the nasals. Crowcroft (1967) indicated that variation in this character distinguished between geographic races of modern *L. latifrons.*

Mandibular fragments from Wellington Caves exhibit few taxonomically useful characters. The single lower incisor available (AM F58704) is wider and deeper than I_1 of *L. latifrons,* and similar in size to I_1 of the Clermont wombats. Other dental dimensions are within, or only slightly greater than the observed ranges of *L. latifrons.* The fossils resemble wombats from Deniliquin in the more anterior origin of the coronoid process (ectalveolar groove) at the level of the anterior lobe of M_4. Other characters, such as the depth of the masseteric fossa and presence or absence of a masseteric foramen, are variable and have been shown to have no taxonomic value at the species level. Thus the data from mandibles alone would not exclude the possibility that *L. latifrons* was present in the Wellington Caves deposits, as suggested by Owen

(1872a). However, there are insufficient data to support the recognition of more than one species in that deposit. All mandibular specimens from Wellington Caves which are referable to a species of *Lasiorhinus* have here been referred to *L. krefftii* as part of the topotypical sample.

Wilkinson (in Merrilees, 1973) has reported *L. krefftii* from late Pleistocene deposits at Lake Tandou, Lake Menindee and Lake Victoria in New South Wales. These specimens were not available for this study. The present disjunct distribution of *L. krefftii* in the modern fauna supports the hypothesis that these populations represent relicts of a previously greater range from southeastern Queensland, through inland New South Wales, to northern Victoria as suggested by Wilkinson (in Merrilees, 1973).

?Lasiorhinus angustidens De Vis, 1891

Phascolomys angustidens was named by De Vis (1891) for three mandibular fragments (see Mahoney and Ride, 1975) from the eastern Darling Downs, Queensland. De Vis (1891) only compared this material with Owen's fossil *Phascolomys mitchelli,* shown here to be a subspecies of *Vombatus ursinus.* That the material referred by De Vis (1891) to *angustidens* represents a species of *Lasiorhinus* is indicated by the proportions of the alveolus of I_1 (character 9, Table 1), by the shape of P_3 (character 11, Table 1), and the anterior extent of the 'ectalveolar groove' (character 12, Table 1) in QM F2921, selected here as the lectotype of *Phascolomys angustidens* De Vis, 1891. The present study has indicated that characters of the mandible alone are generally insufficient to distinguish between species of *Lasiorhinus.*

Wilkinson (in Hope and Wilkinson, 1982) has suggested that *angustidens* belongs in *Phascolonus,* although he has given no justification for this decision. Several features of *Lasiorhinus angustidens* argue against such allocation. It does not have a vertical labial groove on P_3, considered by Dawson (1981) to be a derived feature in *P. gigas,* nor are the molar lobes of *L. angustidens* separated by a deeply U-shaped median valley, as in *Phascolonus gigas.*

Dawson (1983) has pointed out that *'Phascolomys' medius* is dentally very similar to species of *Lasiorhinus,* although features of its palate differ greatly from species of *Lasiorhinus.* With this in mind it is conceivable that the mandibular fragments here assigned to *L. angustidens* could represent *'Phascolomys' medius.* They are much smaller than mandibles referred to *'P.' medius* by Owen (1872b), but could represent juveniles of that species, as *Phascolomys parvus* Owen represented juveniles of *Vombatus ursinus* (Merrilees, 1967). There is, however, no way to test this hypothesis at present. Until more conclusive evidence becomes available the name *angustidens* must be considered to be available for a species of *Lasiorhinus.*

Genus *WARENDJA* Hope & Wilkinson, 1982

Warendja wakefieldi Hope & Wilkinson, 1982

This species is known from two mandibles, and some isolated upper teeth (premolars and molars) from Pleistocene deposits in McEacherns Cave, Victoria. The characters of the mandible and its ascending ramus, as described by Hope and Wilkinson (1982) are atypical of other known wombats, but are apparently plesiomorphic among diprotodonts. With one exception (the depth of I_1 relative to its width) all dental characters of *W. wakefieldi* are plesiomorphic for vombatids according to the criteria described by Dawson (1981, 1983). Because of the preponderance of plesiomorphic characters in material described so far it is not yet possible to establish the phylogenetic relationships of *W. wakefieldi* to other Pleistocene or Tertiary vombatids.

GENERAL DISCUSSION

The preceding study has clarified taxonomic concepts of small fossil wombats from the Pleistocene, at least as far as possible with current understanding of the taxonomy of related modern forms. The Northern Hairy-Nosed Wombat, now extant only at Clermont, Queensland, apparently represents a relict population of *Lasiorhinus krefftii,* once widely distributed throughout New South Wales and southern Queensland. However, there is, as yet, no indication of the origin, or past distribution of the modern Southern Hairy-nosed Wombat, *Lasiorhinus latifrons.*

The correct taxonomic status of geographic variants of the Common Wombat, *Vombatus ursinus,* both fossil and modern, has yet to be established. Preliminary studies of variation in *V. ursinus* (Merrilees, 1967, and the present study) indicate the possibility that the geographically and stratigraphically isolated groups recognized here and by Tate (1951) as subspecies of *V. ursinus* could represent full species. A comprehensive study of modern populations, based on characters such as chromosome number and morphology, serology, or allozymes is needed before the taxonomic significance of morphological variation in these wombats can be fully understood. If such a study supported the recognition of more than one species of *Vombatus* in the modern fauna, it is likely that *V. mitchellii* from Wellington Caves could represent a distinct species of *Vombatus* rather than a sub-species of *V. ursinus* as designated here. Recognition here of *Vombatus hacketti* from Mammoth Cave as a full species is a reflection of the more complete cranial material available for that species.

The poor understanding of morphological variation in both 'common' and hairy-nosed wombats obscures knowledge of the stratigraphic range and the phylogeny of these small vombatids. Tooth and jaw fragments in the size range of species of *Lasiorhinus* and *Vombatus* are known from many Pleistocene deposits throughout Australia, but without cranial material (at least) their specific status cannot be confidently established, at present.

As yet no representatives of *Vombatus, Lasiorhinus* or *Warendja* are known from Tertiary faunas. The only record of any Tertiary vombatid resembling the modern species in size is a partial molar recorded by Rich (1980) from the Pliocene Hamilton fauna of Victoria. Large species representing at least three other vombatid genera (*Phascolonus, Ramsayia* and *Rhizophascolonus*) have been described from Tertiary faunas (Archer and Bartholomai, 1978; Dawson, 1981). However, the phylogenetic relationships of these genera, and of *Lasiorhinus* and *Vombatus* are still obscure (see Dawson 1983). Cladistic analysis of vombatid dental and palatal characters (Dawson, 1981, 1983) has indicated that *Vombatus ursinus* is the most plesiomorphic species of Quaternary and modern faunas. *Warendja wakefieldi* was not included in those analyses. The scant material so far described suggests that this species is so far removed from other fossil and modern wombats that it may even represent a distinct subfamily.

ACKNOWLEDGEMENTS

This work was part of a study for the degree of Ph.D. from the University of New South Wales. I wish to thank my co-supervisors, Dr Michael Archer and Dr Alex Ritchie for their support, advice and encouragement. Dr Ritchie also kindly made available the collections and facilities of the Australian Museum, Sydney. I also wish to thank Dr Anthony Sutcliff of the British Museum (Natural History), London, Dr Bill Clemens of the University of California Museum of Paleontology, Berkeley, Dr Alan Bartholomai of the Queensland Museum, Dr Tom Rich of the National Museum of Victoria, and Dr Neville Pledge of the South Australian Museum for allowing me to study collections in those institutions. Dr Ken Macnamara of the Western Australian

Museum kindly lent the skull of *Vombatus hacketti*. I would also like to thank Dr M. O. Woodburne for constructive criticism of Chapter 7 of my Ph.D. thesis, part of which is incorporated in this paper, and Mr Ken Aplin for his comments on this manuscript. This study was supported by a Commonwealth Postgraduate Award and partly by a grant-in-aid from the Trustees of the Australian Museum, Sydney.

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A new Australian Species of *Charletonia* (Acarina: Erythraeidae)

R. V. SOUTHCOTT

SOUTHCOTT, R. V. A new Australian species of *Charletonia* (Acarina: Erythraeidae). *Proc. Linn. Soc. N.S.W.* 107 (2), (1982) 1983: 125-130.

Charletonia keyi n. sp., parasitic on the grasshopper *Greyacris profundesulcata* (Carl) (Pyrgomorphidae, Monastriini), is described from Australia.

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INTRODUCTION

Sixteen of the 32 species left by Southcott (1966) in the larval genus *Charletonia* Oudemans (Erythraeidae: Callidosomatinae) were Australasian. Treat and Flechtmann (1979) described another species from South America, and Yano and Ehara (1982) referred to an unidentified species parasitic on plant hoppers, *Nilaparvata lugens* (Stål) and *Sogatella furcifera* Horváth, from paddy fields in Japan.

Ishii (1954), Treat (1980) and Rosa and Flechtmann (1980) showed that *Charletonia* Oudemans, 1910 is a prior synonym of *Sphaerolophus* Berlese, 1910 (see Southcott, 1961: 528-529; 1966).

Some 14 postlarval species of *Charletonia* have been described, as *Sphaerolophus* spp., from Europe, South America, Africa, Australia and the Malayan region (see Southcott, 1961: 531-533), and Feider and Chioneau (1977), Treat (1975, 1978, 1979) and Witte (1977) further studied the morphology, biology and distribution of the genus as larvae, active nymphs or adults.

A new species of larval *Charletonia* parasitic on an Australian grasshopper (Pyrgomorphidae) is described below.

DESCRIPTION AND DISCUSSION

Charletonia keyi n. sp.

HOLOTYPE LARVA (Figs 1 **A-F**, 2 **A-E**, 3)

Colour in life not recorded, presumably red. Idiosoma ovoid, 480μm long by 340μm wide (partially fed, slide-mounted); total length of animal from tip of cheliceral blades to posterior pole of idiosoma 595μm.

Dorsal scutum generally rounded, wider than long, with a slightly concave (sinuous) anterior margin. Anterolateral angles rounded, posterior sensillary bases projecting from posterior end, with a notch between them, making PL borders somewhat concave. All scutalae close to scutal margin; AL scutalae arising somewhat back from AL angles; ML scutalae about midway between AL and PL scutalae; PL scutalae somewhat behind equator of scutum. Scutalae curved, tapering, terminally blunted, with light barbs. ML scutalae shorter than the ALs (longest) and PLs. Scutum moderately chitinized, with generalized fine puncta, but without striations.

Eyes 1 + 1, cornea circular, 18μm across.

Dorsal idiosomalae tapering, pointed or slightly blunted at tip, lightly barbed, arranged in vague transverse lines across idiosoma, about 58 in number. Two 'ocular' setae (Oc.) near each eye.

Venter: between and behind coxae I a pair of setae, well-branched with long cilia, 35μm long; between coxae II a pair of pointed ciliate setae 42μm long; in area between

Standard Data, etc., of Holotype

AW	74	ASens	38
MW	85	PSens	71
PW	94	ASBa/ISD	.44
SBa	11	DS	33-60
SBp	17	MDS	32-40
ASBa	24	PDS	33-60
ISD	54	'Oc.'	42-46
L	85	GeI	93
W	102	TiI	118
A-M	14	GeII	86
A-P	31	TiII	107
AL	54	GeIII	95
ML	32	TiIII	147
PL	46	TiI/W	1.16

coxae II and III a row of four setae, tapering, pointed, ciliate, 31-35μm long.

On opisthosoma behind coxae III about 19 ventralae, similar to last, but becoming blunter posteriorad, and there resembling posterior dorsalae, 27-36μm long.

Coxala I long, strong, tapering, pointed, ciliate, ca 70μm long. Medial coxala II at last, 51μm long; lateral coxala II tapering, slightly blunted, ciliate, 36μm long. Medial coxala III as for II, 55μm long; lateral coxala III as for II, 33μm long. Supracoxala present to leg I, a blunted peg 5μm long.

Legs normal for genus, I 565μm long, II 545μm, III 625μm (all lengths including coxae and claws). Tarsus I 120μm long (excluding claws and pedicle) by 22μm high where thickest; tarsus III 123μm by 19μm similarly. For other leg metric data, see Table above. Ratio TiI/GeI 1.27, TiIII/GeIII 1.55. Femoral to tibial segments more or less cylindrical; tarsi asymmetrically spindle-shaped, thicker proximally. Leg scobalae pointed, lightly ciliate. Basifemoral formula 4, 4, 2, telofemoral 5, 5, 5.

Genu I with specialized setae SoGeI.83d and VsGeI.88pd; most distal scobala coded ScGeI.80a. Tibia with specialized setae CpTiI.65d + SoTiI.67d ('duplex pair'), SoTiI.77d, and VsTiI.86pd. Tibia III with specialized seta SoTiIII.15d.

Pedotarsal claws normal, slender. Anterior claw without cilia, posterior claw with several long cilia, forming a sparse brush, the cilia shortening distally.

Gnathosoma normal, robust, moderately chitinized. United chelae bases (slightly damaged) about 109μm across by about 114μm long to tip of cheliceral blades. Blades normal, terminal cutting edge without barbs. Hypostomal lip well fimbriated, normal. Galeala normal, tapering, pointed, simple except for about two cilia, about 27μm long. Anterior hypostomala pointed, tapering, simple, 13μm long. Posterior hypostomala slender, with long cilia, about 30μm long.

Palpal formula 0, 1, 1, 3, 7. Palpal supracoxala slender, 4μm long. Palpal tibial claw with two somewhat unequal, slightly separated prongs.

Locality data

Holotype, labelled M6736 and ACA2012, parasitic on grasshopper *Greyacris profundesulcata* (Carl) (Acridoidea, Pyrgomorphidae, Monastriini), ♀, Mt. White, 2 miles (3 km) S. of Coen, Queensland, 30.iv.1962, K. H. L. Key, attached on left mesepimeron (to be deposited in Australian National Insect Collection). Dr Key advises (pers. comm., 1 November 1982) that this species of grasshopper is 'cited in

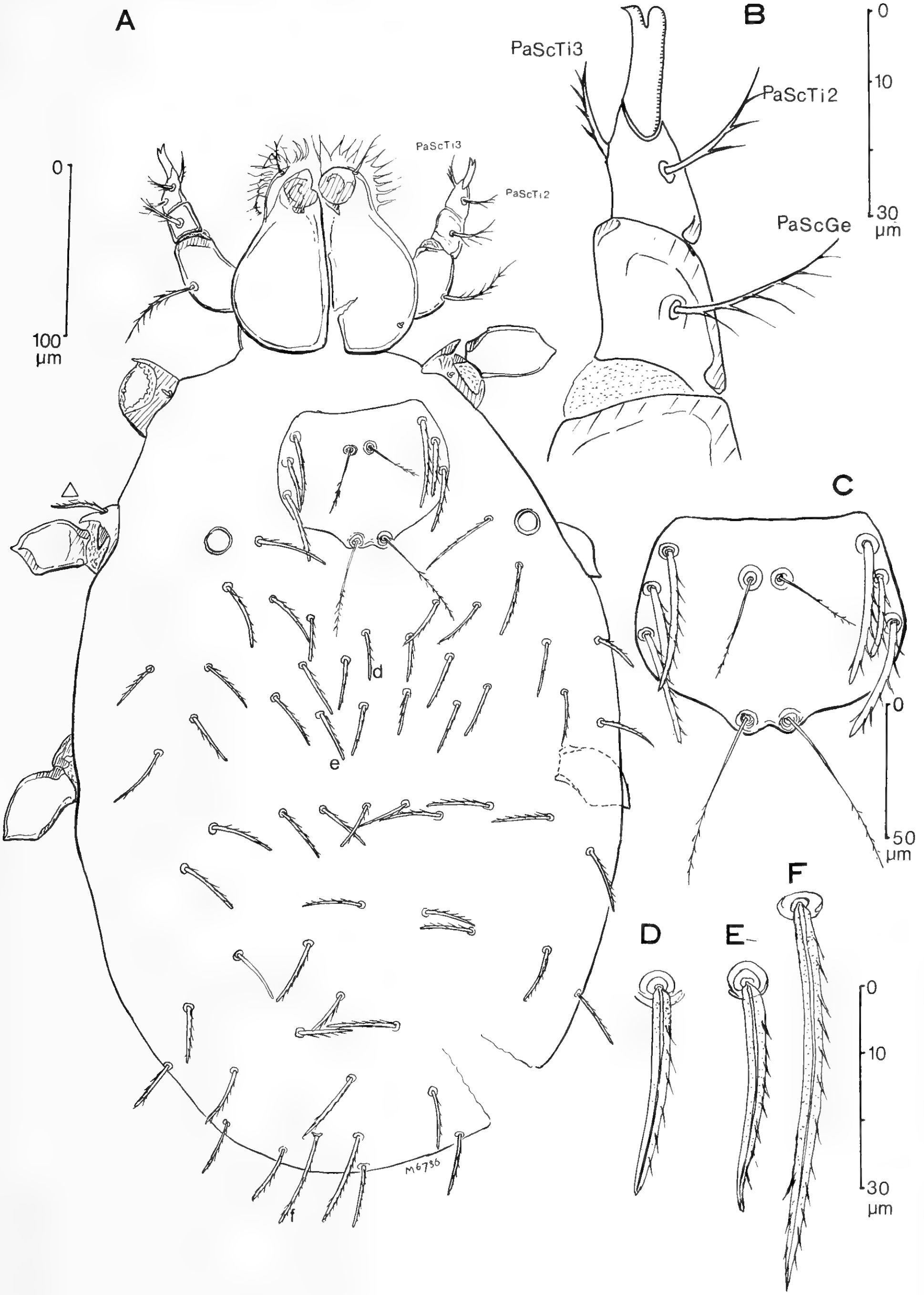

Fig. 1. Charletonia keyi n. sp. Holotype larva. **A**, Dorsal view, legs mostly omitted. **B**, Dorsal view of right palp, showing palpal tibial scobalae 1 and 2, also palpgenuala. **C**, Dorsal scutum. **D, E, F**, Dorsal idiosomal setae (d, e, f, respectively in **A**). (All figures to nearest scale).

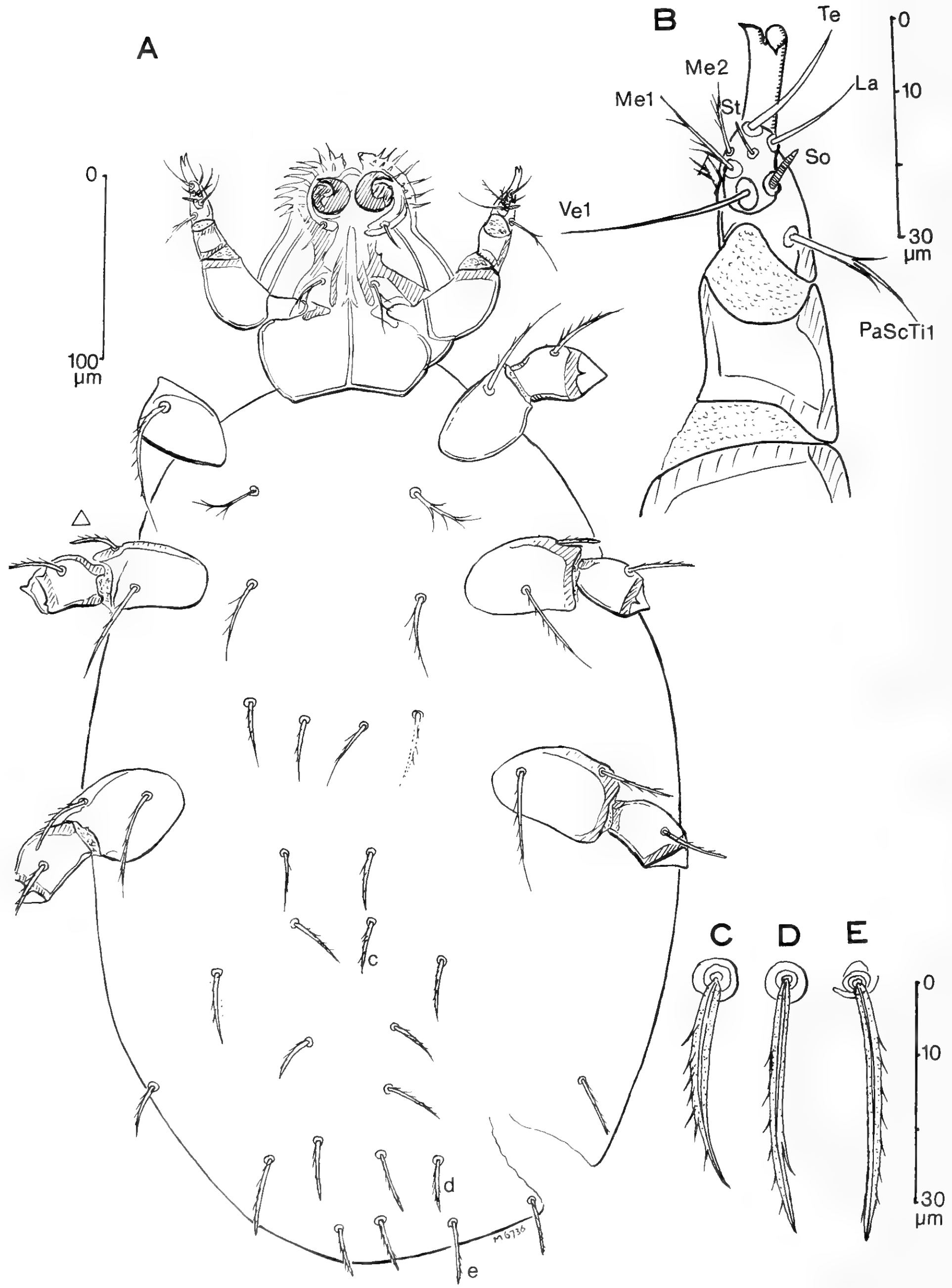

Fig. 2. Charletonia keyi n. sp. Holotype larva. **A**, Ventral view, legs mostly omitted. **B**, Ventral view of right palp, by transparency, with codings for palpal scobotibiala 1 and tarsal setae (Ve1, first ventral seta, Me1 and 2, first and second medial tarsal setae, Te terminal seta, St subterminal, not clearly seen in preparation, La lateral distal seta, So solenoidala). **C-E**, Opisthosomal setae (c, d, e, respectively in **A**). (All figures to nearest scale).

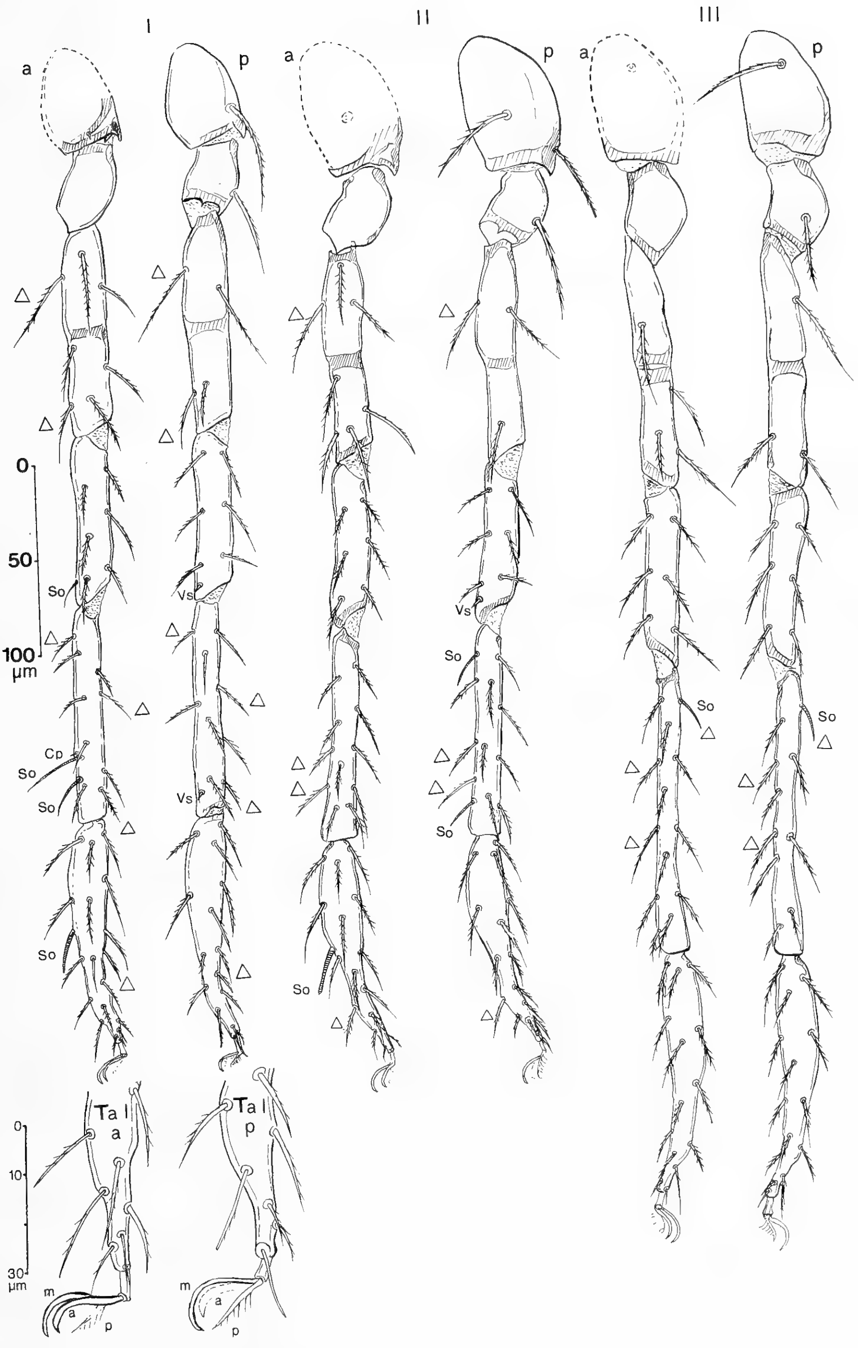

Fig. 3. Charletonia keyi n. sp. Holotype larva. Legs I, II and III, anterior and posterior aspects, to standard symbols, to scale on left. Below, tip of tarsus I, anterior and posterior aspects, to adjacent scale.

existing literature as *Monistria profundesulcata* — syn. *M. roseipennis* Sjöstedt, but assigned to *Greyacris* in my paper now in preparation'. (See Key, 1969, for further references to these grasshoppers.)

Nomenclature

Dedicated to the collector, Dr K. H. L. Key, who was responsible for instigating the CSIRO 'grasshopper mite project'.

Remarks

Charletonia keyi comes nearest to *C. banksi* Southcott, 1966, but differs in having the lateral border of the dorsal scutum convex instead of concave, in the DS being only adnately barbed, the smaller number of DS (58 instead of 89), in the smaller ratio of TiI/W (1.16 instead of 1.37-1.50), etc.

Evidently it is a rare species, only a single specimen having been submitted among the parasites of several thousand Australian grasshoppers.

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Cainozoic Stratigraphy at Wellington Caves, New South Wales

R. A. L. OSBORNE

OSBORNE, R. A. L. Cainozoic stratigraphy at Wellington Caves, New South Wales. *Proc. Linn. Soc. N.S.W.* 107 (2), (1982) 1983: 131-147.

A sequence of Cainozoic sediments infills karst cavities of the Devonian Garra Formation at Wellington Caves, N.S.W. The sequence is divided into two formations, the older Phosphate Mine Beds and the younger Mitchell Cave Beds. These are subdivided into informal lithostratigraphic units.

The Phosphate Mine Beds are composed of laminated clays, phosphorites, and indurated entrance facies deposits, along with osseous sandstones and conglomerates deposited by turbidity currents in a nothephreatic environment. The Mitchell Cave Beds consist of entrance facies and bone breccia.

An unconformity separates the two formations, and has a complex geometry. It is the product of a period of phreatic speleogenesis that excavated cavities within the Phosphate Mine Beds. The Mitchell Cave Beds infill these cavities. The Mitchell Cave Beds are most likely Pleistocene-Recent in age while the Phosphate Mine Beds may extend back into the Tertiary.

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manuscript received 31 March 1983, accepted for publication 18 May 1983.

INTRODUCTION

The Wellington Caves, located 8 km south of the town of Wellington in central western N.S.W. (Fig. 1), have attracted scientific attention since Cainozoic vertebrate fossil remains were first discovered in them during the 1830s. The history and significance of these discoveries has been outlined by Lane and Richards (1963) and Dugan (1980). More recently Dawson (1982) has re-examined fossil material held in museum collections.

Seven significant caves — Cathedral, Gaden-Coral, Mitchell, Gas Pipe, Lime Kiln, Triplet, and Water; and three large man-made excavations — Phosphate Mine, Big Sink, and Bone Cave, are located in an area less than 50,000 m^2 (Fig. 1).

The major excavations and all but three of the caves were surveyed and described in detail by Frank (1971). Of the remainder, Water Cave, (now inaccessible) was described by Trickett (1906), Lime Kiln Cave by Osborne *et al.* (1981) and Triplet Cave by Osborne (1982).

The caves have developed as a result of nothephreatic solution in massive limestone of the Garra Formation while the excavations, along with many vertical blind shafts, are the result of phosphate mining (Carne, 1919) and palaeontological excavation.

Colditz (1943) first investigated the relationship between cave development and local geomorphic history. Following Colditz's approach, Frank (1971) related cave development to the inferred capture of the Bell River by Catombal Creek. Frank's conclusions suggested that the caves formed during the Pliocene. Francis (1973) questioned the basis of Colditz's work and suggested a Miocene age for the caves based on the radiometric ages of basalts near Stuart Town.

Sediment, rather than limestone, forms the floors of most of the caves. By excavating shafts to depths of 11.5 m in Mitchell Cave and 11 m in Cathedral Cave in search of vertebrate fossils, Ramsay (1882) demonstrated that the sediment had a considerable thickness. Most of the strata described here are exposed in the Phosphate Mine where mine passages are excavated through an almost completely sediment-filled cave.

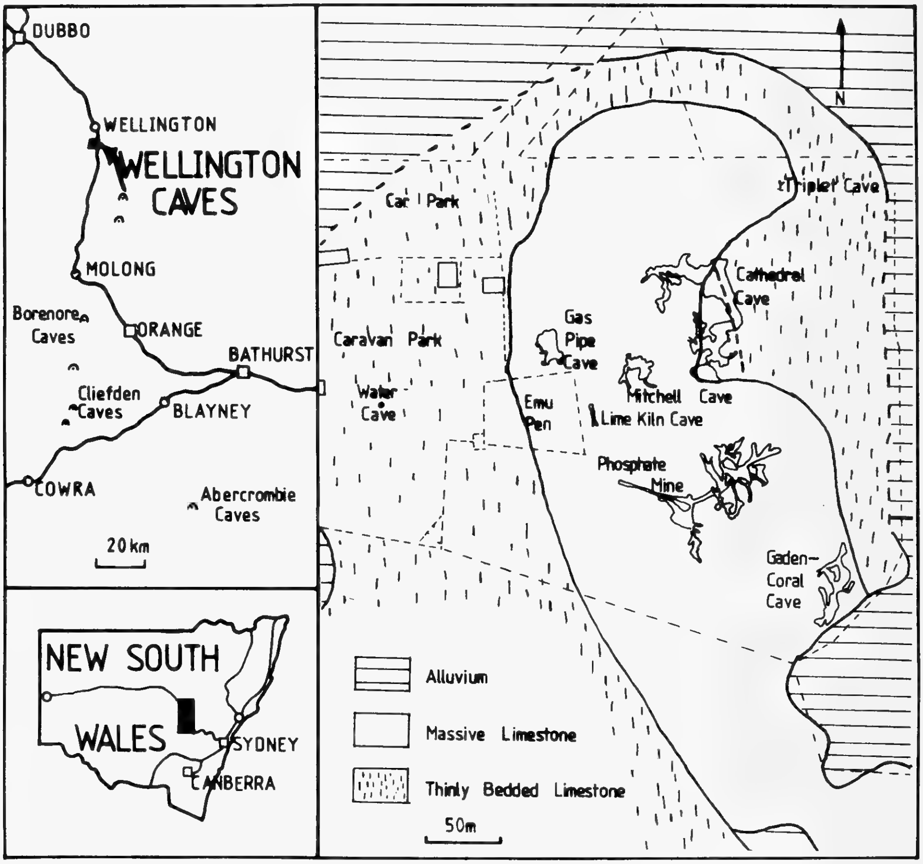

Fig. 1. Location. Semicircles with dots are limestone cave localities.

Despite 150 years of palaeontological research at Wellington Caves the only previous stratigraphic study of the Cainozoic deposits is that of Frank (1971) who proposed a division into three units with a number of sub-units. The stratigraphy is found here to be more complex than Frank's interpretation, with at least three unconformities and a possible disconformity in the succession.

The letters USGD and SUP followed by a five digit number refer to specimens housed in the petrological and the palaeontological collections respectively of the Department of Geology and Geophysics, University of Sydney.

STRATIGRAPHY

The Cainozoic sequence unconformably overlies and is partly enclosed within massive limestone of the Devonian Garra Formation (Strusz, 1965). A maximum stratigraphic thickness of 37 m has been measured. The stratigraphy is summarized in Fig. 2.

A. *Phosphatic rim rock*

This white phosphatic deposit is up to 300 mm thick and encrusts bedrock (Devonian Garra Formation) cave walls and ceilings. It is only developed in Phosphate Mine, Big Sink and Bone Cave. The phosphatic rim rock is laminated parallel to the

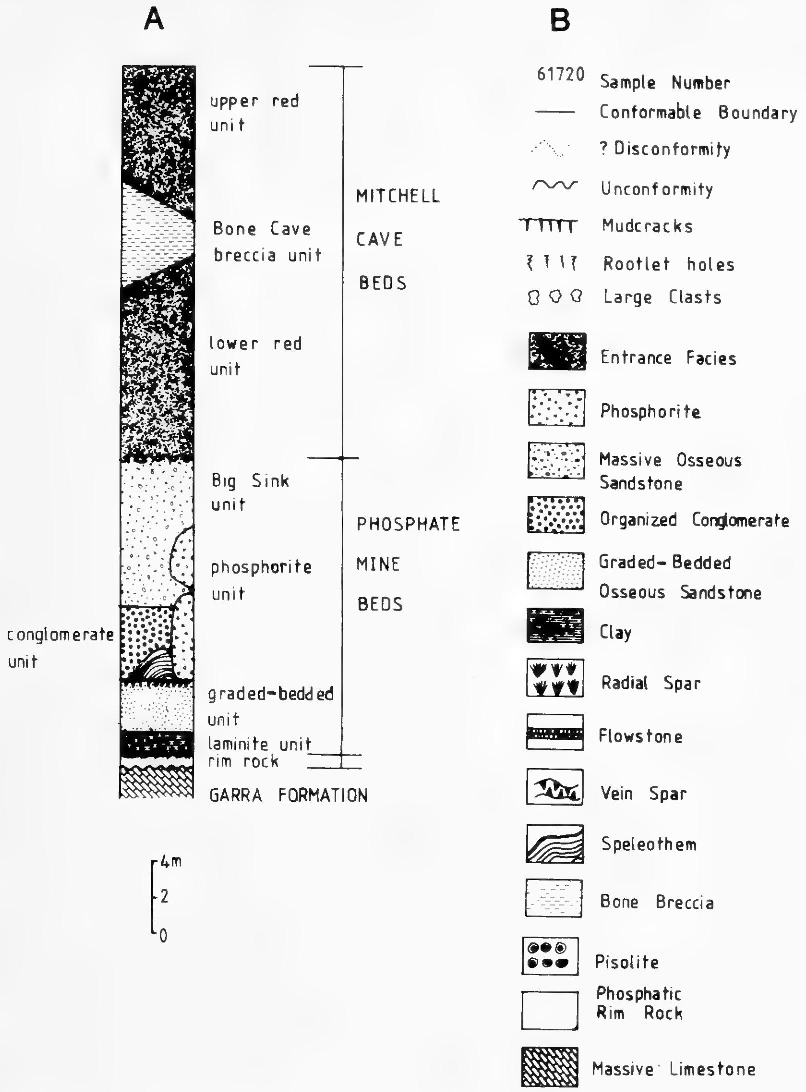

Fig. 2. **A**: Stratigraphy. **B**: Key for stratigraphic columns.

surfaces to which it adheres making its boundaries with both the Garra Formation and the Phosphate Mine Beds unconformable.

B. *Phosphate Mine Beds*

The Phosphate Mine Beds are a sequence of laminated clays, osseous sandstones, conglomerates, and phosphorites exposed in Big Sink, Phosphate Mine and Bone Cave. They take their name from the Phosphate Mine in which they are best exposed. Neither a complete section nor the base of the formation is exposed. A composite section (Fig. 3) is formed from exposures in the Phosphate Mine and Big Sink (localities 1, 4, and 7, Fig. 8).

The Phosphate Mine Beds are divided into five informal lithostratigraphic units.

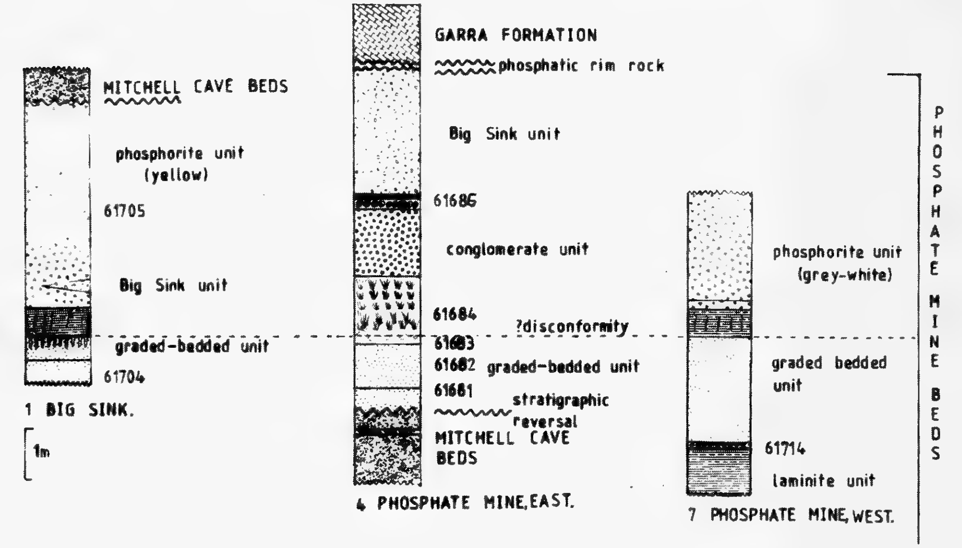

Fig. 3. Phosphate Mine Beds, composite type section.

B.1. *Laminite unit*

This unit, of which 1.3 m is exposed, consists of laminated clays with well-developed mud cracks. Spar has been deposited between laminae and in mud cracks sometimes resulting in brecciation. The top of the unit is marked by a bed of very pale yellow laminated clay.

Laminae range in thickness from a few millimetres to 15 mm. Unlike the 'cap muds' of Bull (1977) and the 'layered clay fill' of Osborne (1978) the laminae represent periodic deposition of similar material rather than distinct compositional changes. X-ray diffraction study of USGD 61698, 61699 (Fig. 5) and 61714 (Fig. 3) indicated that the main component is quartz along with a kandite phase, probably kaolinite.

Finely laminated clays are the product of a stable, low energy environment. In caves they may be deposited in pools perched above the water table or in a low energy phreas like that described as a nothephreas by Jennings (1977). Since laminated clays occur with the same stratigraphy at widely separated parts of the Phosphate Mine it seems most likely that they were deposited in the phreas. Desiccation features indicate variations of the water table level at the time of deposition.

B.2. *Graded-bedded unit*

The graded-bedded unit conformably overlies the laminite unit and consists of 2.7 m of well-cemented, graded sandstone beds up to 170 mm thick interbedded with thin parallel-laminated, ripple-laminated, and mud-cracked horizons (Fig. 4**A**). The top of the unit is marked by a bed with prominent mud cracks, 80 mm deep, filled with

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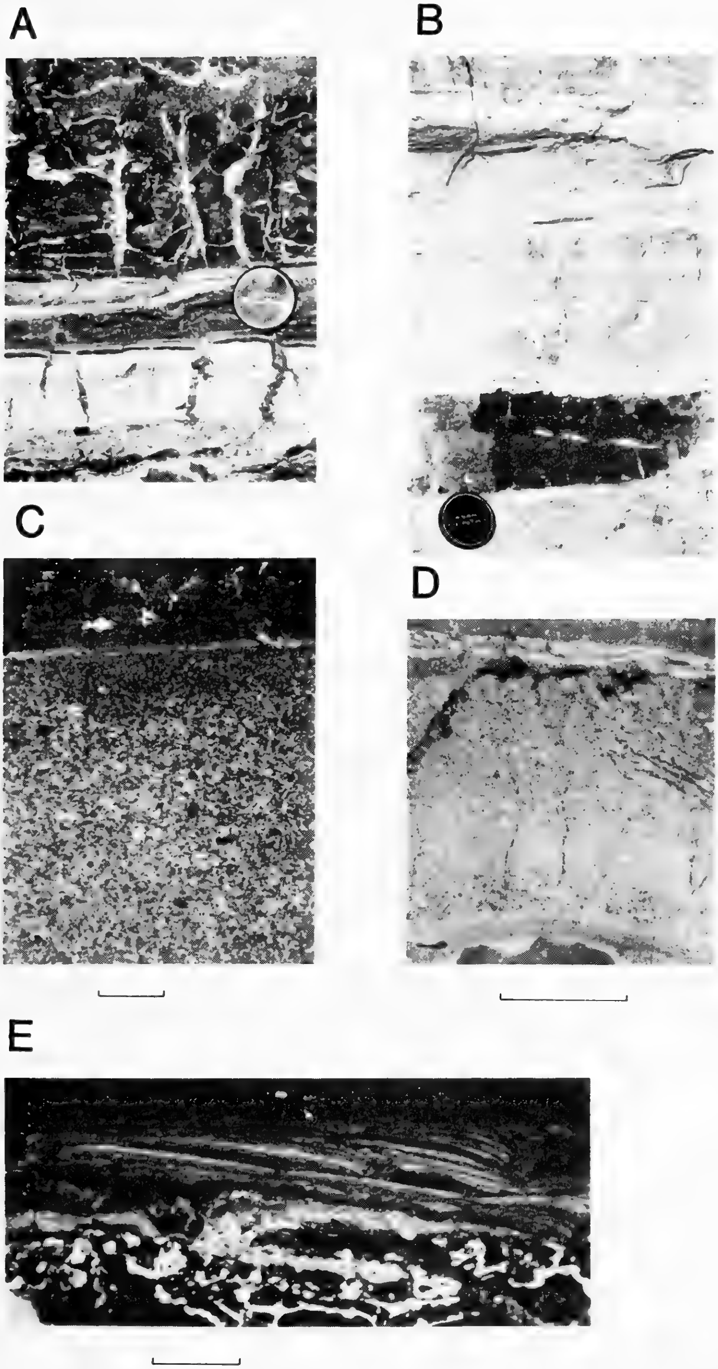
Fig. 4. **A**: Graded bedded unit exposed in wall of Phosphate Mine at locality 11, Fig. 8. Note mudcracks and laminated bed. Lens cap 55 mm in diameter. **B**: Graded bedded unit exposed in wall of Phosphate Mine at locality 2 Fig. 8. Note phosphate filled 'rootlet' structures. **C**: Polished block of osseous sandstone from the graded bedded unit, USGD 61704, Fig. 3. Note lower graded bed and upper laminated bed. Scale bar 10 mm. **D**: Polished block of thin graded bed from the graded bedded unit, USGD 61697, locality 11, Fig. 8. Scale bar 5 mm. **E**: Polished block of ripple laminated bed from the graded bedded unit, USGD 61695, Fig. 5. Scale bar 10 mm.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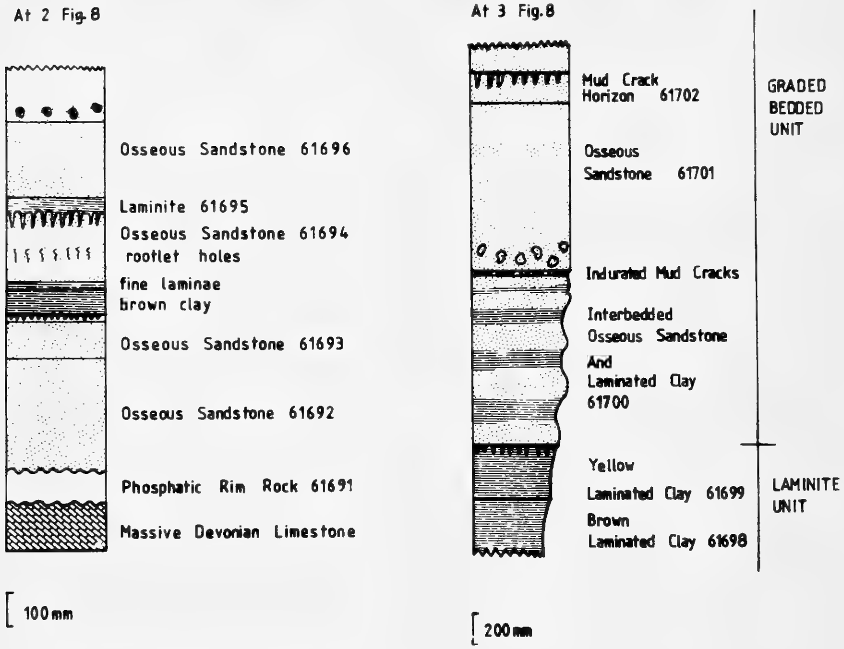

Fig. 5. Graded bedded unit, sections in Phosphate Mine.

opaline phosphatic speleothem. Within the unit are vertical tubes filled with phosphate (Fig. 4**B**) interpreted by Frank (1971) as invertebrate burrows. Piearce (1975) has shown invertebrates can produce casts and burrows in cave sediments, but since tree roots presently penetrate sediments in the Phosphate Mine, it seems more likely that these structures are phosphate-filled rootlet holes.

The relationships between the various types of beds are shown in Figs 4 and 5. In Fig. 4**C** a graded sand bed is overlain by a bed of parallel-laminated mud, Fig. 4**D** is of

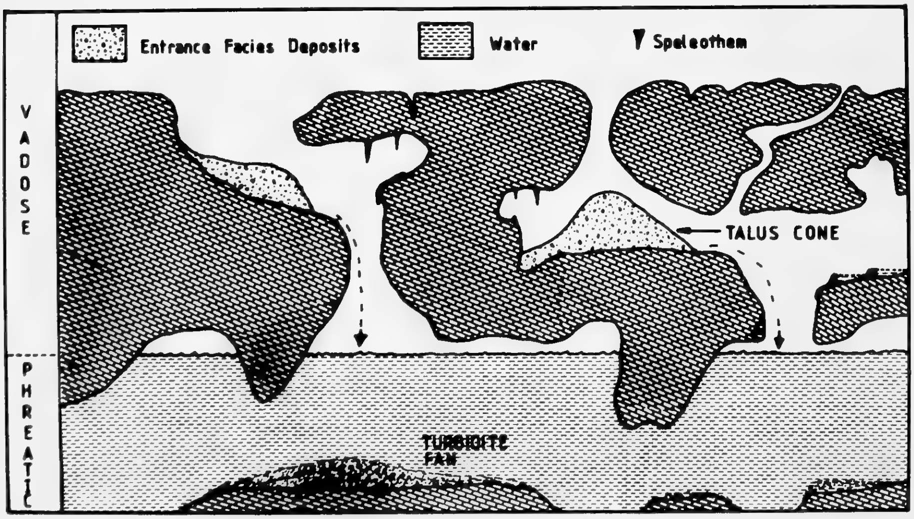

Fig. 6. Deposition of turbidites in caves.

a thin graded bed only 10 mm thick, while Fig. **4E** shows ripple- and convolute-laminated beds.

These structures are similar to those found in classic turbidites (Bouma, 1962) and suggest that turbidity currents may have been the depositional agents for the graded-bedded unit. Turbidity currents have usually been invoked for the deposition of coarse clastics in deep water environments. They were first recognized in inland lakes and reservoirs (Grover and Howard, 1938) where turbid flood waters interacted with less dense ponded water.

Similar conditions to those in lakes can exist in caves. Where a nothephreas is separated from the surface by air-filled caves (Fig. 6) coarse sediments will be trapped in talus fans, so that under normal conditions only fines will reach the phreas. Where such caves do not have active vadose streams (as is the present case at Wellington Caves) coarse clastics will only reach the phreas as a result of either slumping or flood rains. These will both result in the rapid introduction of sediment into the phreas and may produce turbidity currents. Due to the network geometry of nothephreatic caves a turbidity current is likely to cause deposition some distance from its point of initiation.

Osseous sandstone

The sandstones of the graded-bedded unit have their sand fraction composed almost entirely of bone and tooth fragments, and are therefore described as *osseous sandstones*.

Osseous sandstones are hard, light tan-coloured rocks with large spar crystals visible to the naked eye on broken surfaces. In thin section three main components are recognized: bone and tooth fragments, equant spar and clay (Fig. 7**A**).

Fragments include long bone (which may be up to 5 mm long), membrane bone and enamel. In polished blocks bone fragments appear as elongate dark specks which are oriented parallel to bedding. Heads of long bones often display complex involute textures, while marrow cavities of long bones are filled with spar. In thin section under plane polarized light bone fragments are pale yellow in colour. They have a low birefringence and a longitudinal fibrous structure resulting in irregular extinction. Small dark spots on fragments of long bone mark the ends of the canaliculi (Fig. 7**A**).

Two types of carbonate cement occur in osseous sandstones. Equant spar, the more common type, forms crystals up to 2 mm in section with most falling in the range of 0.5 to 1 mm. Equant spar is a secondary cement, filling spaces between bone fragments and replacing clay. In some cases (USGD 61681, Fig. 3) the clay has been reduced to thin coatings on bone fragments. The other type of carbonate cement is acicular plumose cement which is found both in brecciated phosphorite and osseous sandstones.

Brecciated phosphorite from the entrance to Bone Cave (USGD 61690) contains acicular plumose cement which forms an iron-stained rim around the outside of clear equant spar crystals (Fig. 7**B, C**). The plumose rim and the clear equant spar extinguish together between crossed polars. Where plumose cement occurs without an equant spar centre it extinguishes in large masses that behave in a similar way to equant spar grains. Osborne (1978) reported acicular plumose cement from deposits in Cliefden Caves and believed it to consist of calcite pseudomorphs after subaqueously precipitated aragonite. It seems likely that equant spar cement is produced by neomorphism of acicular plumose cement.

Phosphates occur as minor, secondary vadose cements in osseous sandstones with collophane and, to a lesser degree, dahllite filling mud cracks and voids. In USGD 61693 (Fig. 5) botryoidal masses of collophane with rims of dahllite surround and are embayed into equant spar grains. In USGD 61695 (Fig. 5) collophane has invaded

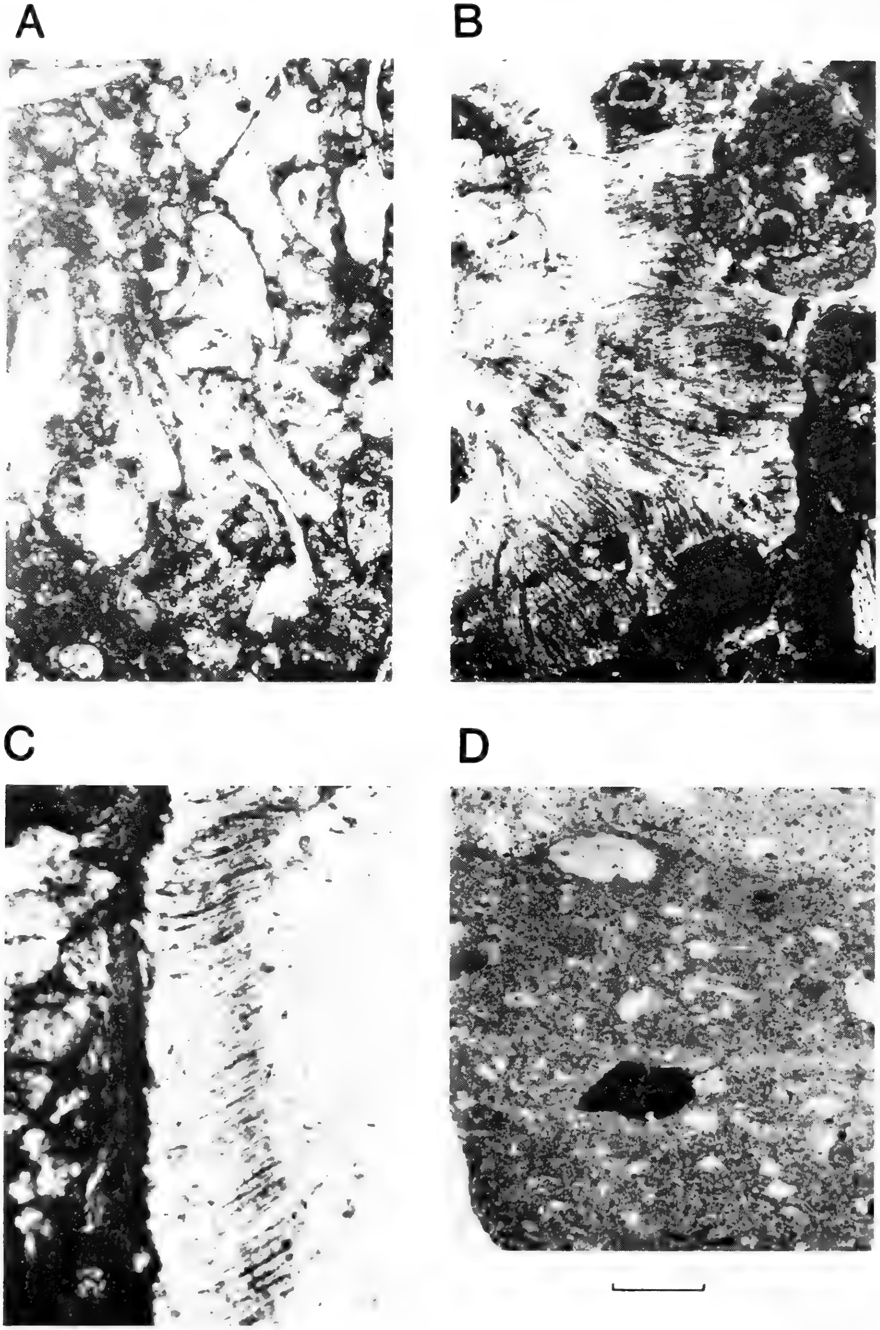

Fig. 7. **A**: Thin section of osseous sandstone, USGD 61704, Fig. 3, crossed nicols, x63. Note bone fragments, light grey. Black dots on bone fragments are canaliculi. **B**: Thin section of brecciated phosphorite, USGD 61690, from the Bone Cave entrance, crossed nicols, × 63. This shows a zone at the edge of a large spar crystal. Note acicular plumose structure. **C**: USGD 61690, plane polarized light, × 130. Shows plumose edge zone of spar. **D**: Polished block of conglomerate from the conglomerate unit, USGD 61706, locality 5, Fig. 8. Note alignment of clasts. Scale bar 10 mm.

TABLE 1

Point Counts of Osseous Sandstones

Sample	Bone Fragments	Spar	Clay	Phosphate	Others	Total Points
61681	55%	31%	14%	—	—	954
61693	47%	10%	17%	26%	—	834
61704	40%	23%	23%	12%	2%	1671

between equant spar grains while in USGD 61700 (Fig. 5) a vein is filled first with collophane, then with dahllite and finally with spar.

Point counts of osseous sandstones, Table 1, show bone fragments forming up to 55% of the rock. Such high concentrations require a significant source of bone in the caves prior to deposition.

Deposits of bones are not uncommon in caves. Small bone fragments are found as undigested residue in the faeces of carnivorous mammals and in pellets regurgitated by birds of prey. Kukla and Lozek (1958) note that owls can produce extensive deposits of bone. Unlike the bone in the osseous sandstone this bone is usually not broken (Lundelius, 1966). Since the fragments in the osseous sandstone are of small bones they were probably introduced into the caves by small carnivores. Transport and re-deposition may have been responsible for breakage of membrane bones but is unlikely to have resulted in the observed breakage of long bones.

B.3. *Conglomerate unit*

The 4 m-thick conglomerate unit overlies the graded-bedded unit. Its lower boundary is exposed at two places in the Phosphate Mine (localities 4 and 5, Fig. 8). At locality 4 the conglomerate unit is separated from the graded bedded unit by 830 mm of speleothem while at locality 5 the conglomerate unit overlies the mud-cracked horizon at the top of the graded-bedded unit. Both the mud cracks and the speleothem suggest that the lower boundary of the conglomerate unit may be disconformable.

The conglomerate is poorly sorted, consisting of horizontally aligned angular fragments of clay, phosphatic mudstone, bone and teeth in a porous matrix in which birdseye structures are developed (Fig. 7**D**). In thin section (USGD 61707, locality 5, Fig. 8) the matrix is seen to consist of blocky spar, clay, fine bone fragments, and small clasts of phosphatic mudstone. X-ray diffraction indicated that quartz and hydroxyapatite are the main non-carbonate phases present.

Like the graded-bedded unit, the conglomerate unit was probably deposited by turbidity currents in the phreas, the larger grain size resulting from deposition close to the point where clastics entered the phreas. This is equivalent to the inner fan area proposed by Walker (1975) as the locus of deposition for re-sedimented conglomerates with a preferred clast orientation.

B.4. *Phosphorite unit*

Three types of phosphorite — grey-white, yellow, and brecciated — occur within the sequence at about the same stratigraphic level. Grey-white phosphorite overlies the graded-bedded unit in the western part of the Phosphate Mine (Fig. 3). Yellow phosphorite overlies the graded-bedded unit and has Big Sink unit interbedded with it in Big Sink, while brecciated phosphorite is overlain by Big Sink unit at the entrance to Bone Cave.

In the Bat Chamber of the Phosphate Mine and at the northern end of the Main Drive, sheets of phosphatic speleothem have blocked off sections of the cave,

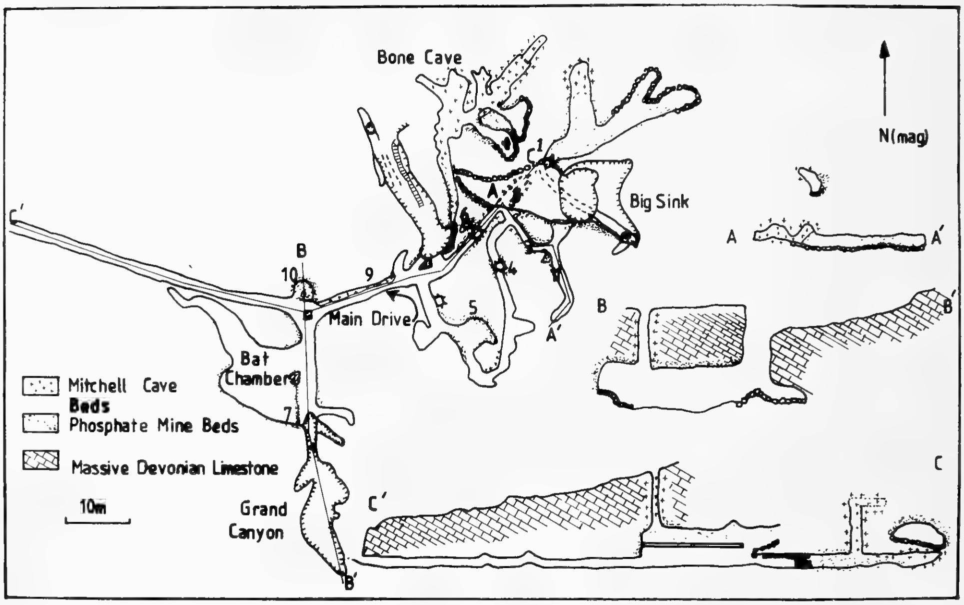

Fig. 8. Phosphate Mine, Bone Cave and Big Sink. Plan and sections after Frank (1971).

preventing the deposition of grey-white phosphorite. In these pockets are complex non-clastic sediments that appear to be time equivalents of the grey-white phosphorite.

The three types of phosphorite and the non-clastic sediments are grouped together to form the phosphorite unit which is considered to be a lateral equivalent of the conglomerate and Big Sink units.

B.5. *Big Sink unit*

The Big Sink unit is the uppermost unit of the Phosphate Mine Beds and takes its name from Big Sink where an 8 m section is exposed, forming the southern wall of the doline. It is also exposed in Bone Cave, the Phosphate Mine, in a small subsidence doline near the entrance to Bone Cave (locality 6, Fig. 8) where it conformably overlies the conglomerate unit, and at the surface in the flat area between Big Sink and the entrance to Bone Cave.

The unit is composed of beds of osseous sandstone interbedded with thin layers of structureless mud. The osseous sandstones are indurated and graded bedding is not developed. Bone and tooth fragments, which may be locally concentrated, are randomly oriented. In some places bedding has a high initial dip, suggesting that the unit consists of cemented entrance facies deposits.

The Big Sink unit is the only unit of the Phosphate Mine Beds readily correlated with the stratigraphic scheme of Frank (1971) being equivalent to his 'Unit 1 BG'.

The Phosphate Mine Beds — Mitchell Cave Beds Boundary

The boundary between the Phosphate Mine Beds and the Mitchell Cave Beds is exposed in the Phosphate Mine, Big Sink and Bone Cave. At the entrance to Bone Cave the Mitchell Cave Beds are surrounded completely by the Phosphate Mine Beds. Further along the entrance passage of Bone Cave the boundary between the formations is vertical (Fig. 9**A**). In the Phosphate Mine (locality 8, Fig. 8) the boundary is marked by a layer of flowstone separating Big Sink unit from lower red unit. Frank (1971) mapped this boundary but was unaware of its significance. Also in the Phosphate Mine

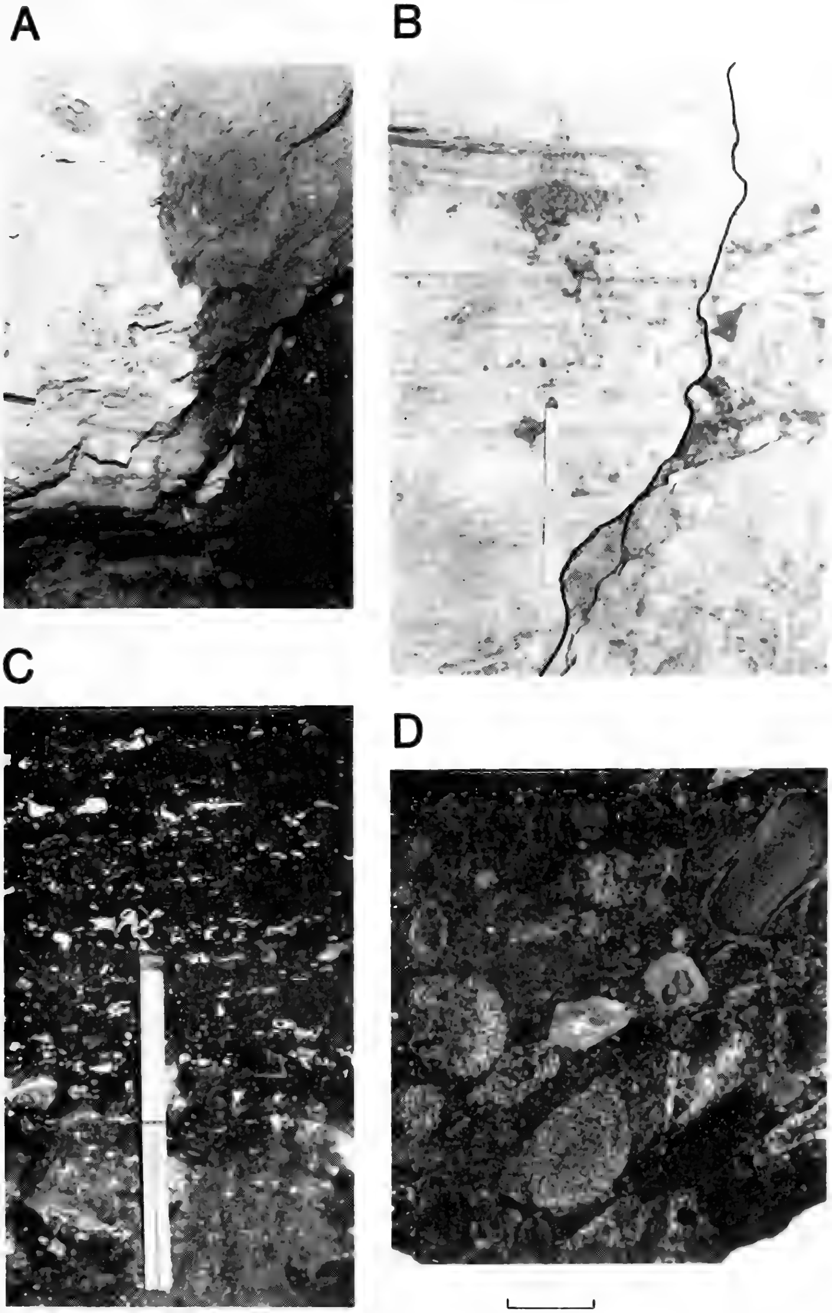

Fig. 9. **A**: Outcrop of unconformity in entrance passage to Bone Cave. Phosphate Mine Beds (grey) are exposed on the left while Mitchell Cave Beds (dark) are exposed on the right. The unconformity surface here is a vertical plane. **B**: Outcrop of unconformity in wall of Phosphate Mine at locality '3' Fig. 8. Unconformity surface is retouched dark line. Graded bedded unit is exposed to the left of the surface and undifferentiated Mitchell Cave Beds to the right. **C**: Bone Cave breccia unit exposed in wall of Bone Cave. Note alignment of bone fragments and large cobbles at base. **D**: Polished block of disorganized conglomerate, USGD 61707, from locality 9, Fig. 8. Scale bar 10 mm.

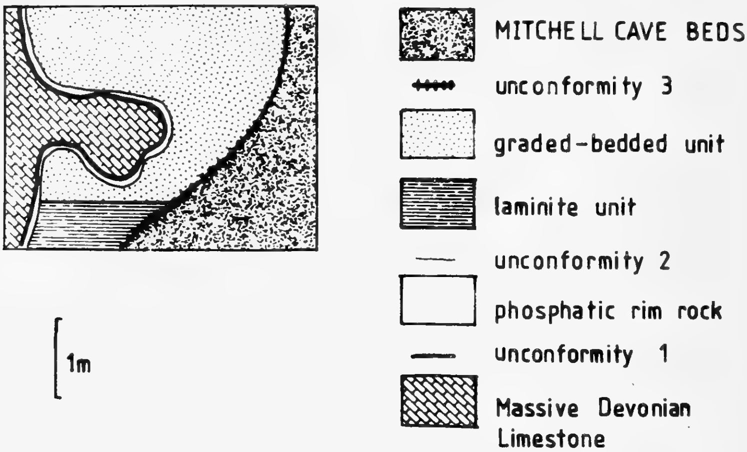

Fig. 10. Unconformities exposed in Phosphate Mine at locality 3, Fig. 8.

(locality 3, Fig. 8) a sloping boundary between the graded-bedded unit and the Mitchell Cave Beds is exposed (Figs 9**B**, 10).

The geometry of the boundary between the two formations indicates that they are unconformable and that the Mitchell Cave Beds were deposited in caves that developed within the Phosphate Mine Beds (see idealized cross section through the Phosphate Mine Fig. 11).

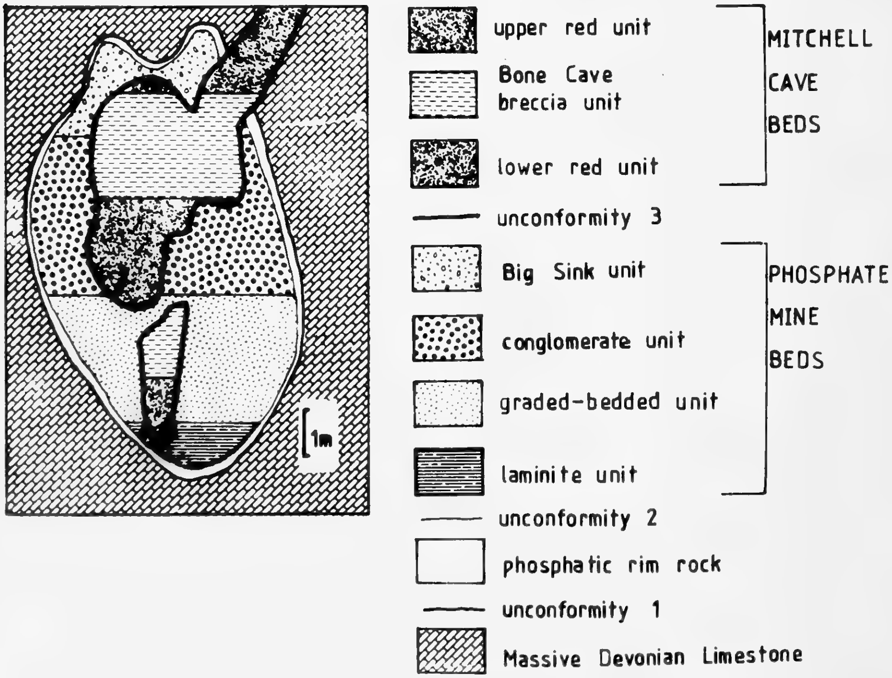

Fig. 11. Idealized section through Phosphate Mine.

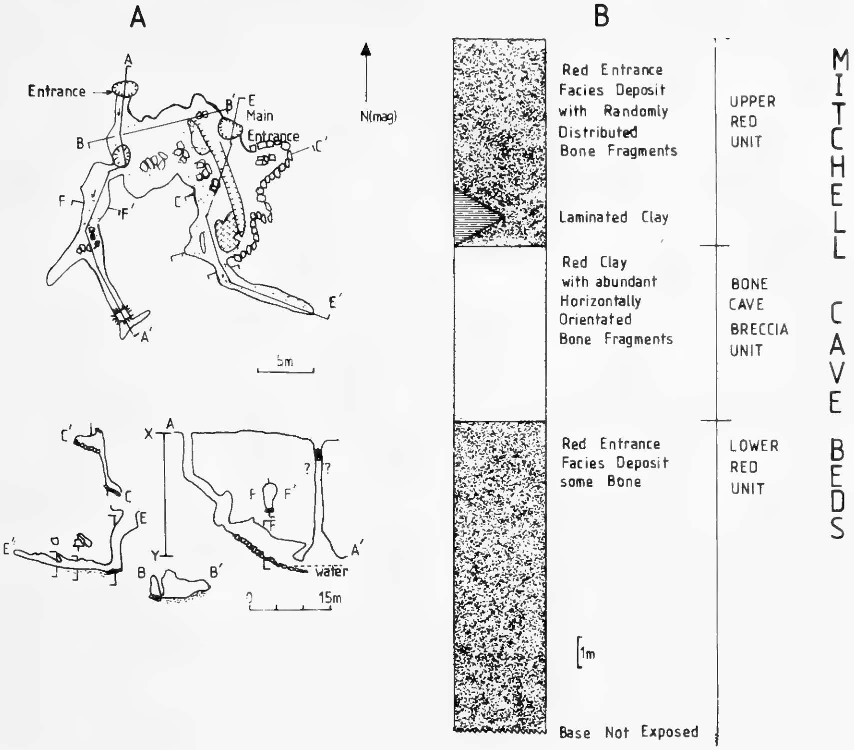

Fig. 12. **A:** Plan and sections of Mitchell Cave after Frank (1971). **B:** Type section for Mitchell Cave Beds.

C. *Mitchell Cave Beds*

The Mitchell Cave Beds consist of entrance facies deposits and bone breccias. They unconformably overly the Phosphate Mine Beds and take their name from Mitchell Cave where their type section (Fig. 12) is located. They are divided into three informal lithostratigraphic units and are laterally more extensive than the Phosphate Mine Beds. In Bone Cave, Big Sink and the Phosphate Mine, the Mitchell Cave Beds have been deposited in cavities developed within the Phosphate Mine Beds while in Mitchell Cave they directly overlie limestone bedrock.

C.1. *Lower red unit*

The lower red unit forms the base of the sequence in Mitchell Cave and is also exposed in the Phosphate Mine. It is a red, poorly-consolidated, unbedded entrance facies deposit consisting of sparse bone and tooth fragments in a matrix of red friable clay mainly composed of quartz with a small amount of kaolinite. The lower red unit attains a maximum thickness of 9.2 m in the Mitchell Cave section.

C.2. *Bone Cave breccia unit*

The Bone Cave breccia unit is named after Bone Cave where a 2 m thick exposure has been the source of much vertebrate fossil material (Lane and Richards, 1963). It is found conformably overlying the lower red unit in Mitchell Cave and the Phosphate Mine and is equivalent to 'Unit 3 R.B.' of Frank (1971).

The unit consists of a partially cemented breccia of bone and tooth fragments (up to 0.25 m long) and limestone cobbles (up to 0.5 m in diameter) in a red clay matrix. The bone fragments are horizontally aligned (Fig. 9C). The boundary between the

Bone Cave breccia unit and the Big Sink unit, the wall of the cavity in which the Bone Cave breccia unit was deposited, is exposed in the eastern wall of Bone Cave. The horizontal alignment of the bone and tooth fragments continues undisturbed right up to this boundary.

Numerous theories have been advanced to explain the deposition of this unit with its profusion of bones and teeth. Some theories of historic interest have been outlined by Lane and Richards (1963). Lundelius (1966) proposed that the marsupial 'lion', *Thylacoleo carnifex,* introduced the bones by using the cave as a den. Frank (1971) suggested that the unit was deposited primarily by gravity with some slight contribution by water.

The horizontal alignment of the bone and tooth fragments suggests that the unit is neither a result of the activity of carnivores nor is it a gravity-deposited entrance facies deposit since both of these tend to be poorly bedded with a high initial dip.

It is proposed that this unit was originally deposited as entrance facies deposits, containing bones (either from pit traps or carnivore dens), which slumped (or were washed by flood pulses) into shallow still ponds of water in the lower parts of the cave. In such conditions a slurry could be produced that would be viscous enough to support and align the bone fragments. Cobbles would be transported to the ponds by sliding and rolling.

Any taphonomic or stratigraphic relationships that might have existed between bone material in the original entrance facies deposits would have been destroyed during their subsequent transport and re-deposition.

C.3. *Upper red unit*

The upper red unit is an entrance facies deposit very similar to the lower red unit. It attains a thickness of 6.6 m in Mitchell Cave where it is sparsely cemented and contains a few bone and tooth fragments.

Entrance Facies

The term 'entrance facies' (Kukla and Lozek, 1958) is applied here to poorly sorted sediments deposited in cave entrances and talus cones largely by the action of gravity and rain wash. The upper and lower red units are good examples of this type of deposit.

Red entrance facies deposits are found in the majority of the Wellington Caves and were considered to be part of the same unit by Frank (1971). In the type section in Mitchell Cave the upper red unit conformably overlies the Bone Cave breccia unit, however, the stratigraphic positions of similar sediments in other caves referred by Frank (1971) to his 'Unit 3.R' are far from certain. Frank reported rabbit bone in some sediments in Bone Cave while the author has found dog and human skeletal material in the entrance facies deposits of Triplet Cave. Entrance facies are currently being deposited as talus cones in the Bat Chamber of the Phosphate Mine and as rain wash in Gas Pipe Cave.

D. *Strata with Uncertain Relationships*

Two sequences exposed in the Phosphate Mine cannot be correlated with the stratigraphic scheme outlined above. In the Main Drive of the Phosphate Mine (locality 9, Fig. 8) entrance facies deposits are overlain by conglomerate (Fig. 13**A**) consisting of irregularly arranged subangular clasts, up to 16 mm across, in a tan coloured matrix (Fig. 9**D**). The clasts are laminated clays and phosphorites while the matrix (USGD 61707, Fig. 13) is composed of sand-sized quartz grains in a fine phosphatic mud. Some clasts of amorphous phosphorite are recrystallizing into fine acicular crystals of apatite. This conglomerate is probably the result of slumping of cave-derived detritus, the clasts being produced by breakdown of cave passages ex-

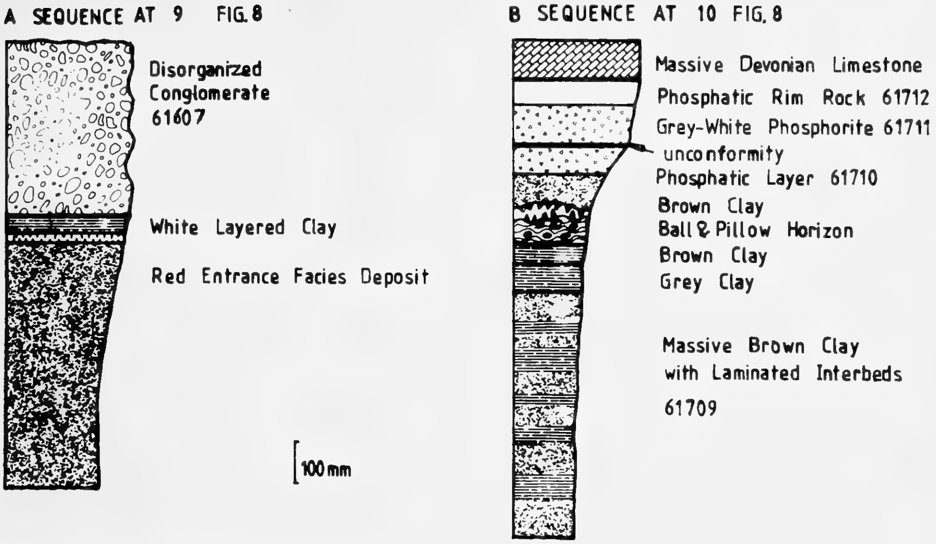

Fig. 13. Strata with uncertain relationships.

cavated through the Phosphate Mine Beds. The sequence is therefore younger than the Phosphate Mine Beds but its relationship with the Mitchell Cave Beds is uncertain.

In the western part of the Phosphate Mine (locality 10, Fig. 8) phosphorites of the Phosphate Mine Beds overlie apparently younger clays (Fig. 13**B**). Reverse stratigraphy is indicated as the clays fill a tunnel eroded in the phosphorite. As with the sequence described above, the relationship between these clays and the Mitchell Cave Beds is unclear.

AGE OF THE STRATA

The maximum age for the strata is determined by the time of excavation of the caves. Attempts to date this event by geomorphic means by Colditz (1943), Frank (1971), and Francis (1973) suggest that it took place between the Middle Miocene and the Late Pliocene. Thus the strata in the caves could range in age from Middle Miocene to Recent.

Frank (1971) reports ^{14}C ages for his 'Unit 3 R.B.' (equivalent to the Bone Cave breccia unit) of 30,610 ± 2,110 and 22,570 ± 610. He also presents a series of dates for flowstone in the Phosphate Mine of about 40,000 years. While these datings are open to some doubt, being at the limit of the technique employed, they do indicate that the Mitchell Cave Beds extend well into the Pleistocene. Until recent work by M. Archer *et al.* in October, 1982 no stratigraphically-controlled collection of fossils had been made at Wellington Caves. What is presently known of the mammal material in museum collections (most of which is probably derived from the Bone Cave breccia unit) is consistent with a Pleistocene age. Dawson (1982) in reviewing the museum collections noted the absence of modern species of *Macropus,* and suggested a minimum age for the fauna of at least 20,000 years, and possibly greater than 37,000 years. On more tenuous grounds she argued that the fauna could be as old as 128,000 years. A Pleistocene-Recent age may therefore be assigned to the Mitchell Cave Beds.

The age of the Phosphate Mine Beds is problematical. Their unconformable boundary with the Mitchell Cave Beds and the outcrop of the Big Sink unit at ground level indicate a significant period of phreatic speleogenesis and surface erosion between the deposition of the Phosphate Mine Beds and that of the Mitchell Cave Beds. In their models for speleogenesis, Colditz (1943), Frank (1971), and Francis (1973) considered that the last time the water table was high enough to place the caves in the phreatic zone was during the Pliocene or Miocene. If this is the case then the unconformity must be at least Late Pliocene in age and the Phosphate Mine Beds a Tertiary deposit.

Preliminary palaeontological evidence as to the age of the Big Sink unit is equivocal. Some small tooth fragments extracted from it (SUP 14972) are from rodents and marsupials (J. A. Mahoney, pers. comm). These two groups have Australian histories extending into the Tertiary (Archer and Bartholomai, 1978) and more work is required before an age can be assigned to this material. L. Dawson (pers. comm.) has collected remains of *Protemnodon* sp. from the unit which, on the basis of present knowledge, are Late Pliocene to Pleistocene in age. Should the Big Sink unit be found to be Pleistocene in age the caves must have been in the phreatic zone more recently than Colditz, Frank, or Francis have inferred.

CONCLUSIONS

Wellington Caves were excavated by groundwater solution under low energy phreatic (nothephreatic) conditions which persisted while the phosphatic rim rock and lower units of the Phosphate Mine Beds were deposited. The level of the water table was not constant during this period and desiccation features in the laminite unit and the graded-bedded unit were produced at times of low water.

Following deposition of the graded-bedded unit a significant lowering of the water table took place leading to large scale mud cracking and the deposition of speleothem. After this phreatic conditions were again established and the conglomerate and phosphorite units were deposited. The water table again fell and vadose conditions were established in Big Sink, Bone Cave and the Phosphate Mine. Entrance facies deposits accumulated forming the Big Sink unit.

Following deposition of the Big Sink unit the water table rose significantly and a second period of cave excavation was initiated. This formed new caves within the Phosphate Mine Beds and enlarged those in bedrock. A period of surface erosion that planed off the surface, exposing the Big Sink unit, occurred at the same time as the caves were enlarged.

Vadose conditions were again established and the Mitchell Cave Beds deposited. The lower red unit and the upper red unit were deposited under dry vadose conditions similar to those existing in the caves today while the Bone Cave breccia unit was deposited under wetter conditions.

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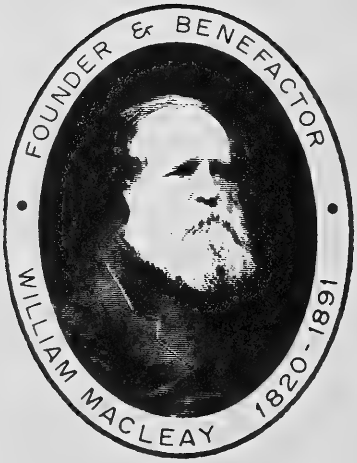
NATURAL HISTORY IN ALL ITS BRANCHES

THE LINNEAN SOCIETY OF NEW SOUTH WALES



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Cover motif: *Stigmodera imitator* (Coleoptera: Buprestidae), New South Wales and Queensland.
Adapted by Len Hay from *Proc. Linn. Soc. N.S.W.* 55, 1930, plate IV(6).

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LINNEAN SOCIETY
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VOLUME 107
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FOREWORD

Evolution & Biogeography of Early Vertebrates

From 16-26 February 1983, some twenty-five invited research workers from China, France, U.S.A., U.S.S.R., U.K. and Australia met to discuss problems of early vertebrate faunas. This meeting was the third of a series that began in Stockholm in 1967, and continued in Tallinn in 1976. Seminars were held in Sydney and Canberra, and field excursions organized to Forbes, Grenfell, Braidwood, Wee Jasper and Cobar.

In all, twenty-six papers were presented for discussion. Many of these were not intended for publication, but rather to provide new data or new interpretations for consideration by research workers active in the field. All the papers submitted for publication are presented in this volume.

We are grateful to the Council of the Linnean Society of N.S.W. for agreeing to publish this symposium, and to Prof. T. G. Vallance for his work as Honorary Editor.

We also wish to express our thanks to the following organizations for making funds available to bring overseas workers to the meeting:

25th I.G.C. Fund Committee of the Australian Academy of Science
Australia/China Council
Australian Museum
Australian National University.

In addition, we extend the thanks of the participants to the Australian Museum and the Australian National University for the use of conference facilities, and to these organizations, the Bureau of Mineral Resources (Geology & Geophysics), and Monash University for field support.

K. S. W. CAMPBELL
A. RITCHIE
J. W. WARREN
G. C. YOUNG

Editorial Note:

Dr Ritchie's paper, printed in this number, was not in fact presented at the Symposium.

The Choana, Maxillae, Premaxillae and Anterior Palatal Bones of Early Dipnoans

K. S. W. CAMPBELL and R. E. BARWICK
(Communicated by A. RITCHIE)

CAMPBELL, K. S. W., & BARWICK, R. E. The choana, maxillae, premaxillae and anterior palatal bones of early dipnoans. *Proc. Linn. Soc. N.S.W.* 107 (3), (1983) 1984: 147-170.

The attempt by Rosen *et al.* (1981) to demonstrate the presence of a choana in dipnoans revolved around the identification of the bones forming the rostrum and the anterior end of the palate of *Griphognathus whitei* as homologues of the vomers, palatines, maxillae and premaxillae of tetrapods. These homologies were postulated on the basis of similar patterns of bones in the two groups. Studies of the function of the bones in question and of their evolution from the primitive dipnoan condition, have shown that these conclusions cannot be sustained. *Griphognathus whitei* is a highly derived species with neomorphic bones formed in response to an unusual mode of feeding. The rostral ossification is formed by the fusion of bones after the dipnoans separated from their parent group, and it does not contain homologues of the premaxillae. In this instance, the attempt to establish relationship by outgroup comparisons without an analysis of the ingroup relationships in evolutionary and functional terms, is inappropriate. Studies of pattern and process must proceed hand in hand.

K. S. W. Campbell, Geology Department, and R. E. Barwick, Zoology Department, Australian National University, G.P.O. Box 4, Canberra, Australia 2601. *A paper read at the Symposium on the* Evolution and Biogeography of Early Vertebrates, *Sydney and Canberra, February 1983; accepted for publication 18 April 1984, after critical review and revision.*

INTRODUCTION

Dipnoans have either lost or never had marginal tooth rows. Since they appeared in the fossil record in the Early Devonian, they have had palatal and prearticular teeth which have displayed a variety of grossly different patterns and functions (Campbell and Barwick, 1983). Recently, several attempts have been made to interpret the nature of the dentition in primitive lungfishes. This is a matter of some importance, as the recent work of Rosen *et al.* (1981) has raised again the issue of the relation between the Dipnoi and the Amphibia, suggesting that they are sister groups. Implicit in that hypothesis is the view that marginal tooth rows were present in the ancestors of the Dipnoi, and persisted in that group at least during its early evolutionary phase, becoming modified as palatal teeth became more effective.

It was the supposed identification of the choana in the Late Devonian dipnoan *Griphognathus whitei* that suggested to Rosen *et al.* the need to reinvestigate dipnoan/tetrapod relationships. In that species, the identification of the choana is dependent on the recognition of the homologies of its surrounding bones, a point that is made clear in their introduction to the topic (Rosen *et al.,* 1981: 178-182). The choana in early tetrapods, exemplified by *Ichthyostega,* is surrounded by the vomer, the palatine and the maxilla, and these three bones were said to be recognized in *G. whitei.* The homologies proposed by Miles (1977) were abandoned. In our view, their case depends on special pleading, takes no account of variation in the number and the position of the bones present, ignores the fact that this species shows many derived characters quite unknown in earlier dipnoans, and makes no attempt to understand the structures concerned in functional terms.

In the ensuing discussion the arrangement of the bones in question will be described for *G. whitei,* their positions in other primitive dipnoan species will be discussed, an attempt will be made to interpret the structure of *G. whitei* in functional terms, the homologies of the bones will be outlined, and as a consequence it will be shown that no evidence supporting the presence of a choana in the Dipnoi can be derived from *G. whitei.* This being so, the case for the dipnoan/tetrapod relationship proposed by Rosen *et al.* is considerably weakened.

For discussion purposes, the bone names used by Miles (1977) and Rosen *et al.* (1981) are employed, but they are placed in quotation marks to indicate that we question their validity.

BONES AROUND THE ANTERIOR END OF PALATE OF *GRIPHOGNATHUS WHITEI*

'Dermopalatines 1 and 2' or 'Vomers'

At the anterior end of the palate is a pair of bones ('dermopalatine 1' of Miles, 1977, and 'vomer' of Rosen *et al.,* 1981), which can be recognized in all specimens examined to date. They continue the contours of the pterygoids. In some specimens, an elongate element ('dermopalatine 2' of Miles, and 'palatine' of Rosen *et al.*), which moulds itself around the inner margin of the posterior naris, lies posterior to the 'dermopalatine 1'. It separates the posterior nostril from the pterygoid in the specimen considered to be typical by the above authors. As Miles (1977: 163) indicated, this bone is not invariably present, and where it is present it varies considerably in length. In some specimens the same space is occupied by the expanded pterygoid, and in others a single dermopalatine (or vomer) flanks the pterygoid between the mid-line and the posterior naris (see Fig. 2**A-C**). It is necessary to justify the assumption that

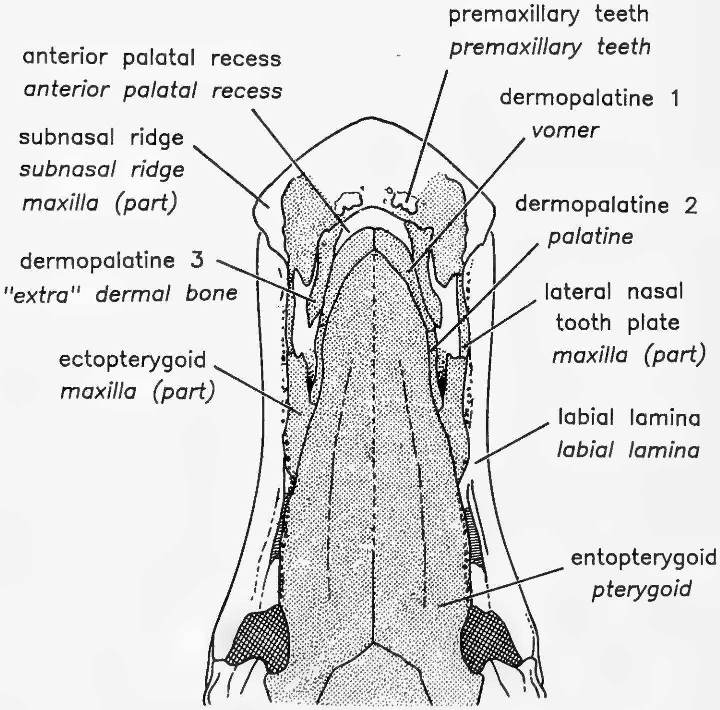


Fig. 1. Anterior part of the palate of *Griphognathus whitei* copied from Miles, 1977: fig. 6, and labelled with his bone identifications and those of Rosen *et al.,* 1981. The upper label (upright letters) is from Miles, and the lower label (italics) is from Rosen *et al.* Note that we consider the presence of dermopalatines 1 and 2 to be abnormal.

'dermopalatines 1 and 2' are typical of *G. whitei* and that this represents the primitive condition.

In the primitive genera *Uranolophus* (Denison, 1968), *Dipnorhynchus* and *Speonesydrion* (Campbell and Barwick, 1983) a single bone occupies the space on each side anterolateral to the pterygoid between the mid-line and the postnasal wall. The position in *Fleurantia denticulata,* in which Graham-Smith and Westoll (1937) have restored a single dermopalatine, is not clear. Because a single bone occupies the same space in several specimens of *G. whitei,* and a similar situation occurs in *G. sculpta* (Schultze, 1969: fig. 14), it is reasonable to conclude that this is the typical condition in *Griphognathus.* The second bone (i.e. the one labelled 'dermopalatine 2' by Miles and palatine by Rosen *et al.*) is an individual variation within *G. whitei* and is of no significance in determining homologies. Its presence is functionally related to the great increase in the distance between the postnasal wall and the anterior end of the palate. The occurrence of a single bone in all other Devonian genera indicates that this is the primitive condition and the use of the specimen of *G. whitei* with two 'dermopalatines' as typical of the primitive condition is unjustified.

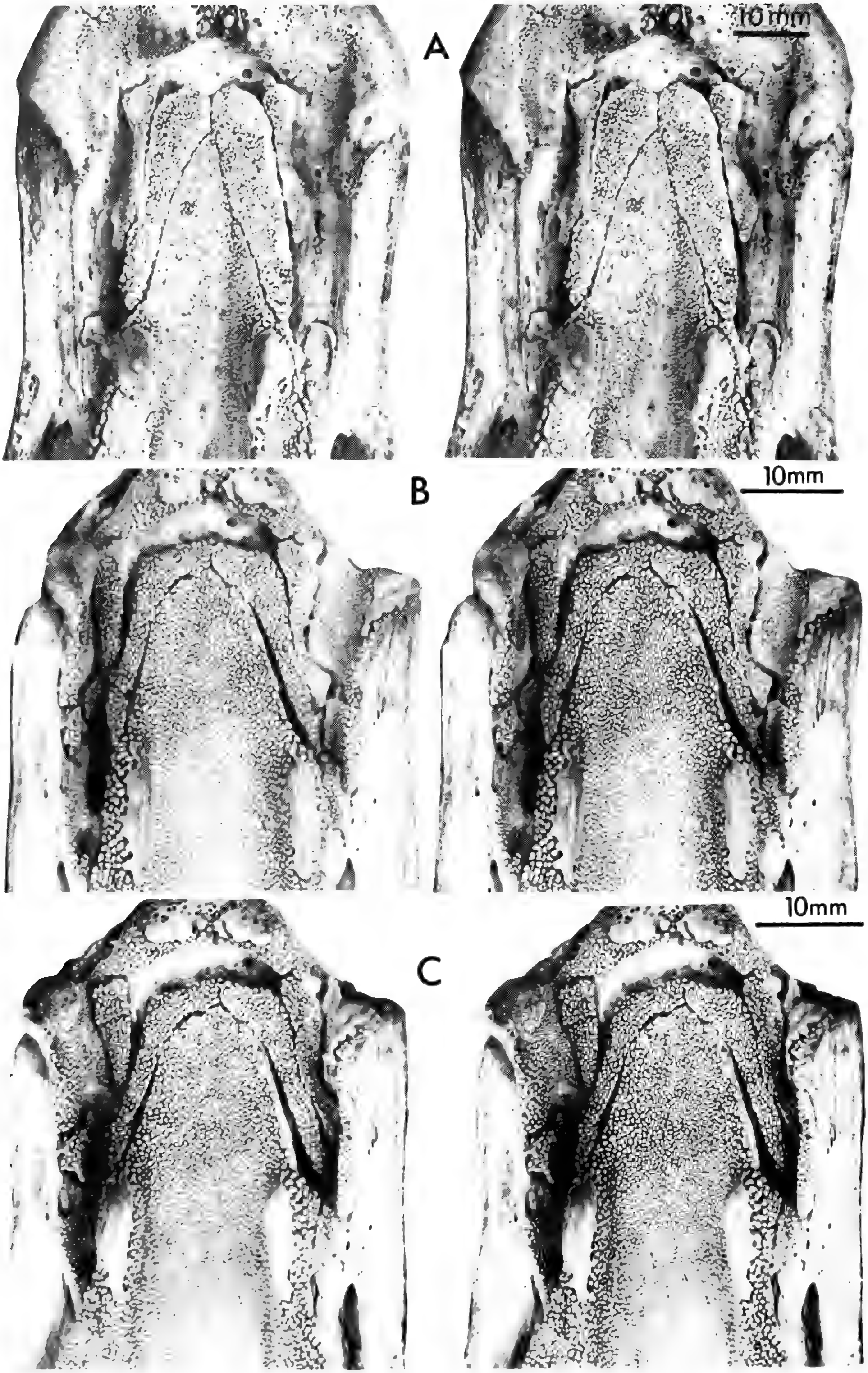
For present purposes the homology of the single bone between the midline and the post-nasal wall is not a matter of consequence, except in so far as it has quite the wrong relationships to be a palatine, a point to which we return later.

'Ectopterygoid' or 'Maxilla'

The bone immediately posterior to the 'dermopalatine' has similar characteristics, but it does not form part of the arcade continuing the palatal contours. Instead, its inner edge stands up abruptly from the pterygoid and then moulds itself to the ventral surface of the postnasal bar. This latter structure is well ossified in all Devonian dipnoans, and runs laterally to form a broadly expanding buttress against the inner surface of the roofing bone that contains the anterior part of the suborbital lateral line (Fig. 2**A-C**). The bone in question, which is interpreted as the 'ectopterygoid' by Miles (1977: fig. 57), and as part of the 'maxilla' by Rosen *et al.* (1981: 185, fig. 7A), is very thin, denticulated, and appressed to the surface of the postnasal bar. Laterally it is sutured against the concave and sharply defined labial lamina which is discussed below. It lies around the lateral and posterior edges of the posterior naris. Miles (1977: 180) gave a good account of the bone and its relationships. There is no doubt that it lies on the lateral face of the tectum nasi (above which lie the ramifying sensory tubules of the snout) as well as on the postnasal bar. Its outer edge, on which the denticles are slightly enlarged, is aligned with the outer edge of the lateral nasal tooth plates. It is clearly sutured against the ridge labelled 'endoskeletal ridge supporting tooth-ridge' by Miles (1977: fig. 78), as is shown on Fig. 2**A**, **B**.

'Lateral Nasal Tooth Plates' or 'Maxillae'

The anterior edge of the bone designated as maxilla by Rosen *et al.* (1981: fig. 7a) is not clear. In at least some of our specimens it is a short bone, and this is probably the norm. In ANU35641 one, or possibly two lateral nasal plates (Miles, 1977: 181) lie between its anterior edge and the subnasal ridge (Fig. 2**B**, **C**). These lateral nasal tooth plates consist of an almost horizontal outer, lateral sector, and a vertical inner sector that turns inwards slightly along its dorsal edge, partly to join with the 'dermopalatine 3' of Miles (see below), and partly to form the lateral margin of the anterior naris. They broadly follow the contours of the ventral surface of the tectum nasi. More than one lateral nasal tooth plate may be present, as was indicated by Miles (1977: 181), but it is difficult to distinguish between cracks and sutures on most specimens. The anterior edges of the lateral tooth plates are generally clear, though they vary slightly in position from specimen to specimen. Their contours continue smoothly into the concave ventral face of the rostral capsule.


A
10mm
B
10mm
C
10mm

It is of importance to establish that these tooth plates are sutured against endocranial bone, and that the sutures frequently open allowing them to fall free. Some confusion may arise from the identification by Miles (1977:180, fig. 78) of a separate entity named the labial lamina, which he characterized as 'an internal lamina of anterior bones in the infraorbital lateral-line series'. This lamina is said to lie against an endoskeletal ridge that supports the ventral edge of the lateral nasal tooth plates. The edges of the external dermal bones (probably 1a-c) are not inflected along this edge. Topographical relations and thin sections both show that the endocranium is deflected outwards to meet the external bones to form the main lamina (Fig. 3). The boundary between the endocranium and the dermal bones is difficult to distinguish clearly in the sections, but it is clear that the lamina as well as the ridge supporting the lateral nasal tooth plates is of endocranial origin. The tooth plates are not in contact with the external dermal bones 1a-c.

Such an arrangement is possible in *G. whitei* only because the dermal bones 1a-c are so elongated and the snout is so depressed. Species such as *Chirodipterus australis* have the postnasal bar standing up much more steeply so that it makes contact with bones 1a-c only along their dorsal edges (Figs 4**A**, 5**B**).

'Dermopalatine 3' or 'Extra Dermal Bone'

One other loosely articulated bone is present in this region in all specimens examined. It is labelled 'dermopalatine 3' by Miles, and as an 'extra dermal bone' by Rosen *et al.* (1981: fig. 7A). In both ventral and lateral aspects this bone is always strongly flexed. Its lateral edge forms the margin of the anterior naris, which must have been directed anteriorly from the nasal capsule. Its posterolateral edge was probably loosely articulated with the inner edge of the lateral nasal tooth plate, thus forming a continuous but flexible roof over the entrance space to the anterior naris. As Miles (1977: fig. 80a) has shown, this flexible junction is sometimes lost by fusion of the adjacent bones. In some specimens (BM P56054 and ANU35641), the 'dermopalatine 3' articulates with the posterior denticulated edge of the rostral capsule, but in others there is a gap at its anterior edge. This gap may have been occupied in life by yet another denticulated plate.

No equivalent of 'dermopalatine 3' is known from any other dipnoan. One may have been present in other long-headed forms such as *Fleurantia* or *Soederberghia,* but further material is needed. No short-headed species shows evidence of such a bone. Indeed, one would not be expected, because the anterior naris in such forms is situated well forward, immediately behind the edge of the notch in the rim of the rostral capsule. A similar argument would apply to *Uranolophus wyomingensis* in which the posterior edge of the notch for the anterior naris is sharply defined and stands up to form a steep non-denticulated rim.

Miles and Rosen *et al.* have been unable to homologize this bone with bones in osteichthyans or amphibians. The conclusion that it is neomorphic seems inescapable.

'Vomer' — A Median Unpaired Plate

Was a median unpaired bone present at the front of the palate of *G. whitei*? Miles (1977: 165) found the possibility of such a bone attractive because it 'would occupy the same morphological position as the vomer in *Chirodipterus* and *Holodipterus*'. He found no bone *in situ* in this position in his material, and we have found none in ours. One median non-denticulated bone (Miles, 1977: fig. 83) was treated as a possible candidate, but neither its shape nor its structure support this identification. Moreover, *G.*

Fig. 2. Views of the anterior part of the palates of two specimens of *Griphognathus whitei* showing the arrangement of the various denticulated structures. **A** and **C** are full ventral views of CPC22593 and ANU35641 respectively. **B** is of ANU35641 tilted slightly to the right. Scale = 10 mm.

whitei normally has neurocranial shelves to support the loose bones such as 'dermopalatine 1' and 'dermopalatine 3', but no shelf is present to support a median dermal bone. We consider that no such bone was present.

The only Devonian species for which unequivocal evidence of a median anterior unpaired bone exists is *Chirodipterus australis*. *Scaumenacia curta* as figured by Jarvik

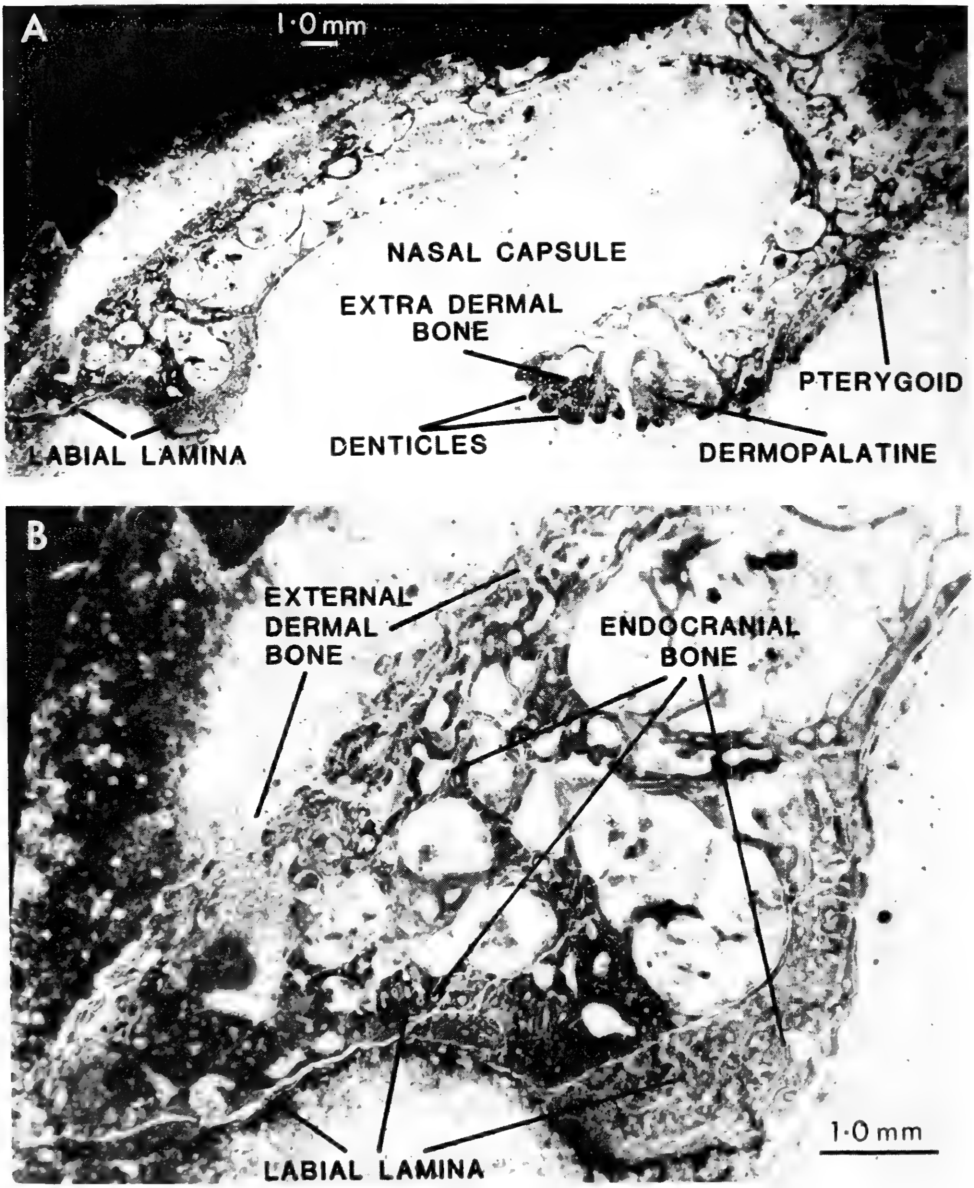


Fig. 3. Cross section of the nasal capsule of *Griphognathus whitei*. **A.** General form of the endocranial bone, lining the capsule; the denticle-bearing 'dermopalatine' and 'extra dermal bones' lying against the 'pterygoid' and the external dermal bones and labial lamina, the latter without the 'lateral nasal tooth plates' covering its inner surface. **B.** Enlargement of the labial lamina which is formed entirely of endocranial bone without an inflected cover of external dermal bone. Dark field illumination.

(1967: pl. 6, fig. 5) is said to show a bone of this type. Examination of the specimen has left one of us (KSWC) unconvinced. In addition to the specimens of *C. australis* mentioned by Miles, ANU35638 shows the median unpaired bone admirably (Fig. 5). None of the specimens of *C. australis* have the 'dermopalatines 1' meeting in the mid-line as they do in all three Early Devonian genera *Uranolophus, Dipnorhynchus* and *Speonesydrion.* Miles expressed the view that the 'dermopalatines 1' primitively met in the mid-line and paired bones (the vomers) lay in front of them. According to this view the 'dermopalatines 1' in *Chirodipterus* have become smaller and withdrawn from the mid-line, leaving a median space into which the now fused vomers have moved. Miles (1977: 175) has argued that the vomer 'is primitively paired in choanates, actinistians and actinopterygians', and that paired vomers are known in all the recent dipnoan genera as well as the late Palaeozoic *Sagenodus, Uronemus, Conchopoma* and *Monongahela.* Unfortunately no reason is given for homologizing the paired bones in these genera with the median unpaired bone in *Chirodipterus* (the 'vomer') rather than the paired lateral bones (the 'dermopalatines 1'), an hypothesis that seems to us to be at least equally probable. The outgroup comparison argument is irrelevant for purposes of determining whether these bones are the homologues of the 'dermopalatines' or the median unpaired 'vomer'. We conclude that no case has been made in support of the view that paired bones or an unpaired bone lay in front of the 'dermopalatines 1' in *Griphognathus whitei.*

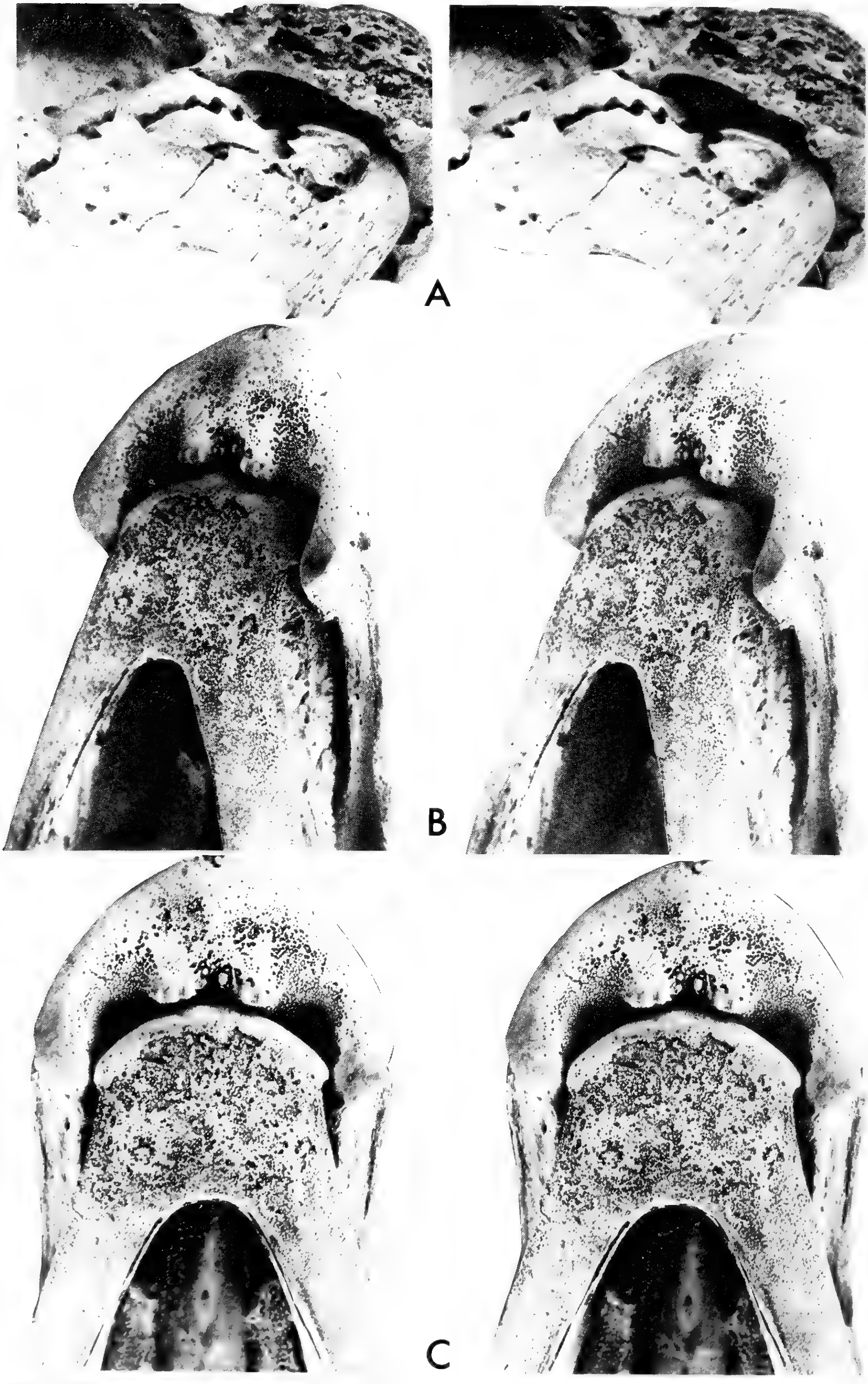
The Rostral Ossification

The denticulated parts of the rostral ossification remain to be discussed. This is a massive structure, largely covered by a sheeting of dentine and enamel (Smith, 1977: 33) that breaks down into denticles in the region of the notches leading to the anterior nares. Unlike most Devonian dipnoans, this structure has an extensive ventral surface produced from backwardly deflected external bone that forms a ventral cover for the anterior part of the ethmoid capsule. The lateral part of this cover, which forms the subnasal ridge of Miles (1977), lies well behind the anterior edge of the palate. This relationship is possible only because of the attenuation of the snout in *Griphognathus whitei.* It is quite impossible in shorter-headed forms, be they of the tooth-plated type like *Chirodipterus* or the non-tooth-plated type like *Holodipterus.*

No sutures are present on this surface, but topographically it is divided into three elements — a pair of pre-oral eminences, very prominent subnasal ridges, and very broad anterior narial notches. The pre-oral eminences usually carry a few coarse tubercles on their crests and smaller denticles on their lateral and posterior faces. The notches are broadly rounded and lined with a thin layer of denticulated dermal bone that extends posteriorly a considerable distance to meet the edge of 'dermopalatine 3', and then runs lateral to that bone until it meets the lateral nasal tooth plates. This surface continues laterally in a smooth curve up the inner face of the subnasal ridge.

Rosen *et al.* (1981: 180-181) refer to the tubercles on the pre-oral eminences as 'premaxillary teeth', and they believe that these eminences 'represent premaxillae that have fused with the bone of the snout'. It is not clear where these supposed 'premaxillae' and the 'bone of the snout' join. They also regard the slightly enlarged denticles that occur on the subnasal ridge in some specimens as 'maxillary teeth'. As has been shown above, the subnasal ridge is quite separate from the more posteriorly placed lateral nasal tooth plates, which they also regard as 'maxillary', but this ridge cannot be separated from the remainder of the rostral ossification which is not part of the 'maxillary'.

Interpretation of these bones should be made in terms of what is known about the rostral region of other Devonian dipnoans rather than by outgroup comparison. When that is done, a completely different picture emerges, as is shown below.


A
B
C

THE ANTERIOR AND POSTERIOR NASAL OPENINGS IN *G. WHITEI*

As was clearly shown by Miles (1977: fig. 57), the nasal capsules are relatively small and lie more posteriorly than in most other species. They are also more protected on the ventral side by the pterygoids than in any short-headed dipnoan known to us. The anterior opening for the nasal capsule must have been situated in the notch in the 'dermopalatine 1', and it must have entered the capsule from a slightly anterolateral direction. It would have had a depressed oval outline, and it must have been in a more posterior position than that indicated by Miles (1977: fig. 57). The posterior naris was in the position indicated in that figure, but its shape cannot be defined from the material at our disposal. The bone edges around the space for this naris are not always 'finished', and presumably the actual opening was in loose skin.

The anterior naris was therefore well behind the anterior nasal notch in the rostral capsule, quite unlike the situation in any known short-headed dipnoan with tooth plates. Forms such as *Dipnorhynchus* and *Chirodipterus* (Fig. 8) have large nasal capsules situated anterior to the dentition, and the anterior naris was placed immediately posterior to the anterior nasal notch. Similar comments seem to be applicable to *Uranolophus,* which is the most primitive of all the denticulated types, though in *U. wyomingensis* the capsule details are not completely clear. However, even the relatively short-headed denticulated types such as *Holodipterus* have much smaller nasal capsules that are partly covered by the pterygoids and adjacent denticulated plates, and the anterior naris must be situated well back from the anterior nasal notch which is itself denticulated.

The posterior naris in *G. whitei* was in a very posterior position relative to the front of the palate. It was tucked into the angle formed at the junction of the postnasal wall and the pterygoid. With a similarly small nasal capsule, the posterior naris of *Holodipterus* must also have occupied a posterior position. On the other hand, the posterior naris in *Dipnorhynchus* and *Chirodipterus* would have been further forward, being about half way along the length of the 'dermopalatine 1' (see Thomson and Campbell, 1971: fig. 29; Miles, 1977: fig. 67).

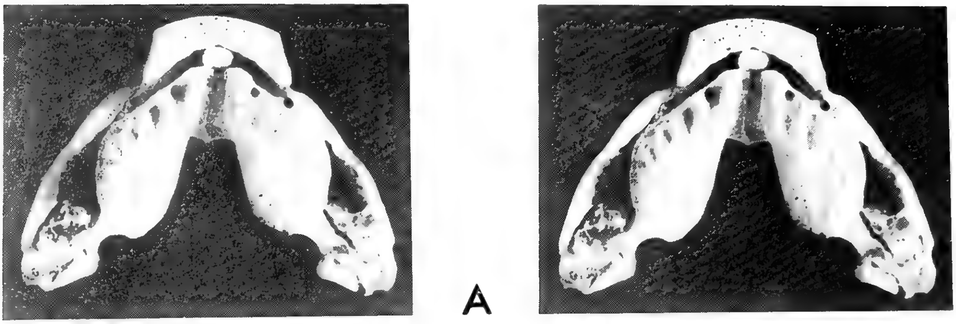
OCCLUSION IN *G. WHITEI*

The arrangement of the bones around the nasal capsules in *G. whitei* can be understood only if the occlusal pattern of the jaws is appreciated. Other long-headed dipnoans may share a similar pattern, but the only genus for which the specimens are sufficiently well preserved for this to be established unequivocally is *Griphognathus.* Several undistorted specimens of *G. whitei* have been found with the mandible preserved in position. These illustrate a number of points:

1. The largest 'prearticular' tusk passes lateral to the large pterygoidal tusk, and meets the ventral face of the postnasal bar. On some specimens, this bar has a distinct pit to receive the crest of the 'prearticular' tusk. Clearly the denticulated dermal bone (maxilla of Rosen *et al.*) on the surface of the postnasal bar served as a protection during full occlusion and also assisted with the holding of food. Such a relation is not possible in other dipnoans.

2. The crest of the 'dentary' passes with a shearing action between the den-

Fig. 4. **A.** Ventrolateral view of a weathered specimen of *Chirodipterus australis* (ANU35640) with the lower jaw in position showing the relation of the tooth plates to the postnasal bar. **B, C.** Two views of a specimen of *Griphognathus whitei* (CPC22593; see also Fig. 2**A**) showing the extent to which the lower jaw occludes the anterior nasal notches and the space along the inner edge of the labial lamina. Note that the lateral nasal tooth plates are missing, leaving a larger slit than would have occurred in life. Compare this situation with that of *C. australis* shown in Fig. 5**C**. Natural size.



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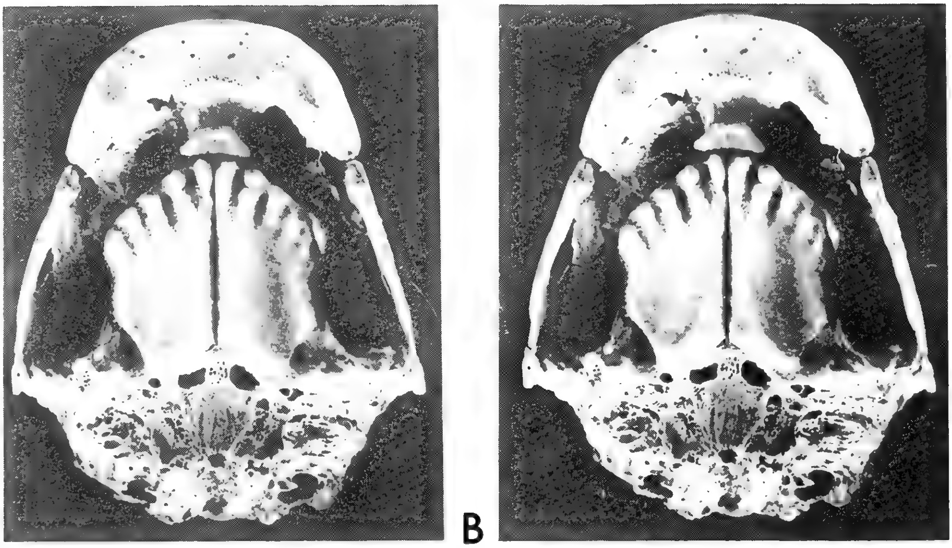

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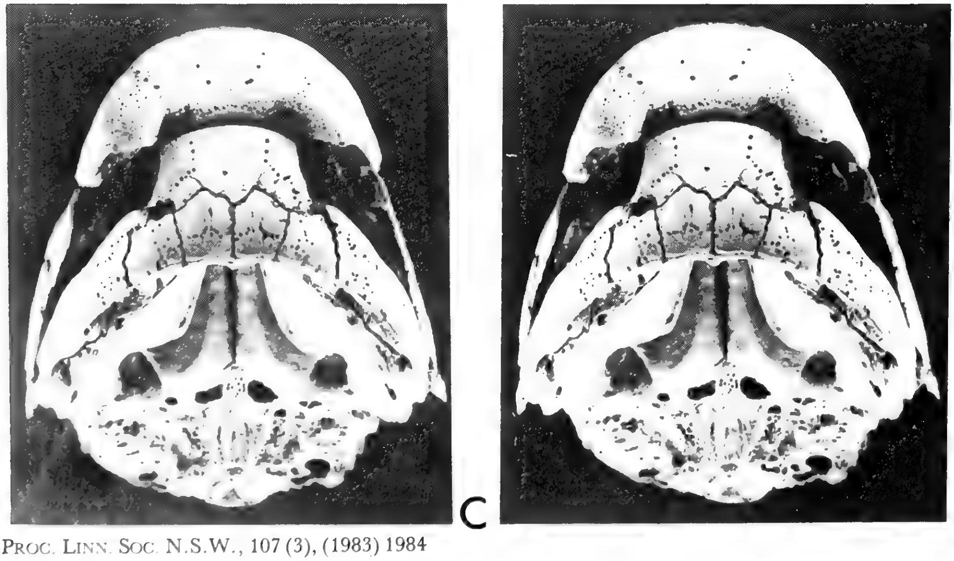

C

ticulated surface of the subnasal ridge and the lateral nasal tooth plates on its outer side, and the 'dermopalatines' on its inner side. Its crest then fits neatly into a groove that is roofed in part by the anterior palatal recess, the backwardly deflected bone of the rostral capsule, 'dermopalatine 3', and the inflected edges of the lateral nasal tooth plates.

3. The anterior edge of the 'dentary' lies behind the preoral eminences of the rostral capsule, and does not even contact the denticles on the posterior surfaces of these eminences. Articulated specimens show that the fit of the lower jaw is so tight that it cannot be moved forwards to make such a contact. The relationship indicates either a grasping or a shearing action which is almost exactly the same as that between the lateral parts of the 'dentary' and the lateral nasal tooth plates. The only difference is in the increase in size of the denticles on the preoral eminence. This modification would be expected in the light of the fact that the mouth opening was restricted to the space between the subnasal ridges (see Campbell and Barwick, 1983: 41), and special grasping structures would be necessary in this position.

4. At full occlusion both the anterior and posterior nares are completely covered by the crest of the 'dentary'. A slight gap remains between the 'dentary' and the anterior end of 'dermopalatine 3', but this would have left a very narrow passage between the anterior nasal notch and the anterior naris (see Fig. 4**B, C**). The fit is so close that the nasal apparatus could not be fully functional when the mouth was closed.

The above-mentioned features may not be unique in *G. whitei,* but they certainly are not present in any of the short-headed types with or without tooth plates. Even in *Uranolophus* the bite did not bring the 'dentary' into close contact with the nasal capsule or the post-nasal bar, and hence in this genus as well as in such tooth-plated forms as *Chirodipterus,* denticulated plates to cover these structures were unnecessary. Any explanation of such bones in *G. whitei* has to take into account the fact that they are not primitive but derived to serve a function related to the distinctive bite of this genus. Further, this distinctive bite occludes both the anterior and posterior nasal openings more effectively than does the bite of any of the primitive forms.

FUNCTION OF THE POSTERIOR NASAL OPENING IN DIPNOANS

The emphasis elsewhere in this paper is on structure, but in this section we examine the functional significance of the position of the posterior nasal opening inside the mouth. In so doing we are partly constrained by what is known of the functions of the living dipnoan genera, by what can be inferred of the structure of the nasal organs of fossils from the shapes of their surrounding hard tissues, and by information on the environment in which the early genera evolved.

Dipnoans are now thought to have evolved in the sea, and it is clear that even the most primitive genera had nasal capsules similar in structure to subsequent forms that became adapted to life in freshwater streams and lakes. Therefore we cannot accept the view that the dipnoan nasal apparatus evolved in response to special conditions associated with the freshwater environment, such as relatively anoxygenic standing water bodies, or ephemeral streams in 'old red sandstone' environments.

All three living dipnoan genera gulp air through their mouths. None respire through their nasal capsules (see Atz, 1952, for summary). *Neoceratodus* lives in quiet

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Fig. 5. A single specimen of *Chirodipterus australis* ANU35638. **A.** The isolated mandible showing the adsymphysial plate that occludes with the anterior median plate of the palate shown in **B. C.** Whole specimen with the lower jaw in position and showing the relatively open anterior nasal notch and the large labial spaces which indicate that the passage of water through the nasal capsule was little affected by closure of the mouth. Natural size.

water bodies that are often poorly oxygenated. *Protopterus* and *Lepidosiren* live in lakes or rivers, and have a capacity to aestivate. All three apparently swim to the top of the water and gulp air as required. Primitive dipnoans in the sea may not have been able to do this. They were all heavily ossified bottom feeders. However, even if they were able to use their fins and hydrostatic structures to get to the surface it can be safely assumed that like living species they gulped air and the nasal apparatus took no part in respiration. Even assuming that the so-called marine species were catadromous, and that in the sea they depended on gill respiration but in rivers and lakes they were able to respire by gulping air, the argument that the mouth had to be open to take in air would still apply. Moreover, the body design of these fishes would not permit seasonal, migratory habits, so a catadromous mode of life can be ruled out. We know of no structural or environmental evidence to support the view that primitive genera had a nasal respiratory capacity that has since been lost.

A second possibility is that the opening served a dual function — passage of water for olfaction and water from some accessory structure such as a nasal aspirator. Aspirators are known in some living teleosts that are either sessile or slow moving, and require some additional means for producing a water flow through the nasal capsule (Atz, 1952). Early dipnoans give evidence of being slow moving, but it would be difficult to argue a case for an aspirator unless there was strong morphological support from the structure of the bony lining of the nasal capsules. Inferences can be made from structures preserved in *Dipnorhynchus* (Thomson and Campbell, 1971: fig. 29), *Griphognathus* and *Chirodipterus* (Miles, 1977: 135), but these are not sufficiently precise to support or contradict this hypothesis, which must therefore remain as a speculation. One further point that may argue against the presence of an accessory aspirator is that *G. whitei* has a very small capsule, much smaller than those of the other genera, and little space would have been available for such a structure. In fact, closure of the mouth would compress the capsules, and it may well be that by appropriate use of valves water could be forced through the capsules by this means. However, we see no evidence to support an argument for a dual function of the posterior nasal opening involving an accessory organ. This does not rule out the possibility of a dual use of the water but, so far as we can determine, no adequate proposal of this kind has been put forward. The suggestion of Atz (1952: 376), for example, that the internal position would allow respiratory water to be used to prevent desiccation of the lungs and gills can only be regarded as improbable in view of the fact that the animals evolved in the sea.

Consequently we are forced to the conclusion that the function of this opening is to allow passage of water for olfaction, which is not surprising in view of the fact that this is its only function in living species.

Having decided that the function is olfactory, it does not necessarily follow that the posterior nasal opening is a posterior naris that has migrated into the mouth. Such a view assumes (a) that the position of the posterior naris outside the mouth is primitive for osteichthyans and (b) that in dipnoans this opening is not a neomorphic structure serving the same function as the posterior naris in other osteichthyans. Miles (1977: 147) has reviewed the first point. We are in agreement with him and with the large number of workers he quotes, that the posterior naris is primitively outside the mouth. Acceptance of the view that the opening is neomorphic, but serves the same function as a posterior naris, would require strong independent support, and this has not been forthcoming.

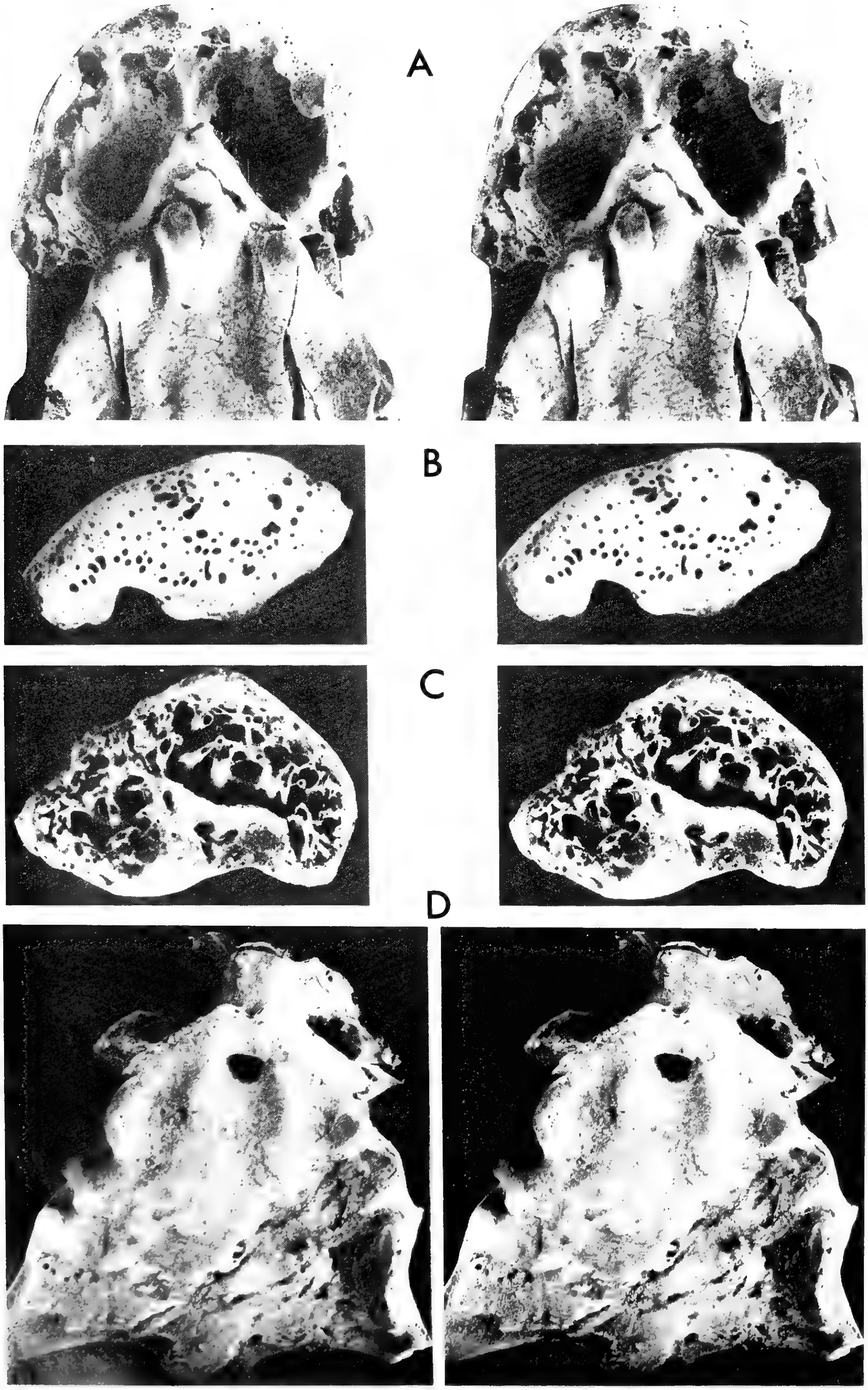
Hence we are left with the hypothesis that in the Dipnoi the posterior naris has migrated into the mouth. This hypothesis was championed by Jarvik (1942), and has received support from many later workers (Bertmar, 1965; Panchen, 1967; Miles, 1977). It has been further developed by Jarvik (1980). Evidence favouring this view rests largely on evolutionary functional morphology, but this does not depend on demonstrating a positive advantage for an internal opening. Rather it depends on showing that it is a concomitant of other adaptive changes characteristic of dipnoans.

Marginal to the mouth in the ancestors of the Dipnoi and other osteichthyans there must have been bones that had developed, or were in a position to develop, marginal teeth. It is not known if these bones were paired to form maxillae and premaxillae, or consisted of a greater number of smaller bones (but see Chang and Yu, 1984). The important point is that as dipnoans gained their distinctive palatal bite, these marginal bones atrophied. The row of suborbital lateral line bones, which were primitive in osteichthyans, thus came to border the mouth laterally. (A similar phenomenon seems to have occurred as early as the Devonian in the Actinistia, though this does not necessarily imply a close relationship between the two groups.) Anteriorly the situation is more complicated. However, assuming that the anterior marginal bones also atrophied, the anterior and posterior nares would have come into positions marginal to the mouth. Associated with this change, modification of the palatal bones must also have been taking place. The so-called 'prearticular' tooth plate was developing to meet the 'pterygoid' and 'dermopalatine' teeth, and these were concentrating to leave a marginal gap between themselves and the outer dermal marginal bones. This gap was skin covered. With further evolution the nares moved into this gap, and then assumed the standard dipnoan arrangement.

This view not only provides a functional interpretation of the movement of the nares, but it also accounts for the peculiarities of the lateral line system in the snout region of dipnoans so frequently commented on since Jarvik (1942) proposed that the incomplete infraorbital lateral line resulted from 'the fact that the lateral nasal wall with the fenestra endonarina communis and associated soft tissues and exoskeletal parts has been bent inwards below the nasal sac' (Jarvik, 1980: 393). If the lateral-line-bearing bones in the region of the nasal capsule were lost, the loss of the anterior end of the suborbital line and the ethmoid commissure would be neatly explained along with the fact that the supraorbital canal terminates anteriorly in a large pore. As has been shown by Campbell and Barwick (1982) the infraorbital canal in *Dipnorhynchus kiandrensis* passes inside the dermal bone in the snout and enters the mass of rostral tubuli. A recently-collected dipnorhynchid from Wee Jasper (see Fig 6**B, C**) shows a row of large pores around the anterior edge of the rostrum in a position approximating to the putative position of a continuation of the infraorbital canal, but these large pores all open into large rostral tubuli. The supraorbital canal, though maintaining its integrity, is also intimately connected with these tubuli.

These observations support the view of Westoll (in Lehmann and Westoll, 1952: 414) that the absence of the ethmoid commissure in dipnoans is secondary, but they do not support his general thesis. Rather, they suggest that the ancestors of the Dipnoi already had a system of rostral tubuli that functioned as seismosensory structures and were innervated by the profundus, ophthalmicus superficialis and buccalis lateralis nerves. When the ethmoid commissure was lost, the lateral line system, which in this region is innervated by the same nerves, became integrated with the tubuli.

We note Westoll's comments (in Lehmann and Westoll, 1952: 418) that Jarvik in his argument that the nares have been turned into the roof of the mouth in dipnoans 'relies heavily on the course of the r. maxillaris V in *Epiceratodus,* internal to the excurrent posterior nostril; but its relations to the vomer are very abnormal. Moreover, in the same fish the r. buccalis lateralis runs *outside* the nasal sac and at least the posterior nostril; in all fishes known to the writer this never passes *ventrally* to the posterior external nostrils'. Neither of these objections carries much weight. As we will show below, the homology of the 'vomers' in the Dipnoi is open to question, and the


A
B
C
D

course of the buccalis lateralis nerve became modified in early dipnoans as its connection with the rostral tubuli probably developed after the loss of parts of the anterior lateral lines.

This provides a feasible morphological and functional interpretation of the bone pattern, the nares and the sensory systems of the rostral region. It requires no assumption of taxonomic relationships.

Set in opposition to arguments of this type are those of Rosen *et al.* (1981) who have attempted to establish without reference to function, evolutionary history or environment, that the posterior nasal opening in dipnoans is a choana. They have relied on the determination of bone homologies in *G. whitei.* We now turn to a discussion of this attempt.

HOMOLOGIES OF BONES AROUND THE ANTERIOR END OF THE PALATE IN DIPNOANS

The pattern of bones in this region varies considerably from genus to genus, and there is conflict of opinion on homologies *within* the Dipnoi. Authors usually state their conclusions without indicating what criteria have been used. The situation is further confused by the use of bone names defined for other groups, so that one is unsure if completely unlike bones in the Dipnoi (say the unpaired 'vomer' of *Chirodipterus* and the paired 'vomers' of *Neoceratodus*) are homologized by comparison with non-dipnoan vomers, or by direct comparison with other dipnoans.

The logical approach to this problem is to argue a set of internally consistent homologies for the Dipnoi first, and then to examine the possibility of determining the relations between these and the bones of other groups.

Premaxilla

Miles (1977) and Rosen *et al.* (1981) assert that a premaxilla is present, the former author not attempting to set limits to the bone, and the latter authors restricting it to the dentigerous bone between the anterior nasal notches. As was shown above, there is no evidence to suggest the presence of paired bones in this region of *Griphognathus* (or any other described genus), and consequently argument in favour of homologies with other groups is rendered difficult, if not impossible. Rosen *et al.* (1981: 185) use morphological criteria to identify the premaxillae — 'they bite outside the lower jaw, they are the most anterior teeth in the upper jaw, and lie immediately in front of the anterior palatal recess . . .'. Elsewhere (pp.180-181) these authors add the criterion that they are 'in series with a more posterior upper jaw dentition (as are premaxillae with maxillae) . . .'. Miles (1977:186-187) offers a phylogenetic argument in support of his view — dipnoans are teleostomes that are collateral descendants of crossopterygians, and hence would be expected to share in the possession of premaxillae and maxillae. In addition, he comments that these identifications 'are not seriously contradicted by the criterion of morphological relations, for both the lip area and the lateral nasal tooth plate bite immediately outside the dentary'. What is more, these

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Fig. 6. **A.** Anterior palatal view of *Dipnorhynchus sussmilchi* (ANU18815) showing the fused-in 'dermopalatines' and the boss formed from the anterior median bone, as well as the distance between the occlusal surfaces and the postnasal wall. **B, C.** Anterior and posterior views of a snout fragment from an undescribed dipnorhynchid from Wee Jasper, N.S.W. (ANU36519). Note the pores (1) associated with the main lateral line canal which is indicated by the arrow, and the irregular row of pores (2) in the position of the infraorbital canal, but which open directly into the tubes of the ethmoid capsule. **D.** An isolated palate of *Speonesydrion iani* (ANU35646) showing the fused-in 'dermopalatines' and the space where the anterior median bone has failed to ossify or has fallen out. Compare this with the specimen of *D. sussmilchi* figured by Thomson and Campbell (1971: fig. 72). Natural size.

identifications 'avoid the assumption that the lip area and lateral nasal tooth plates are new structures'.

As indicated above, the matter should be approached first using data derived from the dipnoans themselves. After all, a statement of dipnoan relationships may be seriously modified by an interpretation of the homologies of these bones *within* the Dipnoi. It is illogical to decide first what the broad relations of the Dipnoi are, thus restricting the options in any discussion of homologies within the Dipnoi especially as these homologies are then used to identify a choana which becomes a significant part of the argument supporting the initially-accepted statement of broad relations.

It has been known for years that primitive dipnoans had highly ossified snouts, which seemed to be formed of a single massive rostral structure. Posterior to this was a large number of small dermal bones. These features are well shown by *Dipnorhynchus,* and they also occur in *Speonesydrion.* Denison's discovery that in *Uranolophus* the small bones continue over the rim of the snout to the edge of the anterior palatal recess, showed that in the most ancient genus no paired marginal bones had yet formed. We have examined Denison's material and agree completely with his interpretation of both the snout and the anterior bones of the mandible, which shows similar small plates. There is no evidence that the plates result from cracking — several show finished edges. (Incidentally, this pattern of small bones is retained in some species until the Late Devonian). *Uranolophus* indicates to us that the Dipnoi separated from the stock that was ancestral to them and their nearest neighbours *before* the bilateral symmetry of the paired external dermal bones of the rostral capsule of osteichthyans became established. (For further discussion, see below). No dipnoan described up to the present time shows pairing of these bones, but rather a single continuous sheet of bone. The pairing referred to by Rosen *et al.* is merely the bilateral symmetry of a single fused entity, which developed long after the dipnoan line was established.

In the second place, these bones are not tooth-bearing in the normal sense. In some genera they carry crude irregular tuberosities which no doubt enabled the animal to grasp passive food more effectively than it could with smooth bone. However, in other genera, including the most primitive ones — *Uranolophus, Dipnorhynchus* and *Speonesydrion* — no such tuberosities are present. In the genera in which tuberosities occur, the front edge of the mandible passes close behind them on closure, producing a grasping or shearing action. In the more primitive genera such a relation had not developed. The tuberosities are best regarded as secondary, derived several times, and of no phylogenetic significance.

In the third place, the fact that they bite outside the lower jaw is strictly irrelevant for the identification of maxillae and premaxillae. If the marginal bones of the Dipnoi were derived independently within the group by the fusion of a number of small bones, precisely the same situation could occur. After all, marginal bones in the two jaws should have some occlusal relationship. What else would one expect if they were to form an efficient system? But Miles comments that the relationship is not simply between these bones and the lower jaw, but specifically with the 'dentary', making it necessary to argue for the existence of that bone. As indicated by Denison (1968: 378) a good case can be made for the view that the 'dentary' like the 'premaxilla' is the result of fusion of small bones, and this fusion must also have occurred *after* the dipnoan stock became isolated.

Fourth, the argument that the bones lie in front of the anterior palatal recess is difficult information to handle. The recess is a space of unknown function anterior to the palate, and found in a variety of primitive actinopterygians, crossopterygians and tetrapods. Being only a space, and lying in different relationships with the bones behind it, can we say that it is a homologous 'structure' in all these groups?

Finally, the argument that these bones are in series with more posterior dentigerous bones identified as maxillae is really only a statement that they believe that the subnasal ridges are parts of maxillae, a position that Rosen *et al.* make no attempt to justify.

We conclude that no sound argument has yet been proposed to support the view that the median part of the rostral capsule with its tuberosities is the homologue of the premaxillae in other vertebrates.

On the other hand, the presence of an unconfined anterior narial opening in all dipnoans, and the presence of numerous bones at the rostral margin in the primitive forms, suggests that their upper lips are formed of external dermal bones that have been reflexed to various degrees on to the ventral surface of the rostrum. In some long-headed genera, such as *Griphognathus,* this reflexed area is very extensive and bears tuberosities that are merely irregularities in the enamel-coated dentine covering a continuous unpaired rostral bone. If bones homologous with the premaxillae of tetrapods were ever present in dipnoans, they have been lost during this reflexing process. The rostral capsule was formed by the fusion of small bones that were all originally on the dorsal and anterior surfaces of the head, posterior to the margin of the mouth.

Anterior Median Bone

In *Chirodipterus* the bone considered by Miles to be a vomer is opposed by a single bone in the mandible. No articulated specimens of *Dipnorhynchus* are available, but it is clear that the dentary would occupy most of the anterior palatal recess, and the triangular median area on the mandible (the adsymphysial plate) would oppose the anterior ends of the joined 'dermopalatines'. Consequently, there is no possibility of a median palatal bone of the same type as in *Chirodipterus* lying in front of the 'dermopalatines' in *Dipnorhynchus.*

However, ANU 18815 shows the median anterior palatal boss to be composed of three sections. Two are on the anterior ends of the pterygoids, and the unpaired median one is semi-isolated from them. The interpretation of this single boss has been difficult. Does it result from the inwards growth of the 'dermopalatines'? If so, why is it unpaired? Is it an isolated element? Another dipnorhynchid from Wee Jasper (ANU36508) has a space from which the median bone appears to be broken out cleanly, suggesting that it was a single element. The position is complicated by the presence of a natural gap in this position in one specimen of *D. sussmilchi* BMP33699, and in the only known palate of *Speonesydrion.* These gaps could be best explained by the failure of a median element to ossify rather than by the failure of the well-developed 'dermopalatines' to occupy the space.

If it is agreed that a single median bone is present in these primitive forms, a new explanation for the median bone in *Chirodipterus* becomes possible. As the 'dermopalatines' retreated in the manner suggested below, the median element came to lie at the front edge of the palate. This process would be accompanied by the gradual isolation of the median 'adsymphysial plate' in the lower jaw. During subsequent evolution, these median plates in both the palate and the mandible have been lost.

This solution to the problem of the median plate has interesting consequences. (a) It explains why the bone is single. Miles in regarding it as a vomer had to explain why the vomers had fused. (b) It offers an adequate explanation of why the isolated adsymphysial plate of the mandible appears and then disappears during evolution. No explanation of this has previously been produced. (c) It accounts for the absence of a median plate in genera such as *Uranolophus* and *Griphognathus.* Other workers have had to assume that the plate had been present, but was not preserved.

We suggest that this bone is unique to dipnoans and that it is present only in

Devonian genera. We have no evidence that it was ever present in the denticulated palate line — certainly there is no evidence of its existence in *Uranolophus* in which the 'dermopalatines' meet the pterygoids apparently without an intervening median bone. However, the sutures between the parasphenoid and the pterygoids in the denticulated types are usually very difficult to observe, and we cannot be sure that the bone under discussion is absent. It will be obvious that we are not suggesting that this bone is the homologue of the bones referred to as vomers in *Neoceratodus* by most workers.

We will refer to this element informally as the *Anterior Median Bone,* preferring to do this rather than provide a new formal name.

Anterior Paired Palatal Bones as Dermopalatines or Vomers

As indicated above, these bones are represented by single paired elements in the primitive genera *Uranolophus, Dipnorhynchus* and *Speonesydrion,* in all of which they are sutured against or fused with the 'pterygoids', meet in the mid-line anteriorly, extend back to the postnasal wall, and flank the posterior naris.

Among later Devonian genera with tooth plates, paired bones in a similar position are known with certainty only in *Chirodipterus.* However, in that genus they are smaller than in the primitives, do not meet in the mid-line, and have become quite free of the 'pterygoids'. Although paired plates that may be homologues have been reported from other Devonian and Carboniferous genera (see Miles, 1977: 174), they are not preserved in position. In the early genera these paired plates are opposed by the anterior parts of the 'prearticular' tooth plates which extend well forward into the arch of the 'dentary'. In *Chirodipterus* the edges of the 'pterygoid' and 'prearticular' tooth plates match precisely. The 'dermopalatines' do not take part in the bite, and consequently they are in process of reduction. In later genera such as *Sagenodus* both upper and lower tooth plates become smaller and more sharply defined, with marginal addition of cusps taking place at a level well outside the occlusal surface (Smith, 1979). Clearly the 'prearticular' dentition was not in contact even with the margins of the 'pterygoid' dentition, and so functional 'dermopalatines' were not possible. It is reasonable to conclude that the trend to reduction seen in *Chirodipterus* was continued in later forms, and that the 'dermopalatines' were lost.

Among Devonian non-tooth-plated genera, paired anterior palatal bones are known in *Uranolophus, Griphognathus, Fleurantia,* and possibly *Holodipterus.* Insufficient detail is available to corroborate their presence in the post-Devonian *Uronemus,* but they seem to be retained in *Conchopoma.* The bones considered by Schultze (1975: fig. 5) to be vomers in *Conchopoma gadiforme,* lie at the front end of the pterygoids and the expanded parasphenoid, and must be adjacent to the posterior naris. We conclude that in this line they are retained because they provide a surface against which the broad flat basibrachial tooth plate can function.

The question of the homologues of these bones must now be considered. Miles considered them to be dermopalatines because he inferred that they lay against the pterygoids and behind the vomers (or vomer). This argument does not hold if the so-called 'vomer', in the primitive forms in which it is known, originated behind rather than in front of them. In any case, the palatines in primitive tetrapods lie well away from the mid-line and are commonly behind the choana. Topographically it is difficult to argue for this homology. Rosen *et al.* consider these bones to be vomers. They ignore the existence of the median bone in *Chirodipterus* and this enables them to avoid one significant difficulty in making the broad general comparison that is the basis of their determination. The pattern alluded to, however, depends also on the regularity of occurrence of the bone behind their 'vomer' — the one they refer to as the 'palatine' (Rosen *et al.,* 1981: fig. 7). We have shown that this bone is irregularly present in *G. whitei* and probably is only an individual variation. Consequently, the general pattern argument fails and it is necessary to develop other criteria for the establishment of the homology of the bone.

Denticulated Bones on the Labial Lamina, Tectum Nasi and Postnasal Wall — are they Ectopterygoids, Lateral Nasal Tooth Plates or Maxillae?

Rosen *et al.* (1981: 186) interpreted these bones as maxillae because their denticles bite outside the lower jaw, and 'in no known gnathostome do palatal teeth bite outside the lower jaw'. This argument assumes that if teeth are not 'palatal' (without defining what is meant by that term) then they must be either maxillary or premaxillary. Another possibility, of course, is that they are associated with neither the normal palatal bones nor the normal marginal bones, but are secondarily developed for some new function. Moreover, these bones do not form part of the external dermal series, as they should if they are maxillaries. As shown above, the anterior bones lie on an endoskeletal ridge against the *inner* edge of the labial lamina (which is of endocranial origin) and form a lining on the neurocranial tissue lateral to the nasal capsule, whereas the posterior bones lie directly on the postnasal bar and extend forwards on to the labial lamina. All along their lateral edges they are well separated from the external dermal bone. These relationships would be entirely unexpected for a maxilla.

The difficulty of maintaining the distinction between 'palatal' and 'marginal' bones implied by Rosen *et al.* in the above quotation, is emphasized by the fact that their maxilla is interpreted by Miles (1977: 163) as an ectopterygoid. Though the reason for this homology is not explicit, it presumably is simply that Miles sees the bone as lying in series behind the dermopalatine, and lateral to the entopterygoid against which it is sutured. Again it is an overall pattern of bones that is being interpreted, and the pattern one sees depends on the model being used for comparison.

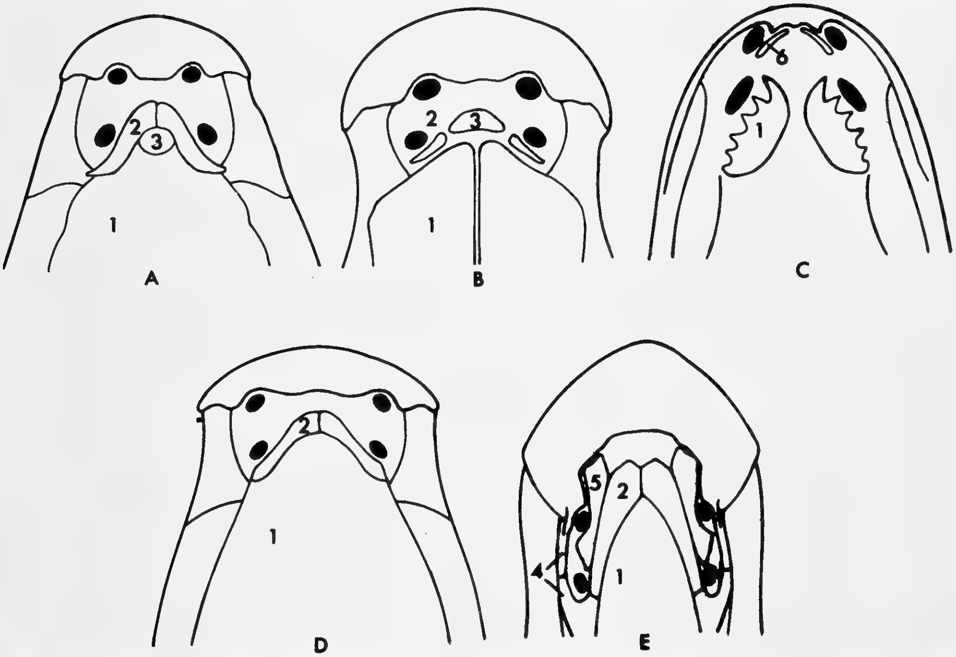

Fig. 7. Diagram showing plate homologies at the anterior end of the palate in **(A)** *Dipnorhynchus,* **(B)** *Chirodipterus,* **(C)** *Neoceratodus,* **(D)** *Uranolophus* and **(E)** *Griphognathus.* The bone names in quotes are not to be considered as homologues of bones of the same name in tetrapods. 1 = 'pterygoid', 2 = 'dermopalatine', 3 = anterior median bone, 4 = lateral nasal tooth plates, 5 = extra dermal bone, 6 = isolated lip bone. Nares black. Each diagram is the same width across the posterior nares.

As has been shown in the section dealing with occlusion, the elongation and depression of the snout, in association with the distinctive mode of feeding, results in the lower jaw coming into contact with the postnasal bar, and the lateral and ventral walls of the nasal capsule. These surfaces not only require protection, but they also form a significant part of the biting surface. The 'dentary' shears past the lateral nasal tooth plates, and the tusks on the 'prearticular' meet the denticles on the postnasal bar. Such an arrangement is not possible in highly arched forms whether they are of the tooth-plated or denticulated types. The postnasal bars of *Chirodipterus, Dipnorhynchus* and *Uranolophus* were situated some distance dorsal to the occlusal surfaces and were embedded in soft tissue (Figs 4**A**, 6**A**; Denison, 1968: fig. 9A). Moreover, the junction of the postnasal bar in *Uranolophus* with the subnasal ridge shows that no labial lamina was present and therefore there would be no lateral nasal tooth plates of the kind seen in *Griphognathus*. If other toothplates were present on the inner face of the postnasal ridge, they have not been preserved. Some denticulated plates are known in *Holodipterus,* but their relationships are unknown (Miles, 1977: 168, fig. 72). They are not necessarily precise homologues of those in *Griphognathus*.

We conclude that the maxillae (excluding the subnasal ridges) of Rosen *et al.* (1981), and the ectopterygoids and lateral nasal tooth plates of Miles (1977), are neomorphic in long headed dipnoans, *Griphognathus* being the only genus in which they are well known.

'Dermopalatine 3' or 'Extra Dermal Bone'

This bone meets the crest of the 'dentary', serving to form part of the bite, and to protect the ventral face of the nasal capsule and the anterior naris. It is also a neomorphic structure in this group. This view is implicitly supported by the work of Miles and Rosen *et al.,* because 'dermopalatines' are not known in this position in any other group, and the term 'extra dermal bone' is an acknowledgement that it has no homologue in other groups.

Summary

Jarvik (1972) and Bjerring (1977), depending mainly on embryological evidence, have also offered an independent interpretation of the bone homologies of the palate. This work is briefly summarized by Jarvik (1980: 397-404), and it is unnecessary to consider most of the detail here. The essential points are: (a) The homologies of the 'vomers' in forms such as *Uranolophus* and *Neoceratodus* are questioned, those of *Uranolophus* being regarded as 'vestiges of the external exoskeleton of the snout which secondarily has been displaced inwards into the mouth cavity', and that of *Neoceratodus* being 'formed by horizontal epal dental plates' of the terminal gill arch (Jarvik, 1980: 402-403). (b) The exoskeleton of the snout that has migrated into the mouth cavity has been 'partly retained in Devonian dipnoans and has disintegrated into a great number of exoskeletal elements. These elements, the subnasal plates, discovered by Miles (1977) and by him referred to as tooth plates or interpreted as ectopterygoids and dermopalatines were all situated in the mucous membrane in the roof of the mouth underneath the nasal cavities. To this category belong also the "lateral nasal plates" which were interpreted as vestiges of the maxillary' (Jarvik, 1980: 430).

We agree that the homology of the 'vomers' has not been established by previous workers, and it will be apparent that we disagree with Jarvik and Bjerring on this point, though we have no comment on the embryological approach as such. We also disagree with the view that the so-called 'subnasal plates' are remnants of the external dermal bones, because they seem to appear only late in dipnoan history associated with the derived flat-snouted types. It is preferable to regard them as new structures developed in the skin below the nasal sacs to serve protective and grasping functions.

The paired anterior tooth-bearing plates in *Neoceratodus,* commonly referred to as vomerine tooth plates, remain a problem. Unlike the paired plates in such forms as *Chirodipterus* (the 'dermopalatines') which lie behind the posterior nares, these plates lie mesial to the anterior end of the nasal capsules, and posteromesial to the anterior nares. Topographically it is difficult to argue a case for the homology of these 'vomerine tooth plates' and the 'dermopalatines' of *Chirodipterus*. It is also impossible to make a convincing argument for homologizing them with the 'anterior median bone' of *Chirodipterus*. Another possibility which is suggested by their position, by the fact that the upper lip turns back into the buccal cavity, and by the lack of ossification of the rostral region in post-Devonian dipnoans, is that these 'vomerine tooth plates' are the remnants of the median part of the upper lip — the so-called premaxillary of Miles and Rosen *et al.* The embryological work of Kemp supports this view. Her illustration of stage V in the developmental series (Kemp, 1977: pl. 4A) shows the vomerine tooth plates erupting just behind the fold of epithelium running between the anterior nares — that is, along the edge of the soft lip.

A summary of the inferred homologies of the various elements in the genera under discussion is given in Fig. 8.

BUT IS IT PARSIMONIOUS?

In suggesting that the anterior part of the palate of *G. whitei* contains several bones neomorphic in long-headed dipnoans, and that other bones such as the 'vomer' in *C. australis* cannot be homologized with bones in similar positions in other osteichthyans and tetrapods, we will be accused of having failed to use parsimonious argument. We reiterate, however, that parsimony is not a mode of argument to be used in the development of hypotheses about homology. If parsimony has any value at all in such discussions, it is only as a device for deciding between two or more hypotheses derived on other grounds, if analysis shows that these hypotheses have equal explanatory merits (Campbell and Barwick, 1982: 520). In such instances it may be preferable to choose the hypothesis that requires the least number of assumptions, but such a choice confers no special value on the hypothesis. It merely becomes the first basis for further work.

We have examined the relationships of cranial bones within the Dipnoi, taking into account a) the evolution of structures during the Devonian, b) the functional relationships of the bones around the anterior end of the palate and those in the lower jaw, as well as the tooth plates and other food reduction mechanisms, and c) the precise relationships of the bones in question to one another, to the neurocranium and to the nasal capsule. This examination leads to the conclusion that certain bones marginal to the buccal cavity in Devonian dipnoans were not in that position in their ancestors, and that other bones are neomorphic. In other words, account has been taken of evidence from morphology, function and sequence to reach conclusions about homologies.

The alternative hypotheses take no account of the level of evolutionary advancement of the animal — they take *G. whitei* to be primitive in the number and arrangement of the anterior palatal bones when it is acknowledged to be advanced in most of its other skull characters, and there is no supporting evidence of the presence of such bones in the genera generally acknowledged to be primitive. Nor do they consider the possibility of special structural requirements for the function of such an aberrant organism as *Griphognathus whitei*. Instead, they depend on the supposed recognition of similar patterns in this animal (taken as a representative primitive dipnoan), and other osteichthyans and tetrapods. That such an approach has led Miles and Rosen *et al.* to such disparate results, without any means of deciding which is correct, shows that pattern recognition of itself does not provide an adequate approach. To claim that their methods are more parsimonious than, and therefore preferable to, one requiring the postulation of neomorphic structures, even though the latter embraces more wide-

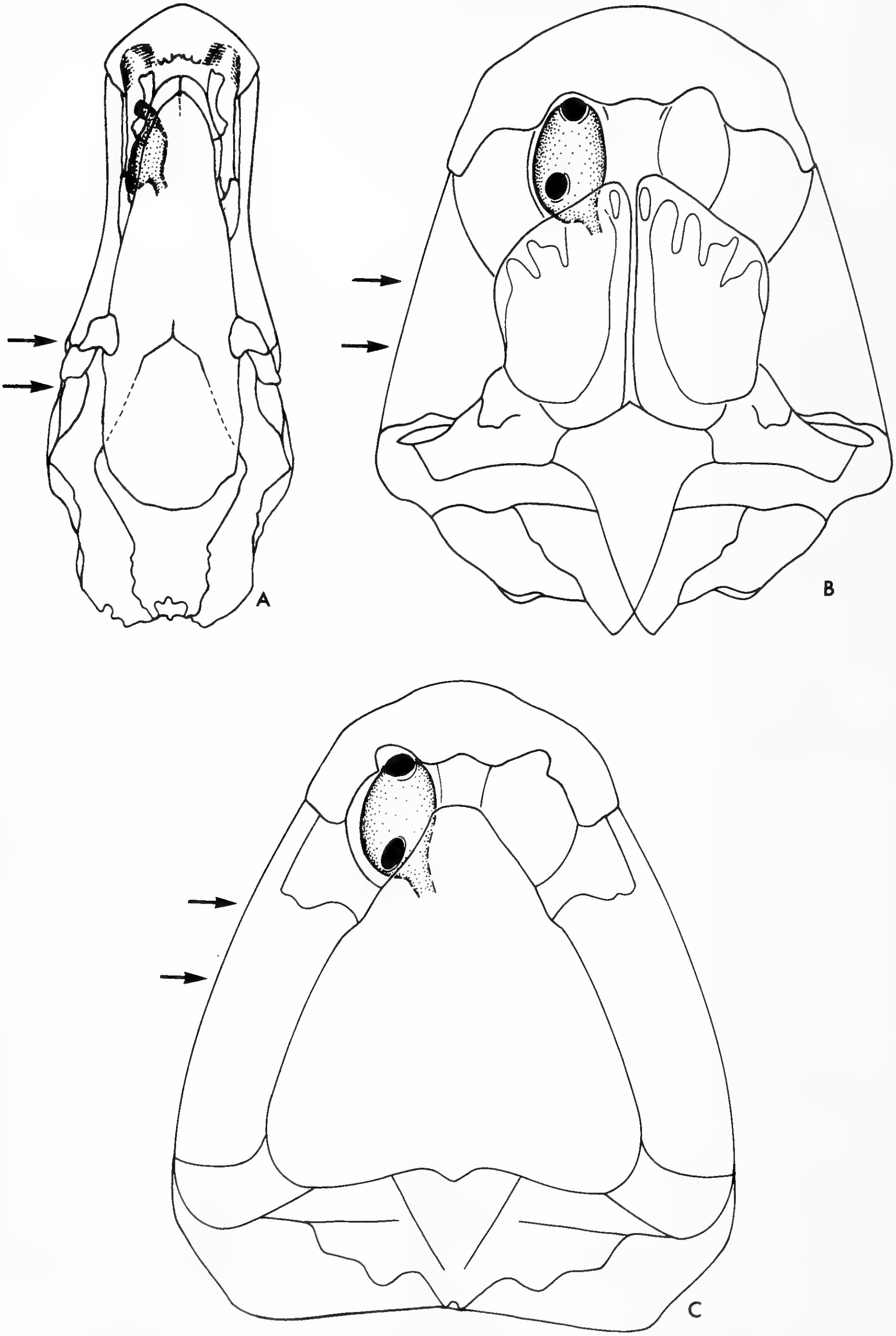

Fig. 8. Comparative diagram of **(A)** *Griphognathus,* **(B)** *Chirodipterus* and **(C)** *Dipnorhynchus* to show the position and size of the nasal capsule relative to the palate and the orbits. Positions of anterior and posterior nares (in black) are inferred from the structure of the surrounding bones, but we have no control on their shapes. Position of orbit indicated by arrows. Skulls reduced to the same length.

ranging data including the bone pattern and its origin and function, as well as the palaeoecological and stratigraphic evidence available from Devonian rocks, is simply irrelevant.

CONCLUSIONS

1. The attempt by Rosen *et al.* to establish the existence of a choana in *Griphognathus whitei* by homologizing bones around the posterior nasal opening with the palatine, maxilla and vomer of tetrapods, fails.
2. Several neomorphic bones are present around the anterior part of the palate of *G. whitei.* These are formed in long-headed dipnoans in response to a derived mode of feeding which is also reflected in the elongated depressed snout.
3. The so-called 'vomer' in *Chirodipterus australis* is an unpaired median bone derived from an element that originally lay behind the paired 'dermopalatine' elements in *Dipnorhynchus* and *Speonesydrion.*
4. The identification of 'vomers' and 'palatines' in dipnoans at all evolutionary stages is called in question.
5. Functional study of the nasal openings in living and fossil dipnoans indicates that they are incurrent and excurrent nares that have migrated into the mouth in response to the loss of marginal bones.
6. The attempt to homologize bones by matching their patterns with patterns in other groups, and then using the inferred homologies as evidence of taxonomic relationships between the groups, is obviously flawed.
7. Comparison of patterns within a group without an understanding of the functional significance and evolutionary origin of the patterns, inevitably produces spurious results. Pattern and process must be examined together.
8. Only after ingroup relationships are established is it safe to attempt an analysis of outgroup relationships.

ACKNOWLEDGEMENTS

Chang Mee-Mann, Hans-Peter Schultze and Gavin Young have assisted considerably by providing stimulating discussion of many issues. A grant from the Field Museum, Chicago, enabled K.S.W.C. to examine *Uranolophus.* The Bureau of Mineral Resources, Canberra, gave access to the Gogo Collection through Gavin Young. Paul Johnston and John Long suggested changes to the manuscript. To these co-workers and organizations we offer thanks.

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Structure and Phylogenetic Significance of *Diabolichthys speratus* gen. et sp. nov., a new Dipnoan-like Form from the Lower Devonian of Eastern Yunnan, China

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CHANG M-M., & YU X. B. Structure and phylogenetic significance of *Diabolichthys speratus* gen. et sp. nov., a new dipnoan-like form from the Lower Devonian of eastern Yunnan, China. *Proc. Linn. Soc. N.S.W.* 107 (3), (1983) 1984: 171-184.

A new dipnoan-like form found in association with *Youngolepis* from the Lower Devonian of eastern Yunnan, China, is described as *Diabolichthys speratus,* gen. et sp. nov. The morphological account covers the dermal skull roof, ventral view of anterior cranial portion, detached pterygoid plates and lower jaw rami. The new form is compared with *Youngolepis,* with previously-described dipnoans, and with other osteichthyans. Analysis of character distribution suggests that *Diabolichthys* is more closely related to dipnoans than to other fishes, and forms the sister-group of all previously described dipnoans. Unique features exhibited by this new form (e.g. skull roof pattern, palatal and lower jaw structure and related palatal bite, position of posterior external nasal opening at the mouth margin lateral to the premaxillary, reduced and attenuated posterior sector of the premaxillary) have possible significance for the current debates concerning the interrelationships of lobe-finned fishes and the origin of tetrapods.

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INTRODUCTION

Some remarkable dipnoan-like specimens associated with *Youngolepis* (Chang and Yu, 1981; Chang, 1982) were discovered by the junior author in 1980-1981 in the Qujing district, eastern Yunnan, China. The material includes two fairly complete skulls, five anterior cranial portions (some complete and some not), five fragmentary (?pterygoid) tooth plates, two right lower jaw rami and one left prearticular. This material is described and compared with previously known dipnoans (Denison, 1968, 1968a; Miles, 1977; Thomson and Campbell, 1971), with *Youngolepis* and *Powichthys* (Jessen, 1975, 1980) and with other sarcopterygians including the problematical 'rhipidistians' (Jarvik, 1942, 1966, 1972, 1980; Rosen *et al.,* 1981; etc.). As the present material is remarkably distinct from all other known forms, a new genus and species, *Diabolichthys speratus,* is hereby erected. Analysis of character distribution suggests that this new form is more closely related to dipnoans than to other osteichthyans and that it constitutes the sister-group of all previously described dipnoans (cf. Miles, 1977: 306, fig. 157).

This new form occurs in the same argillaceous limestone as *Youngolepis* and its age is either Gedinnian, or late Gedinnian to early Siegenian (Li and Cai, 1978). A brief account of the associated fauna and the geological setting can be found in Chang (1982). The present material is earlier in occurrence than the early or possibly middle Siegenian *Uranolophus wyomingensis* (Denison, 1968), which constitutes the earliest dipnoan record so far known. Dipnoan material previously reported from China consists only of a Middle Devonian tooth plate from Yunnan (Wang, 1981) and the

Mesozoic ceratodontid tooth plates from Sichuan (Liu and Yeh, 1957). *Diabolichthys* described in this paper is better preserved and provides more cranial details for morphological and phylogenetic studies. As this new form is generally similar to the associated *Youngolepis* whose braincase and other cranial structures have been studied by the serial grinding method (Chang, 1982), comparison tended to be made with *Youngolepis* during initial observations. However, the necessity to specify synapomorphies at proper levels has always been kept in mind to reduce the risk of circular phylogenetic arguments. While the present paper tries to suggest an explicit phylogenetic scheme involving *Diabolichthys,* previously known dipnoans, *Youngolepis, Powichthys* and some 'rhipidistians', even a tentative scheme is limited by the problematical status of 'rhipidistians' and by many other unsettled problems of morphology and taxonomy. Preparations are under way to make serial grinding sections to provide additional information on the internal cranial structures of *D. speratus,* and the hypothesis suggested in this paper is obviously tentative pending this study.

DESCRIPTION AND COMPARISON

Diabolichthys gen. nov.

Diagnosis: Dermal skull roof with anterior portion relatively long; 'parietals' or I-bones anteriorly separated from each other by median element or B-bone but posteriorly meeting each other in midline; J-bones separated from each other by B-bone and other median elements; snout fairly short and orbit anteriorly positioned, with long intertemporal-supratemporal series (X, Y_1 and Y_2 bones) at skull roof margin; no pineal opening; premaxillary independent; anterior and posterior nasal openings at mouth margin; premaxillary with no marginal teeth but further inward low-crowned teeth forming continuous patch with vomerine teeth; posterior sector or premaxillary thin and narrow; pterygoid and prearticular tooth plate-like, covered with flattened teeth in regular rows; parasphenoid extending forward to vomers and pterygoids not meeting in midline; endocranium deep and narrow and palatoquadrate not fused with endocranium; buccohypophysial opening present; rostral tubuli present in endoskeletal part of snout.
Etymology: diabolus (Latin) = devil; ichthys (Greek) = fish.
Type species: Diabolichthys speratus sp. nov.

Diabolichthys speratus sp. nov.

Diagnosis: see genus diagnosis.
Etymology: speratus (Latin) = to have hope.
Holotype: V7238, I.V.P.P. Beijing.
Locality and Horizon: Xichong,, Qujing district, eastern Yunnan, China: Xitun Member, Cuifengshan Formation (Lower Devonian).
Dermal skull roof: Dermal skull roof bears general similarity to *Youngolepis* (Chang, 1982). No pineal opening exists, although a corresponding elevation on skull roof surface indicates that the pineal body is rather anteriorly positioned. In specimen V7237, the skull roof is wider and shorter than in *Youngolepis,* the length of the skull (from its anterior tip to the posterior margin of the 'parietal' or I-bones) is 1.2 times its maximum width (the corresponding ratio in *Youngolepis* ranges from 1.3 to 1.6). In specimen 7238, the ratio is 1.3 and close to that in *Youngolepis.* However, this specimen is small with the skull roof only half as long as that of specimen V7237; it probably represents a juvenile. The posterior margin of the orbit is more posteriorly situated and the orbit is larger than in specimen V7237 or in *Youngolepis.* This is consistent with the usual observation that the orbit is relatively larger in juveniles than in adults.

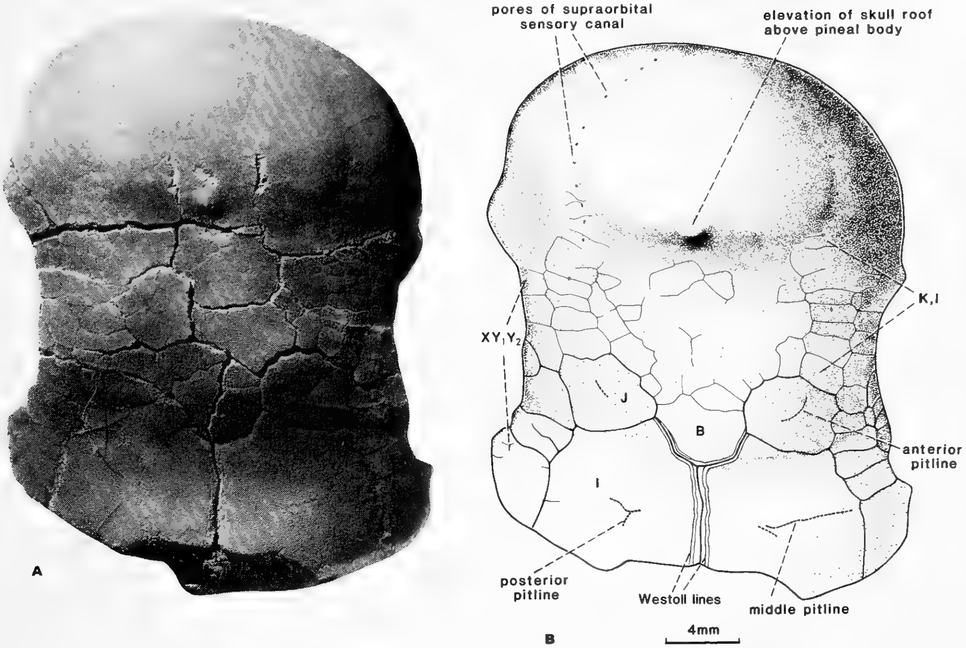
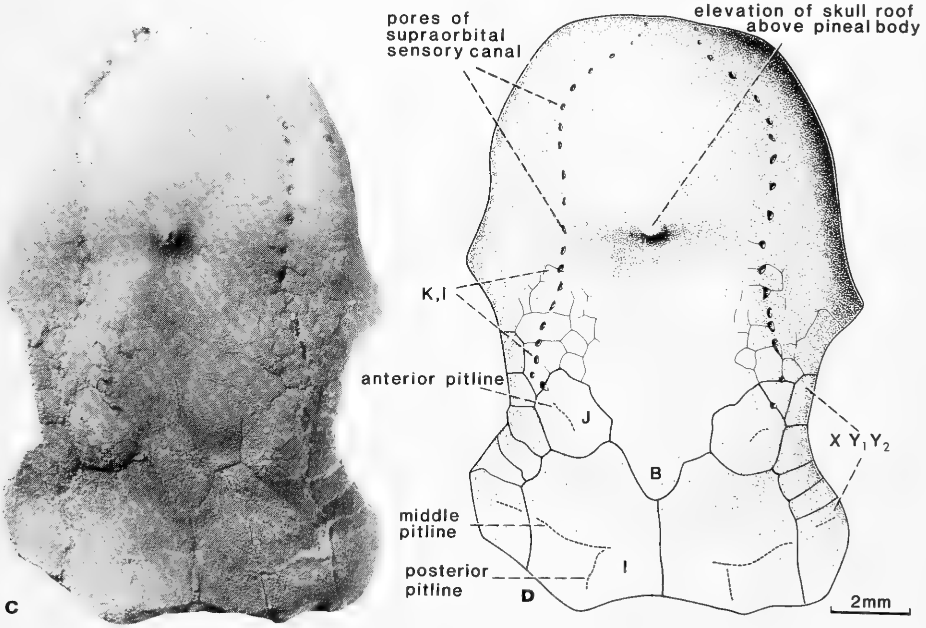


Fig. 1. Diabolichthys speratus gen. et sp. nov. Photographs and sketches of cranial roof in dorsal view.**A, B,** specimen V7237; **C, D,** V7238.



The skull roof elements corresponding to the parietals or the parietal shield of *Youngolepis* are much shorter while the portion anterior to the 'parietals' (I-bones in Fig. 1**B, D**) is much longer than in non-dipnoan osteichthyans; the ratio between the two portions in specimens V7237 and V7238 is 2.4:1 and 3:1 respectively, whereas the corresponding ratio in *Youngolepis* is 1.9:1. Even though the greater part of the 'parietals' still meet each other in the midline, they are anteriorly separated from each other by a median element (B-bone in Fig. 1**B, D**). The supraorbital sensory canal is rather long and its posterior sector is carried by a series of small bones. As noticed in specimen V7238, sutures between these small bones usually form the locations accommodating pores of this canal. The lateral margin of the skull roof is formed by another series of small plates (X, Y_1 and Y_2-bones in Fig. 1**B, D**). Among osteichthyans, the skull roof pattern revealed by this new form comes closer to that of primitive dipnoans than to that of actinopterygians or 'crossopterygians'. When compared with the skull roof pattern in Early Devonian dipnoans, such as *Dipnorhynchus lehmanni* (Lehmann and Westoll, 1952; Lehmann 1956), *Dipnorhynchus sussmilchi* (Thomson and Campbell, 1971) and the North American *Uranolophus wyomingensis* (Denison, 1968, 1968a), the new material from Yunnan reveals the following points of correspondence. The 'parietals' or I-bones are similarly positioned and carry pit-lines corresponding to the middle and posterior pit-lines in dipnoans or the transverse and posterior oblique pit-lines in *Youngolepis* (according to Jarvik's terminology). Anterior to the I-bones lie the well-delineated J-bones, bearing pit-lines corresponding to the anterior pit-lines or the frontal pit-lines in *Youngolepis.* In specimen V7237, the posterior section or terminal point of the supraorbital sensory canal cannot be traced. In specimen V7238, the posterior-most pore-opening for this canal lies at the suture between the J-bone and the anteriorly adjoining element (Fig. 1**D**). It could be assumed that the posterior end of this canal extends backwards into the J-bone and this suggests a similar pattern to that of *Dipnorhynchus sussmilchi* where J carries both the posterior end of the supraorbital sensory canal and the anterior pit-line (cf. Thomson and Campbell, 1971: 26-27, fig. 6A). The median element anterior to the I-bones and lying between the J-bones partially corresponds to the B-bone. In specimen V7237, this element or B-bone is anteriorly delimited by traceable sutures marking out a mosaic of small and variable elements (Fig. 1**B**), whereas in specimen V7238 no traceable sutures exist to indicate the anterior margin of B. The small bones anterior to J and carrying the posterior section of the supraorbital sensory canal, probably correspond to the series including K and L-bones. Lateral to the I, J and K-bones, the small bone series at the lateral margin of the skull roof probably corresponds to the Y_1, Y_2 and X series.

Besides these similarities to primitive dipnoans, the Yunnan specimens manifest the following differences from later dipnoans: the snout and the nasal region are relatively short; the orbit and the pineal elevation are relatively anteriorly positioned; the I-bone and the marginal series corresponding to Y_1, Y_2 and X-series are long; and the I-bones meet each other along a considerable portion of their median margins (Fig. 1**A, B, C, D**).

Ventral view of anterior cranial portion: As in *Youngolepis* (Chang, 1982: 12), the premaxillary is an independent element and the anterior section of the infraorbital sensory canal and the ethmoidal commissural canal probably lie between the premaxillary and the posteriorly adjoining elements. The snout manifests a greater degree of downward and inward bending than that of *Youngolepis,* and consequently a considerable portion of the premaxillary lies inside the mouth cavity and bears no cosmine. However, the relative proportion of the premaxillary which remains outside the mouth cavity and bears cosmine varies with the degree of downward and inward

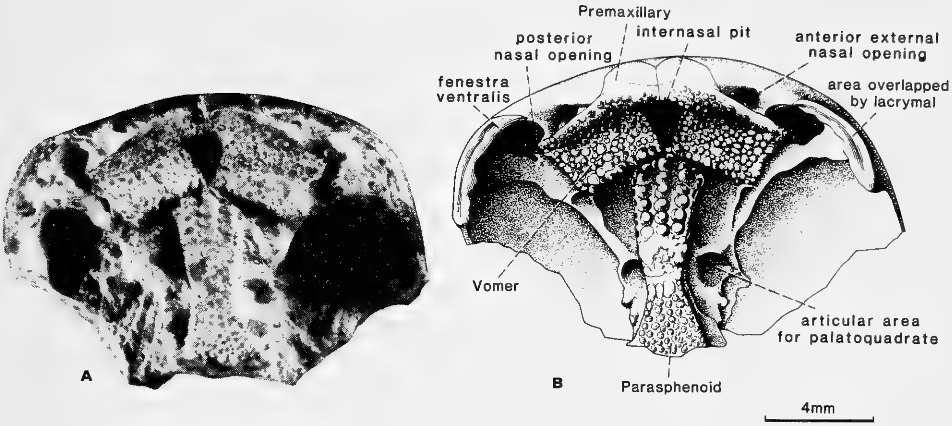
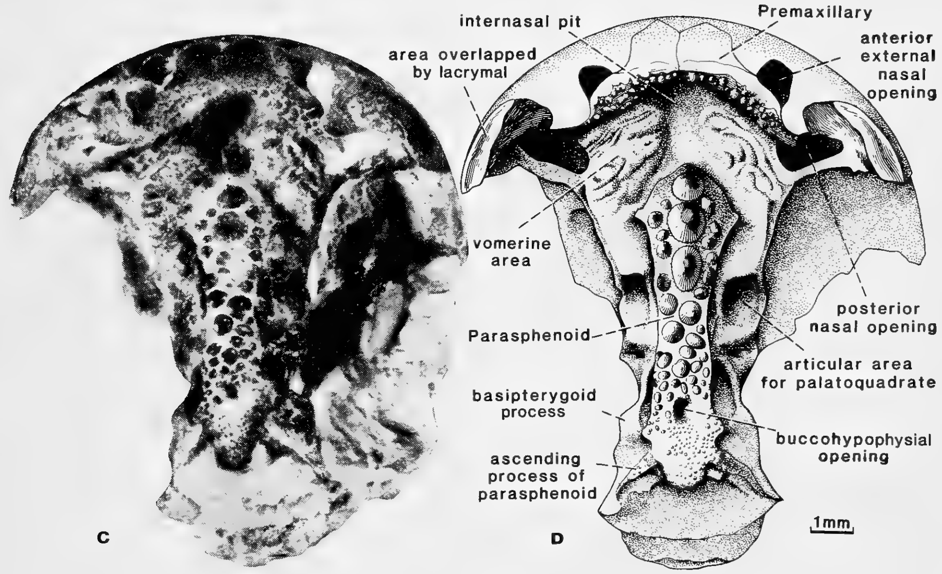


Fig. 2. D. speratus gen. et sp. nov. Photographs and sketches of anterior cranial division in ventral view. **A, B,** specimen V7239: **C, D,** V7240.



bending of the snout. In specimens V7239 and V7240, the portion remaining outside is relatively large, whereas in specimen V7237 it is relatively small. Unlike *Youngolepis,* the part of the premaxillary lying inside the mouth cavity is covered with low-crowned teeth and the mouth margin has no row of large teeth. The ventral portion of the original facial part (cf. pars facialis of Jarvik, 1942) of the anterior sector of the premaxillary, and the entire facial part of the posterior sector, face downward and inward and bear no cosmine at all. Thus the facial surface of the posterior sector of the premaxillary is fully (as in specimen V7239) or almost fully (as in specimen V7240) covered with low-crowned teeth manifesting traces of wear.

The vomer is rectangular in shape and covered with low-crowned teeth similar in shape to those of the premaxillary. Anteriorly the vomerine tooth band merges with the downward and inward facing tooth band of the premaxillary and the two portions form a continuous tooth patch (Fig. 2**A**, **B**, **C**, **D**). All this indicates that the downward and inward facing portion of the anterior sector of the premaxillary and the entire posterior sector of the premaxillary are situated inside the mouth cavity. The possible occlusal relations may be inferred from the lower jaw tooth pattern described later in this paper. The premaxillary is thin and narrow at the posterior end and posteriorly does not reach to the level of the postnasal wall.

In specimens where the vomer is not preserved, the vomeral area has a rugged uneven surface divided by a network of grooves into raised areas of irregular shape and size, rather similar to those of *Youngolepis.* Between the vomeral areas, the ventral surface of the endocranium bears a shallow depression corresponding to the internasal pit in *Youngolepis* (Fig. 2**C**, **D**). In specimens with preserved vomers, a deep depression is formed between the vomers and the premaxillaries because the vomer is so deep (Fig. 2**A**, **B**).

The parasphenoid is long and narrow and extends anteriorly to the ventral side of the most posterior part of the ethmoidal region where it adjoins the vomer. The anterior part of the parasphenoid bears fairly large teeth while the posterior part bears small and irregular teeth which are also low-crowned and flattened. The anterior part of the toothed portion of the parasphenoid is flanked by deep dorsally extending wings, that give a trough-like appearance to the parasphenoid in the anterior two thirds of its total length. This trough accommodates the interorbital portion of the endocranium. The buccohypophysial opening lies in a depression in the posterior part of the parasphenoid. Posterior to the level of this opening, the parasphenoid has a short process extending laterally. More posteriorly, a fairly high ascending process extends dorso-laterally and abuts against the lateral wall of the endocranium at a level posterior to the basipterygoid process (Fig. 2**C**, **D**). The parasphenoid does not cover the ventral surface of the otico-occipital region.

The anterior external nasal opening lies precisely at the mouth margin. The posterior nasal opening agrees with that in *Youngolepis* in certain respects but differs in others. As in *Youngolepis,* specimens with no preserved vomers reveal a fairly large fenestra in the posterolateral portion of the floor of the nasal cavity and this fenestra is divided into medial and lateral portions by the posterior sector of the premaxillary (Fig. 2**C**, **D**). However, as in *Youngolepis,* specimens with preserved vomers show that the portion of the said fenestra lying medially to the premaxillary is covered ventrally by the vomer which forms part of the floor of the nasal cavity. Consequently, this fenestra has an outlet only through the portion lying laterally to the premaxillary, i.e., through the posterior external nasal opening (Fig. 2**A**, **B**). In *Youngolepis,* the premaxillary is fairly long and wide and bears a row of large teeth at the mouth margin. Beyond this tooth row, the entire facial (external) surface of the *Youngolepis* premaxillary is covered with cosmine and obviously the premaxillary and the posterior external nasal opening lateral to it are both situated outside the mouth cavity (Fig. 3). As distinct from *Youngolepis,* a considerable portion of the facial part of the premaxillary in the new form bears a broad band of low-crowned teeth which must have been situated within the mouth cavity. The posterior sector of the premaxillary is not only covered with low-crowned, close-set teeth on the facial surface, but also it is shorter and narrower than in *Youngolepis.* In some specimens (e.g. V7240), the posterior end of the premaxillary is very thin. All this suggests that, unlike in *Youngolepis,* the entire posterior sector of the premaxillary not only lies inside the mouth cavity but is attenuated and possibly reduced. Consequently, the posterior nasal opening immediately lateral to the posterior sector of the premaxillary lies at the very margin of the mouth cavity.

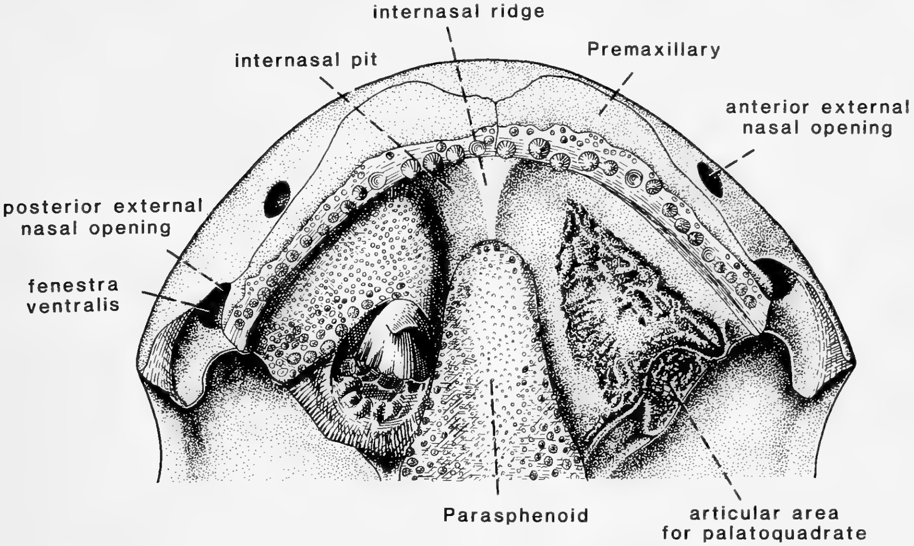


Fig. 3. Youngolepis precursor Chang et Yu. Snout in ventral view. Vomer on left side removed. After Chang, (1982).

So far no maxillary has been found and, except for the lower jaw tentatively allocated to this new form, there is no circumstantial evidence bearing on the presence or absence of this bone. Given the assumption that the maxillary did exist *and* that its anterior end connected with the posterior end of the premaxillary which lies inside the mouth cavity, one could infer that the anterior sector of the maxillary also lay inside the mouth cavity. However, the posterior sector of the premaxillary is so short, and its posterior end so thin and narrow in specimen V7240, that some interruption between the premaxillary and maxillary would not be inconceivable, even if the presence of the maxillary could be assumed.

Lateral to the opening in the posterolateral part of the floor of the nasal cavity, the ventrolateral part of the postnasal wall and the anterolateral wall of the nasal cavity manifest remarkable thickening. In the anterolateral part of the skull roof a long narrow overlapped area on the element probably corresponding to the lateral rostral and anterior tetal (i.e. prefrontal) of the osteichthyans, is visible from the ventral side. This area is probably overlapped by some plate traversed by the infraorbital sensory canal (cf. lachrymal of osteichthyans).

Judging from the prepared portions of the specimens, the endocranium is deep and narrow and the palatoquadrate is not fused with the endocranium. Lateral to the parasphenoid and ventral to the opening for the optic nerve, the ventral wall of the endocranium bears a well-delineated paired depression; there is no periosteal lining in the bottom of the depression and most probably it represents one of the areas where the palatoquadrate articulates with the endocranium. The basipterygoid process occupies a fairly dorsal position. Passing through the dorsal wall of the nasal cavity in specimen V7241, are many tiny tubes, rather like the rostral tubuli found in fossil dipnoans (cf. Thomson and Campbell, 1971: 70, fig. 69; Miles, 1977: 129-132, figs 60, 63 etc.; Campbell and Barwick, 1984). These tiny tubes are also of the same nature as the network of fine canals in the endocranium of *Youngolepis* (Chang, 1982: 29, fig. 13) and *Powichthys* (Jessen, 1975: 219).

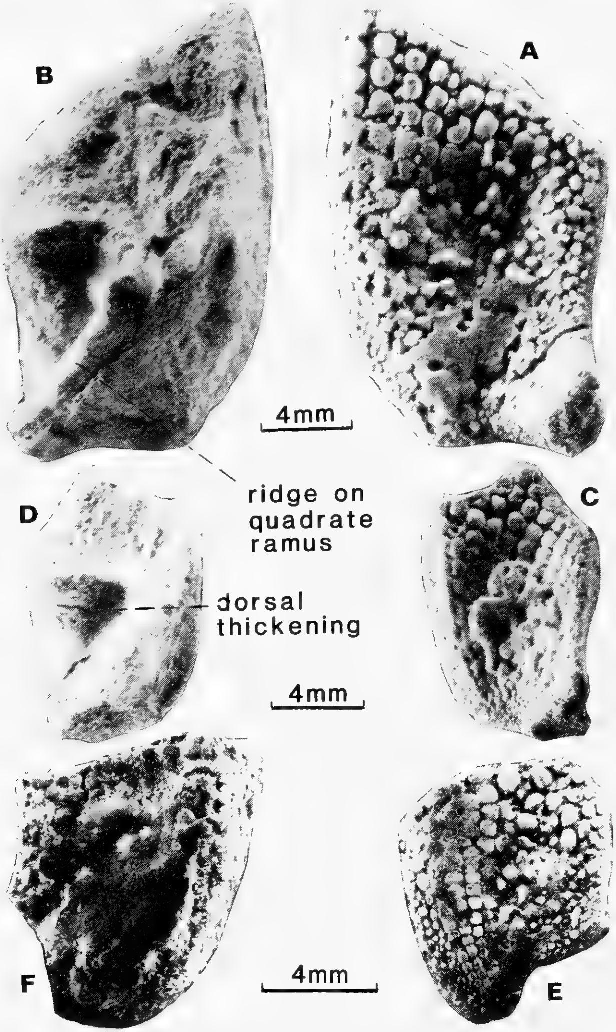


Fig. 4. D. speratus gen. et sp. nov. Left pterygoid in buccal (ventral) (**A, C, E**) and visceral (dorsal) (**B, D**) view, and right pterygoid in buccal view (F). **A, B,** specimen V7246; **C, D,** V7242; **E,** V7244; **F,** V7245.

Detached pterygoid plates: This material also includes some detached tooth bearing plates (Fig. 4). These plates are somewhat similar to those described by Denison, (1968a: 408, fig. 26) and detailed observations show that they can be identified as pterygoids (or endopterygoids). As can be seen in the well-preserved specimen V7246, such plates consist of a horizontal part and a ventrally curved quadrate ramus. In all the specimens so far found, the quadrate ramus is incomplete with its distal portion broken away. The horizontal plate has a medial margin which is slightly convex posteriorly, a straight lateral margin, and a slightly concave posterior margin. The entire buccal surface of both the horizontal plate and the proximal portion of the quadrate ramus, is covered by closely-set small teeth (Fig. 4**A, C**). These teeth are similar to those found on the premaxillary, the vomer and the parasphenoid. They are small in the posterior portion of the plate and larger on the anterior portion. These teeth appear to be arranged in regular rows and the spaces between the rows are taken up by much smaller teeth.

Some of the teeth on the posterior part of the plate are fused with each other in certain specimens (Fig. 4).

The visceral (dorsal) surface of the pterygoid (endopterygoid) has a marked lateral thickening and the quadrate ramus carries a high dorsal ridge (Fig. 4**B**, **D**). This is very similar to the normal structure of fossil dipnoans (e.g., *Dipterus, Chirodipterus, Holodipterus;* cf. Miles, 1977: 165, 168, 170, figs 76-77). Thus the configuration of these tooth-bearing plates, the tooth row arrangement pattern, and particularly the dorsal surface of these plates all correspond with dipnoan pterygoids (or endopterygoids), which bear typical tooth-plates in previously known forms. The only differences are that the teeth on the anterior part of the plate are not completely fused into tooth-plates and the quadrate ramus is covered by closely-set small teeth (at least in the proximal portion).

The allocation of these detached pterygoid plates to the present form, which is mainly represented by anterior cranial portions, is supported by the fact that the morphology of the teeth and the tooth-wear pattern are very similar to those found on the premaxillary, the vomer and the parasphenoid in more complete specimens. As the parasphenoid reaches the ventral part of the ethmoidal region anteriorly and adjoins the vomer, the pterygoid tooth-bearing plates cannot possibly meet in the midline.

Lower jaw: Our collection includes two right lower jaw rami, and an incomplete tooth-bearing portion from a left ramus. As is shown by a well-preserved right lower jaw ramus (specimen V7247, see Fig. 5), the main tooth-bearing portion is probably formed by the prearticular, or by the fused elements of prearticular and coronoid. The teeth have a fan-shaped or radiate arrangement and are similar to the lower jaw plate in *Dipterus valenciennesi* (Jarvik, 1967: 172, text-fig. 6). Most probably this portion occluded with the tooth-bearing pterygoid plate described above. Anterolateral to this main tooth-bearing part, there is a small portion formed by the inward bending of the dentary. This portion is also covered with small teeth and the tooth band thus formed

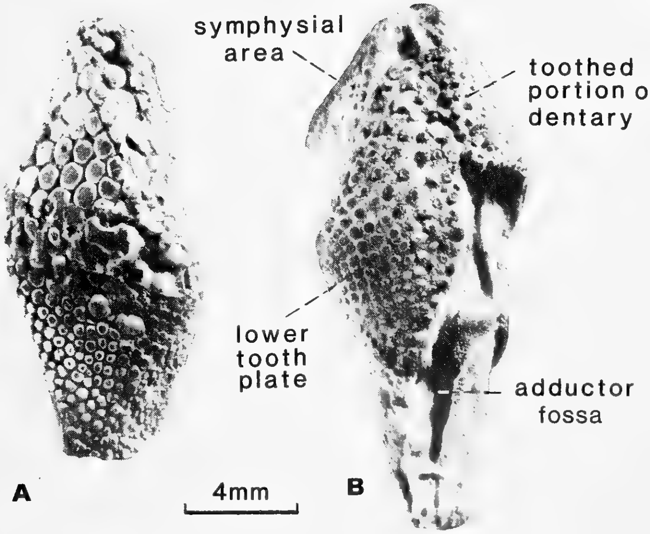


Fig. 5. D. speratus gen. et sp. nov. Right lower jaw ramus (**A**) and left lower jaw tooth-bearing portion (**B**). **A**, specimen V7247; **B**, V7249.

probably occluded with the tooth band formed by the premaxillary and the vomerine teeth lying near the mouth margin in the roof of the mouth cavity. No lateral toothed structure lies posterior to this portion, a point reinforcing the view that no toothed maxillary was present. However, such inferences depend on the validity of the assumption that the lower jaw belongs to the same species as the crania and the detached pterygoid plates.

The adductor fossa in the lower jaw reveals no considerable differences from the condition in previously known dipnoans, and the symphysial area between the right and left rami is fairly broad (Fig. 5). The dermal bones on the external side of the lower jaw can be identified by complete or incomplete sutures. In specimen V7248, the dentary, splenial, postsplenial-angular and surangular bones, as well as openings of the mandibular sensory canal can be observed.

DISCUSSION

Position of Diabolichthys *in relation to dipnoans:* Comparison of cranial features among osteichthyans shows that this new form shares the following unique features with previously described dipnoans rather than with 'crossopterygians' or actinopterygians:

1). The bone series on the skull roof carrying the anterior and middle/posterior pit-lines are separated or partly separated by a median bone, and do not meet their antimeres in the midline. This is similar to the topographical relationship of I, J and B-bones uniquely found in dipnoans, the pattern being specially close to that found in primitive dipnoans such as *Dipnorhynchus* and *Uranolophus*.

2). Corresponding to the downward and inward bending of the snout, a considerable portion of the premaxillary lies inside the mouth cavity and its posterior sector is attenuated and possibly reduced. Moreover, the anterior and posterior external nasal openings occupy a ventral position and lie at the margin of the mouth cavity.

3). The pattern of palatal dermal bones and that of the dermal bones on the lingual side of the lower jaw, together with the tooth pattern of these bones and of the premaxillary, suggest that *Diabolichthys* had developed a palatal bite, which is found in all previously described lungfishes.

4). The anterior portion of the skull roof carrying the supraorbital sensory canal and the anterior pitline (cf. anterior shield, Miles, 1977; fronto-ethmoidal shield, Jarvik, 1942, 1980) is long while the posterior portion with the middle/posterior pit-lines (cf. posterior shield, Miles, 1977; parietal shield, Jarvik, 1942, 1980) is relatively short. The anterior portion in relation to the posterior portion is longer in *Diabolichthys* than in all non-dipnoan osteichthyans, though still not as long as in previously-described dipnoans.

However, as *Diabolichthys* also reveals remarkable differences from previously-described dipnoans (the palatoquadrate not fused with the endocranium and the pterygoids not meeting in the midline due to the forward extension of the parasphenoid to the ethmoidal region), it would be difficult to decide if this new form is a dipnoan without agreement on which characters are necessary and sufficient to define that group. Comparison of previous works involving dipnoan phylogenies (e.g., Bertmar, 1968; Thomson and Campbell, 1971; Miles, 1977; Rosen *et al.*, 1981) suggests that it would be more informative to regard *Diabolichthys* as more closely related to dipnoans than to other osteichthyans, and to conclude that the genus constitutes the sister-group of all previously described dipnoans (cf. Miles, 1977: fig. 157).

Consistent with the above position of *Diabolichthys* are other characters where this form agrees with primitive dipnoans such as *Dipnorhynchus* and *Uranolophus* and differs from later lungfishes. These include such features as the I-bones meeting posteriorly, the orbit anteriorly positioned, the length of the I-bone and the lateral series corresponding to Y_1, Y_2 and X-bone series, and the long parasphenoid (cf. Lehmann and Westoll, 1952: 410, figs 1B, 4B, pl. 24B; Denison, 1968: 372, fig. 8).

Problems in placing Diabolichthys *in a more general phylogenetic scheme:* On the basis of present knowledge of the relevant groups, the position of *Diabolichthys* as the sister-group of previously-described dipnoans is not seriously weakened by any characters uniquely shared by *Diabolichthys* and non-dipnoan osteichthyans. Similarities observed between *Diabolichthys* and other forms, including the associated 'crossopterygian' *Youngolepis,* could be parsimoniously regarded as symplesiomorphies (i.e. more general resemblances defining a more inclusive taxon). Chang (1982) briefly discussed the possible relationship of *Youngolepis,* and she cited several uniquely-shared characters suggesting that *Youngolepis* is more closely related to *Powichthys* (Jessen, 1975, 1980) than to any other forms. Although some of the characters she cited could now be interpreted as primitive features in the light of characters revealed by *Diabolichthys,* the sister-group relationship of *Youngolepis* and *Powichthys* is not challenged by any competing alternatives. There is no character uniquely shared by *Youngolepis* and *Diabolichthys,* while the only character possibly linking *Diabolichthys* and *Youngolepis/Powichthys* (i.e. independent premaxillary and sutural position of anterior section of the infraorbital sensory canal and the ethmoidal commissural canal) is invalidated by its presence in actinistians, and by its variability within taxa.

Given the hypothesized sister-group relationship between *Youngolepis* and *Powichthys,* and that between *Diabolichthys* and previously known dipnoans, it would be possible to define a more extensive group, with *Youngolepis-Powichthys* as the sister-group of *Diabolichthys*-plus-previously-described-dipnoans. This more extensive group is linked by at least one character so far not reported in any other forms (i.e. the presence of rostral tubuli forming a network of fine canals in the endoskeletal part of the snout; cf. Jessen, 1975; Chang and Yu, 1981; Chang, 1982; Miles, 1977; Thomson and Campbell, 1971). The characters associated with the degree of downward bending of the snout and the relatively ventral position of the anterior and posterior nasal openings are basically consistent with this scheme, although the significance of these characters is somewhat dependent on associated notions about the modification of the snout and the nasal openings in the relevant groups.

Attempts to determine the position of *Diabolichthys* in relation to 'rhipidistians', actinistians, and tetrapods are complicated by many unresolved problems (cf. Rosen *et al.,* 1981: figs 4 and 62). In particular 'rhipidistians' make a poorly-defined group, and it is difficult, if not impossible, to determine their relationships with any new group, as was well shown by the study of *Youngolepis* and *Powichthys* (but see Jessen, 1980). However, since no characters have been found which uniquely link 'rhipidistians' or their subgroups with *Youngolepis-Powichthys,* or with *Diabolichthys*-plus-previously-known-dipnoans, the sister-group relationship between *Youngolepis-Powichthys* and *Diabolichthys*-plus-previously-described-dipnoans is not weakened by the probable paraphyletic nature of 'rhipidistians'. It is the intuitive feeling of the present authors that when 'rhipidistians' are divided into monophyletic taxa at various levels, most of them will occupy a range of positions plesiomorphous to that of *Youngolepis-Powichthys* and *Diabolichthys*-plus-previously-described-dipnoans. The present discussion omits consideration of the position of actinistians and tetrapods, an issue that we regard as intractable at present. Our view that 'rhipidistians' occupy a range of plesiomorphous positions in relation to *Youngolepis-Powichthys* and *Diabolichthys*-plus-previously-described-dipnoans does not imply any preconceived notion on the relations between tetrapods, 'rhipidistians' and dipnoans, though the phylogenetic scheme of the present paper could be considered as generally more consistent with some of the competing hypotheses involving sarcopterygians and tetrapods and less consistent with others (cf. Rosen *et al.,* 1981: figs 4, 62).

Comment on the choana problem in the light of Diabolichthys: Previous phylogenetic schemes linking tetrapods with 'rhipidistians' (e.g. Jarvik, 1942, 1972, 1980; Thomson, 1964; Miles, 1977) or with dipnoans (Rosen *et al.,* 1981) depend heavily on the interpreted presence or absence of a choana in 'rhipidistians' and dipnoans. Jarvik and others held that: 1) tetrapods and 'rhipidistians' have a choana as a new formation not homologous with the posterior nasal opening of fishes, whereas the lachrymal duct, supposed to exist in 'rhipidistians' as well as tetrapods, is the homologue of the posterior nasal opening of fishes in general; 2) with the interpreted choana in tetrapods and 'rhipidistians', the premaxillary-maxillary arcade exists in these forms with no interruption; and 3) the palatal opening in dipnoans is the posterior excurrent nasal opening that has migrated onto the roof of the mouth cavity, and this opening lies lateral to the premaxillary-maxillary arcade, which has been subsequently reduced together with the anterior sector of the infraorbital sensory canal. On the other hand, Rosen *et al.* (1981) suggested that: 1) the tetrapod choana is homologous with the posterior nasal opening in fishes, and thus also with the palatal opening in dipnoans, whereas the tetrapod lachrymal duct is homologous with the labial cavity in dipnoans, a structure not found in other fishes; 2) the premaxillary-maxillary arcade exists in tetrapods, 'rhipidistians' and dipnoans; and with the posterior nasal opening assuming a ventral position in the roof of the mouth cavity of tetrapods and dipnoans, the premaxillary-maxillary arcade was interrupted in these two groups. The posterior nasal opening (interpreted as a choana) lies medial to the premaxillary-maxillary arcade both in tetrapods and dipnoans; 3) 'rhipidististians' probably have no palatal nasal opening (i.e. no choana) either as a new formation or as a modified posterior nasal opening.

Given the suggested position of *Diabolichthys* as the sister-group of previously-described dipnoans, it is natural to consider the relation between the premaxillary-maxillary arcade and the position of the posterior nasal opening in this form. Its anterior and posterior nasal openings are situated at the very margin of the mouth cavity, but the posterior one is lateral and not medial to the premaxillary. The attenuated and possibly reduced posterior sector of the premaxillary in *Diabolichthys,* and the evidence of detached lower jaw material allocated to this form, suggest either the absence of a toothed maxillary, or alternatively an interruption between the premaxillary and maxillary (see previous descriptive sections). Without considering the second alternative, the condition in *Diabolichthys* with the posterior nasal opening at the mouth margin but lateral to the premaxillary, might be considered as inconsistent with Rosen *et al.*.*'s* interpretation of the dipnoan condition. However, the possible interruption of the premaxillary-maxillary arcade in *Diabolichthys,* the snout morphology of the genus, and its assumed phylogenetic position, could suggest an alternative scenario in which the posterior nasal opening moved to a ventral position inside the mouth cavity through the gap in the interrupted premaxillary-maxillary arcade. This scenario would not exclude the existence of an *interrupted* premaxillary-maxillary arcade *lateral* to the posterior excurrent nasal opening in dipnoans, and could suggest a possible solution to the dilemma in which one must either quote the existence of the premaxillary-maxillary arcade *lateral* to the posterior excurrent nasal opening, or invoke the total disappearance of this arcade *medial* to the said opening, in order to accept or reject the homology of the dipnoan posterior nasal opening with the tetrapod choana. With the adoption of a ventral position for the posterior nasal opening, and the transition from a marginal to a palatal bite as hypothesized by many authors, the elements of the *interrupted* premaxillary-maxillary arcade could have been modified, and/or fused with other elements, and this could have been the case with *Griphognathus whitei,* as suggested by Rosen *et al.* (1981). The homology or non-homology of the tetrapod choana and the posterior excurrent nasal opening in dipnoans depends primarily on the question of whether the tetrapod choana is homologous with the posterior nasal opening in fishes in general. The latter question depends in turn on the problem of the structure of this region in 'rhipidistians', i.e. whether these forms possess a palatal nasal opening and, if they do, whether this opening co-exists (i.e. is non-homologous) with the posterior nasal opening or a structure which is unquestionably modified from it.

Since Rosen *et al.*'s (1981) analysis was presented, Chang (1982) has described the condition in *Youngolepis,* in which the ventral fenestra of the nasal capsule has no exoskeletal opening into the mouth cavity, and the only outlet is through the posterior external nasal opening. On this basis, the existence of a choana in *Powichthys,* as assumed by Jessen (1975, 1980) was questioned, and variations in the position of the opening in the post-nasal wall of *Euthenopteron foordi* were noted, bringing into doubt the interpreted homology of this opening with the lachrymal duct (or the posterior nasal opening according to Jarvik, 1942). On the basis of personal observations Chang also considers the reported choana in *Porolepis* and *Glyptolepis* as highly speculative, and not supported by morphological details. However, many of the relevant features in the various taxa referred to as 'rhipidistians' are far from clear, and a reasonable solution of the choana problem will require future research in many different quarters.

CONCLUSIONS

1. Analysis of character distribution suggests that *Diabolichthys* is more closely related to dipnoans than to any other osteichthyans and that it constitutes the sister-group of all previously-described dipnoans. In a broader phylogenetic scheme, *Youngolepis-Powichthys* forms the sister-group of *Diabolichthys*-plus-previously-described-dipnoans. However, the hypothesized relationship between the above group and 'rhipidistians' is constrained by the inherent difficulties in choosing between the different phylogenetic schemes of sarcopterygians.

2. Morphological features revealed by *Diabolichthys,* such as the skull roof pattern, palatal and lower jaw structures in relation to the palatal bite, and features associated with the downward and inward bending of the snout, might have significance for current debates on the interrelationships of lobe-finned fishes.

3. In *Diabolichthys,* the posterior nasal opening lies at the mouth margin but lateral to the premaxillary. The attenuated and possibly reduced posterior end of the premaxillary and the condition of the lower jaw, suggest that this form either lacked a toothed maxillary or that there was an interruption between the premaxillary and maxillary. With the assumed interruption in the premaxillary — maxillary arcade, it is possible to suggest an alternative scenario about the snout modification leading towards the dipnoan condition.

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Devonian Vertebrates in Biostratigraphy

D. L. DINELEY

(Communicated by A. RITCHIE)

DINELEY, D. L. Devonian vertebrates in biostratigraphy. *Proc. Linn. Soc. N.S.W.* 107 (3), (1983) 1984: 185-196.

Standards of precision in biostratigraphic dating and correlation of marine formations within the Devonian System now call for similar advances in the stratigraphy of non-marine formations. Vertebrates are amongst the fossils most commonly found in non-marine units but are very rare in the marine facies. Use of palynomorphs, macroplants and invertebrates and intensive study of interbedded marine and non-marine facies in all parts of the world are now urgent in clarification of Devonian world stratigraphy. The efforts of vertebrate palaeontologists are vital in this connection.

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INTRODUCTION

In several parts of the stratigraphic column vertebrates have become recognized as valuable biostratigraphic indices. Vertebrate evolution is comparatively rapid but the disadvantages of vertebrates in biostratigraphy are manifestly well known. Devonian vertebrate biostratigraphy is still in a relatively primitive state, being broadly confined to the continental facies. A notable 'pioneer' Devonian paper was by Gross in 1950 and from the most recent general statement (Westoll, 1979) a summary diagram has been prepared. Between these two mentioned dates Devonian invertebrate biostratigraphy has advanced significantly (House, Scrutton, Bassett, 1979). The International Commission on Stratigraphy, through its Subcommission on the Devonian System, is moving towards the adoption of international formal biostratigraphic definition of the (marine) Series and Stages within the System. So far it has agreed that

a) the base of the Middle Devonian is the base of the *P. partitus* conodont zone. This is approximately the base of the Eifelian stage (Heisdorf-Lauch boundary) in the Rhineland where the stratotype is at Wetteldorf

b) the base of the Upper Devonian is the base of the Lower *Pa. asymmetricus* zone which coincides with the base of the Assize de Frasnes in Belgium

c) while the existing stages of the Middle and Upper Devonian will not be discarded, the choice between the Lower Devonian stages of the Ardennes-Rhineland and those of Bohemia as the international standard has yet to be made. Pelagic fossils (especially microfossils) have been useful in this work but correlation of the marine with the non-marine facies lags behind. There is much evidence to suggest that spores and macroplant fossils will ultimately be of greatest value in this work, though there are dangers in the unquestioning use of spores alone.

In general, the broad recognition of Lower Devonian, Middle Devonian and Upper Devonian vertebrate faunas can be made, and faunas from the two higher Series are found in all continents except South America. Smaller biostratigraphic units based on vertebrates, however, are exceptional, and in the Lower Devonian the faunas tend to differ between four or five palaeobiogeographical provinces (Young, 1981).

As the examination of extensive and critical sections around the Lower/Middle and Middle/Upper Series boundaries has proceeded, it has become obvious that accurate correlation of marine horizons with non-marine is particularly wanting and that

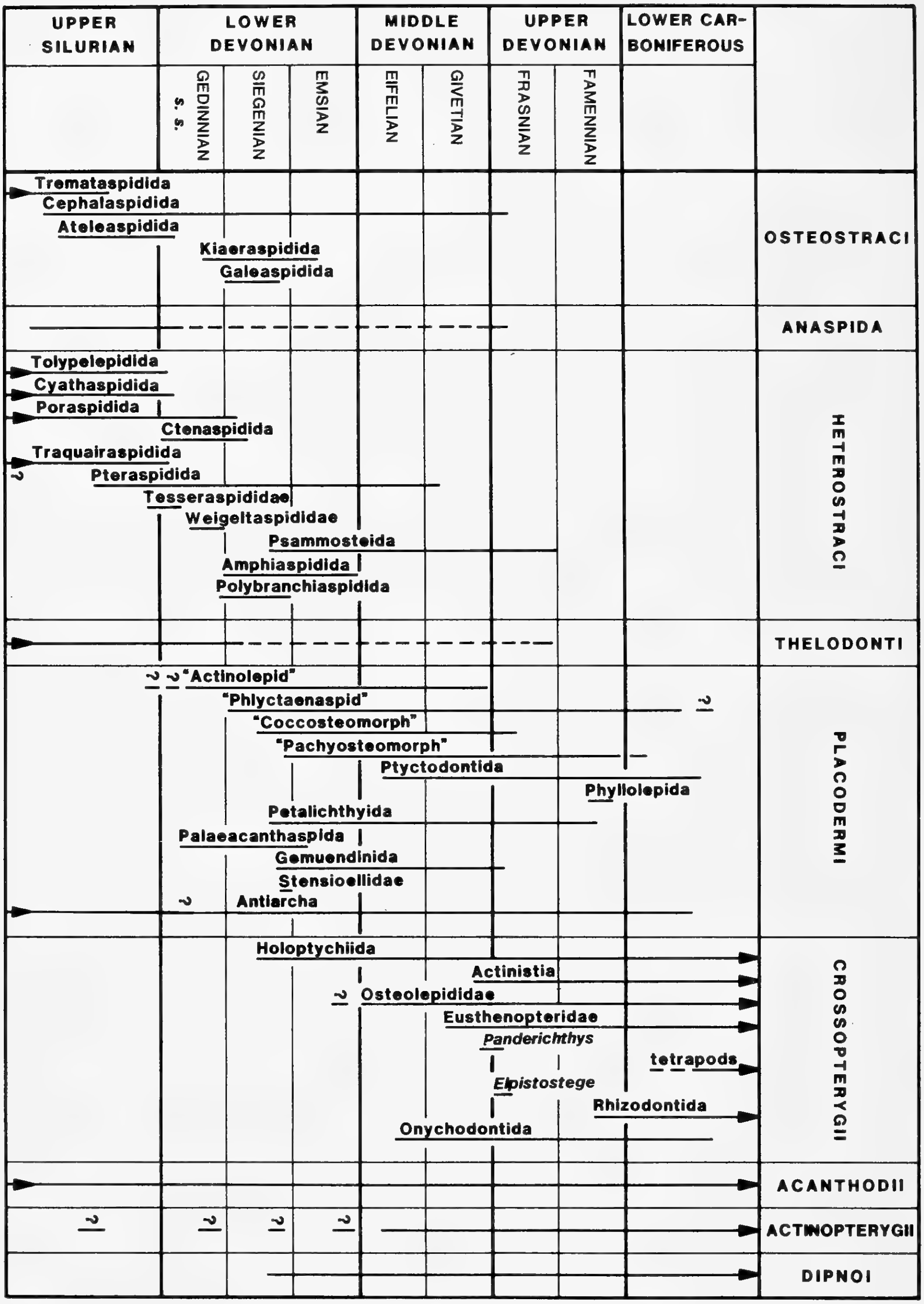

Fig. 1. A summary table of the ranges of vertebrate groups in the non-marine Devonian facies after Westoll (1979) and others.

vertebrate faunas are particularly scarce at those levels. Nevertheless good sections in the non-marine Devonian facies do exist and vertebrate successions within the series are known. This paper calls for efforts to be made to document the stratigraphic distribution of vertebrates and especially for the establishment of reference sections by which correlation from region to region and between facies may be made with greater confidence.

Old Red Sandstone Vertebrate Biostratigraphy, North Atlantic Area

Although attention has been given mainly to the detailed stratigraphic distribution of vertebrates, especially the ostracoderms, in the Old Red Sandstone outcrops of the North Atlantic area (Allen, Dineley and Friend, 1968; Young, 1981; Blieck, 1982) it is probable that other regions may provide better sections for detailed biostratigraphy and inter-facies correlation. China, parts of the Soviet Union and of Australia come to mind. Correlation between marine and non-marine facies in each region or province is the first important step to be achieved if possible and the correlation of non-marine formations and 'horizons' with those identifiable on an international biostratigraphic basis is to be preferred. This should in time allow correlation between different non-marine facies provinces as shown below.

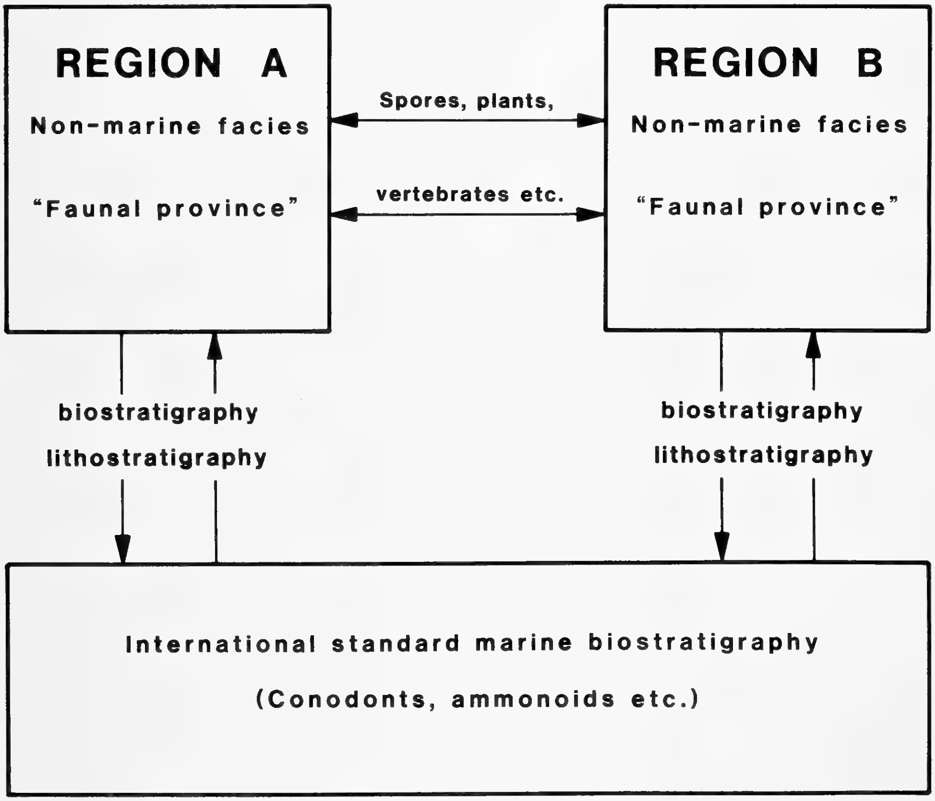

Fig. 2. Correlation between separate sedimentary basins or 'provinces' of non-marine deposits is unlikely to be achieved on the basis of lithostratigraphy and only achieved with uncertainty where there are few taxa in common. There is now a reasonably good basis of international biostratigraphy with which most non-marine Devonian facies may be correlated, given the presence of a few different fossil groups.

The North Atlantic region might be said to illustrate the point well. It includes formations from all three series of the System and where there are not actual unconformities between series the positions of those boundaries are difficult to define. Vertebrate remains are relatively common in the Lower Devonian of western Britain, Spitsbergen, eastern and northern Canada; in the Middle and Upper Devonian of Scotland, and Melville and Bathurst Islands, N.W.T. Canada, and Greenland. Other areas have yielded vertebrates in smaller numbers, others have yet to provide even a minimal number of identifiable taxa. Detailed modern studies in which systematic examination of stratigraphic sections with their vertebrate and palynological record are comparatively few. Of note are those in Wales and the Welsh Borderland (Ball, Dineley and White, 1961), Svalbard (Blieck, 1982a; Blieck and Heintz, 1979), E. Greenland (Friend *et al.,* 1973) and N.E. Scotland (Donovan, Foster and Westoll, 1973). Scattered valuable data have been recorded from many other areas, especially western Europe (Blieck, 1982b). Work on the succession in the Silurian-Devonian of the Canadian Arctic Islands (Elliott and Dineley, 1983) suggests further detailed correlation. For the Lower Devonian a number of 'zones' and 'horizons' have been designated and these are essentially assemblage or acme zones based on thelodont or heterostracan faunas. Material from Somerset and Prince of Wales Islands in the Canadian Arctic may allow zoning on the basis of a phylogenetic sequence of heterostraci originating at a pre-Devonian level. For the rest, phylogenetic sequences of vertebrates are lacking, though tentative phylogenies may be proposed. Continuous stratigraphic sections through the strata in which the assemblage zone fossil occurs in Britain are also wanting (Dineley, 1982). Formal establishment of a zonal sequence based upon unbroken stratotype sections throughout the Lower Devonian is not yet possible.

In the long-studied Middle Devonian of Caithness and the Orkney area a sequence of characteristic 'zones' and faunas has been distinguished by Westoll and his co-workers. (See also Donovan *et al.,* 1973; House *et al.,* 1977). The stratigraphic relationships of these 'zones' are established on the basis of excellent coastal sections, but there remain barren intervals of strata between the boundaries of the 'zones' themselves.

The Upper Devonian or Upper Old Red Sandstone formations of Scotland and Greenland have provided many data on vertebrate distribution and the Baltic-Russian platform outcrops of Middle and Upper Old Red Sandstone have also yielded a wealth of data that has been summarized by Mark-Kurik (1978) and other workers.

Correlation, and the dating, of these vertebrate-yielding formations with the local marine sequences proceeds largely by palynology. Correlation between the Atlantic area and other vertebrate 'provinces' is not so far advanced. While the standard Rhenish or Bohemian stages for the Devonian may be recognized universally and referred to stratotypes in Europe with increasing confidence, the condition of the stages proposed for the non-marine facies is much less satisfactory. A note on the British Old Red Sandstone stages in use may illustrate the point.

DOWNTONIAN Although the term was first used by Lapworth (1879) and later used by Peach and Horne (1899), it was employed for the lowest major division of the Old Red Sandstone in the Welsh Borderlands by King (1934) and White (1950) defined the stage by the incoming of *Hemicyclaspis* and its base in the stratotype sections at Ludlow by the base of the Ludlow Bone Bed. In terms of the marine Silurian-Devonian sequence this is now level with the base of the Pridoli stage, i.e. around the base of the *Monograptus ultimus* zone.

Recently Bassett, Lawson and White (1982) clarified the present status of the Downton Series as the fourth series of the Silurian System, thereby removing it from

	Series or Stage	Banks, 1980	McGregor, 1977	Richardson, 1974
CARBONI-FEROUS	Tn 1b Tn 1a	?		*V. nitidus* *V. pusillites*
DEVONIAN UPPER	FAMENNIAN	*Rhacophyton* Assemblage-zone VII		*S. lepidophytus*
	FRASNIAN	*Archaeopteris* Assemblage-zone VI		*L. cristifer* *optivus-bullatus*
DEVONIAN MIDDLE	GIVETIAN	*Svalbardia* Assemblage-zone V	*devonicus-orcadensis*	*Triangulatus* *Densosporites devonicus*
	EIFELIAN	*Hyenia* Assemblage-zone IV	*velata-langii*	*Rhabdosporites langii* *Acinosporites acanthomammillatus*
DEVONIAN LOWER	EMSIAN UPPER	*Psilophyton* Assemblage-zone III	*annulatus-lindlarensis* *Grandispora*	*Calyptosporites biornatus-proteus*
	EMSIAN LOWER		*sextantii* *caperatus-emsiensis*	*Emphanisporites annulatus*
	SIEGENIAN	*Zosterophyllum*		*Dibolisporites cf. gibberosus*
	GEDINNIAN	Assemblage-zone II	*micrornatus-proteus*	*Emphanisporites micrornatus* *Streelispora newportensis*
SILURIAN	PRIDOLIAN	*Cooksonia* Assemblage-zone I	*chulus-?vermiculata*	*Synorisporites tripapillatus*

Fig. 3. Palynological and conodont zones and macroplant assemblages useful for international correlation in the Devonian System (after Banks, 1980, and others).

the Devonian System and formalizing its status. A description of the stratotype is given, parastratotypes designated and a correlation of the Downton Series with E. Canada and Europe given on the basis of invertebrates, vertebrates and spores. For all intents and purposes, the term Downtonian as a *stage* name should now be discontinued and reference to a Silurian Downton Series made instead.

DITTONIAN Based on his Ditton Series around Ditton Priors, Shropshire, this stage was designated by King (1934) as having at its base a *Cephalaspis* Sandstone (not identifiable elsewhere). Later practice has been to use the main *Psammosteus* Limestone

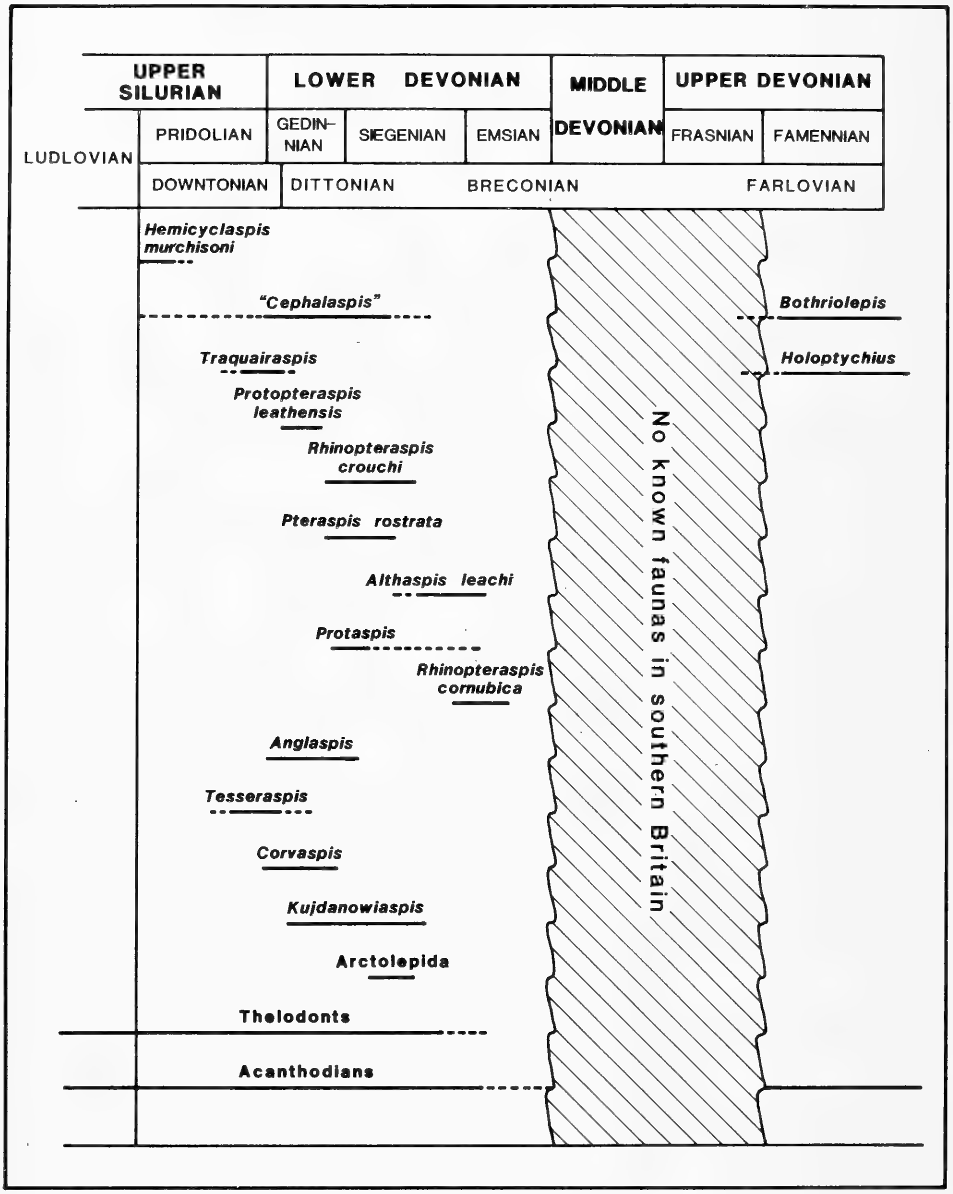

Fig. 4. Vertebrate 'zones' for the Lower Devonian of the North Atlantic province (after Dineley and Loeffler, 1976; Blieck, 1982).

as the mappable base, but to define the base of the stage (and hence the top of the Downtonian) as the base of the lowest bed yielding *Pteraspis (Protopteraspis) leathensis* (see White, 1950; Allen and Tarlo, 1963). Tarlo (1965) subsequently decided that the base of the *Monograptus uniformis* zone (the base of the Devonian System, McLaren, 1977) should occur at about the level of the Downtonian/Dittonian boundary. Direct

		N.E. SCOTLAND	E. BALTIC
UPPER DEVONIAN		*P. magnus*	*Plourdosteus*
MIDDLE DEVONIAN	Upper Caithness Flagstones Group	*Millerosteus minor*	*Pycnosteus tuberculatus*
		Asmussia murchisoniana	
		Dickosteus threiplandi	*Pycnosteus pauli*
	Lower Caithness Flagstones Group	*Palaeospondylus gunni*	*Pycnosteus palaeformis*
		Coccosteus cuspidatus	*Schizosteus striatus*
		Thursius macrolepidotus	*Schizosteus heterolepis*

Fig. 5. Vertebrate 'zones' for the Middle Old Red Sandstone of the Orcadian basin and a possible correlation with the Baltic area (after Donovan *et al.*, 1973, and others).

correlation has yet to be made between the graptolite and the vertebrate horizons but via the use of ostracodes a correlation has been suggested (Martinsson, 1967).

BRECONIAN The group of strata is defined as lying between the Dittonian and the Farlovian (Croft, 1953) and was used to include the Senni Beds with *Rhinopteraspis dunensis* and the overlying barren Brownstones (White and Toombs, 1948) in South Wales. This definition is unsatisfactory and the acceptance of a revised Breconian stage for the uppermost Lower Old Red Sandstone or its total abolition is overdue.

ORCADIAN This term has only been used informally for the Middle Old Red Sandstone and has its origins in the successions of Caithness and Orkney. It could be said to encompass the zones listed above but to what extent it is equivalent to the entire Middle Devonian Series cannot be stated.

FARLOVIAN This term (King, 1934; Ball, Dineley and White, 1961) has been used for the Upper Devonian in South Wales and the Welsh Borderland. At Farlow, Shropshire, the Farlow rocks rest unconformably upon Dittonian and Breconian strata and the fauna is neither distinctive nor well known enough to be of much biostratigraphic use.

All in all, these stages cannot be regarded as very satisfactory and only by careful redefinition and reference to specific stratigraphic sections can some be made 'respectable'. Nevertheless, they have been used successfully in broad correlation (see for example Obruchev and Karatajute-Talimaa, 1967). The Orcadian needs special study but the Farlovian should probably be discarded.

'Cosmopolitan' Lower Devonian vertebrates occurring in this and other provinces of Devonian marine and continental deposits include the thelodonts, various placoderm groups and early osteichthyes. Of these the thelodonts are proving to be the most widespread and may have the greatest biostratigraphic significance (Turner, 1973; Turner and Turner, 1974; Turner, Jones and Draper, 1981; Turner and Tarling, 1982).

DEVONIAN VERTEBRATE BIOSTRATIGRAPHY ELSEWHERE

The work of Chinese specialists in fossil vertebrates and in Devonian stratigraphy has been important in recent years, not only in revealing the unique character of the early Devonian vertebrate faunas of China but also in establishing possible phylogenetic lineages of antiarchs (Pan, 1981) and in proposing stages for the extensive non-marine formations there. The work is based upon extensive field data, and palynological correlation with marine facies is improving. In detail, no doubt, revisions will have to be made, but progress appears to be systematic and encouraging. The Russian platform (Baltic area) Devonian has been studied for many years and the palaeontological record there of vertebrates and marine invertebrates is excellent. Summaries and overviews are now providing a wealth of data for particular intervals. Sorokin's (1978) monograph on the Frasnian stage and Lyarskaya's on Baltic Devonian Placodermi (1981) are good examples. In Central Asia and Siberia (Nalivkin *et al.,* 1973) palynological and palaeobotanical studies are being carried on especially in connection with the definition of the boundaries of the Middle Devonian and are important for the equation of continental vertebrate horizons (see e.g. Novitskaya, 1971) with the marine biostratigraphy (see Sokolov, Rzhonsnitskaya *et al.,* 1982).

In the western United States and Canada discoveries of Devonian vertebrates in marine formations or in beds intercalated with marine strata the ages of which are known in detail have recently been numerous (Gregory, Morgan and Reed, 1977). The affinity of some western American species with those from the Baltic area is striking and the intercalated conodont faunas in Nevada are of great importance.

In Australia Devonian continental facies are known to be widespread, especially those in the Middle and Upper Devonian. The stratigraphic distribution of the different vertebrate taxa is dealt with by other authors in the present symposium (see also Long, Turner and Kemp, 1983), and precise non-marine stratigraphic ranges for all known Devonian vertebrate species may be available in the forseeable future. Probably these ranges will be mirrored in Antarctic stratigraphy. Where possible, the identification of intercalated marine beds together with palynology and other studies in both facies will certainly assist in establishing a more detailed biostratigraphic correlation.

Discussion about the palaeontological basis of stages in continental facies has been minimal, but is now urgent. A consensus of opinion should not be hard to reach.

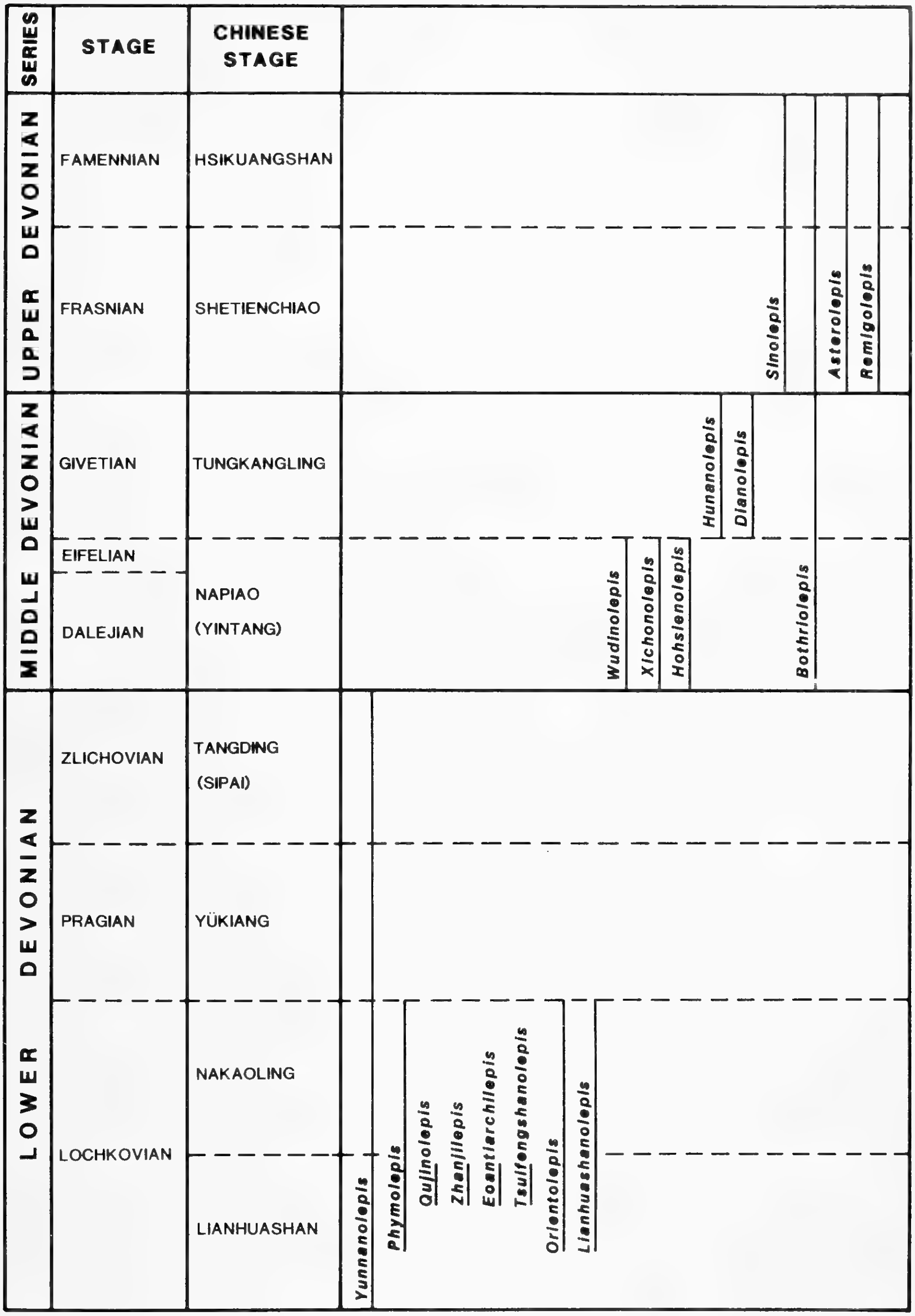

Fig. 6. Stages for the Qilianshan and Qujing (non-marine) facies types and the ranges of characteristic Antiarchi (after Yang, P'an and Hou, 1981; P'an, 1981).
Note that all genera except the three farthest to the right hand side are endemic and that only *Yunnanolepis* is known to reach the top of the Lower Devonian Series. The nature of the record at the upper and lower boundaries of the Middle Devonian is clearly very important and is a topic for special attention.

CONCLUSION AND PROPOSAL

In four of the five Devonian vertebrate provinces designated by Young (1981) there now exists a substantial mass of data that can be examined and assessed for the purpose of setting up successions of biostratigraphic units at 'horizon' or 'zonal' level. These units may also be assessed relative to successions of palynomorphs, macroplants or invertebrate fossils which allow comparison with local, and it may be hoped, the internationally-accepted criteria for Devonian Series and Stages. Local stages established for non-marine successions may be distinguished and be useful on a regional scale but, ultimately, correlation with a world-stratigraphic scale is necessary.

The value of such correlation is great not only in terms of palaeogeographical reconstructions but also in assessing the rates of geological change and organic evolution, migration, etc. In particular the chronology of early vertebrate endemism, migration(s) and of the extinction of particular groups may be revealed.

The evidence to establish good *zones based upon type sections* is less satisfactory but it does exist. To achieve such zonation in each province may require much more work and refined techniques generally regarded as those of ecostratigraphy must be employed.

It is urged that vertebrate palaeontologists and stratigraphers in the regions primarily concerned establish informal local working groups, linked if possible to existing working groups concerned with Devonian stratigraphy. They could most usefully draw attention to and study the best available type areas and putative type sections for vertebrate biostratigraphy. Co-operation with palynologists and palaeobotanists is essential. Correlation of designated type sections and stratotypes with local marine successions must be the aim followed by attempts at correlation with regional and international standard sequences. The liaison and co-operation of groups of workers — North American — W. European, Siberian — Central Asian, Chinese, Australian — Antarctic — with one another and with the Subcommission on the Devonian System is of course a direct and essential consequence. In due course an integration of the work of such working groups or of their representatives with that of the Subcommission would be advantageous. Meanwhile, the case for increasing local and international endeavour, using vigorous stratigraphic methods is now greater than ever before, and the results may be far-reaching. In this the vertebrate palaeontologist is an essential member of the group and he, or she, has perhaps the most to gain from its success.

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Note added at proof stage: At its meeting at Montpellier, France, on 23rd September, 1983, the Subcommission on Devonian Stratigraphy, set up a Working Group on the correlation of the marine with the non-marine facies of the Devonian, the present author to be convener of the Working Group.

Siluro-Devonian Fish Biostratigraphy of the Canadian Arctic Islands

D. K. ELLIOTT

(Communicated by A. RITCHIE)

ELLIOTT, D. K. Siluro-Devonian fish biostratigraphy of the Canadian arctic islands. *Proc. Linn. Soc. N.S.W.* 107 (3), (1983) 1984: 197-209.

Though Silurian and Devonian vertebrates have been well studied in Spitsbergen and western Europe, where they have proved valuable in biostratigraphy, faunas of comparable age in the Canadian arctic have only recently been described. Attempts to use these faunas to date the Canadian strata in relation to the standard European successions have proved difficult as faunal ranges have been incompletely known; some vertebrates appear to have occurred earlier in the Canadian arctic than elsewhere, and European and Canadian faunas probably remained separate until the Early Devonian. More precise correlations can now be made due to recent work on some arctic faunas and revisions of those in Spitsbergen. A fauna from Prince of Wales and Somerset Islands is found to be Ludlovian and Pridolian in age and equivalent in part to the *Hemicyclaspis* zone of the Anglo-Welsh succession. A fauna from Prince of Wales and Cornwallis Islands shows similarities to the fauna of the Vogti horizon of the Ben Nevis Formation in Spitsbergen and the Crouchi zone of the Anglo-Welsh succession.

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INTRODUCTION

The presence of the remains of ostracoderms in rocks of Silurian and Devonian age has been of great significance in geological studies. Since their use (White, 1950; White and Toombs, 1948) as zonal indicators in the Lower Old Red Sandstone of the Anglo-Welsh borders, they have continued to be of great value in stratigraphy. In particular the pteraspidids have been one of the most useful groups of ostracoderms within the Lower Devonian. White (1950) used the faunal break indicated by replacement of the traquairaspidids to mark the boundary between the Downtonian and Dittonian stages in the Welsh borderlands, and the pteraspidid zonal scheme established for the Lower Devonian has provided correlation throughout Europe (Obruchev and Karatajute-Talimaa, 1967, 1968; Schmidt, 1959; White, 1956, 1960), and with Spitsbergen and eastern Canada (Dineley, 1967). Though the fauna from these areas has been well known for a number of years, and much work has been carried out on correlation of sequences, it is only recently that attention has been turned to the vertebrate faunas of equivalent age in the Canadian arctic. Consequently only tentative correlations have been made as yet between these faunas and the better known ones in Europe and Spitsbergen (Blieck and Heintz, 1979; Dineley and Loeffler, 1976).

Rich ostracoderm localities were found on Prince of Wales, Somerset and Cornwallis Islands in the Canadian arctic (Fig. 1) by the Geological Survey of Canada in 1955 (Thorsteinsson, 1958). Since then further localities have been discovered in the same areas, and in the Yukon and British Columbia. Some of this material has been described (Broad, 1973; Broad and Dineley, 1973; Denison, 1963, 1964; Dineley, 1964, 1968, 1976; Dineley and Loeffler, 1976; Elliott, 1983; Elliott and Dineley, 1983; Loeffler and Dineley, 1976; Loeffler and Jones, 1976, 1977). However, many of the faunas are still awaiting description. Correlation of these faunas with the standard

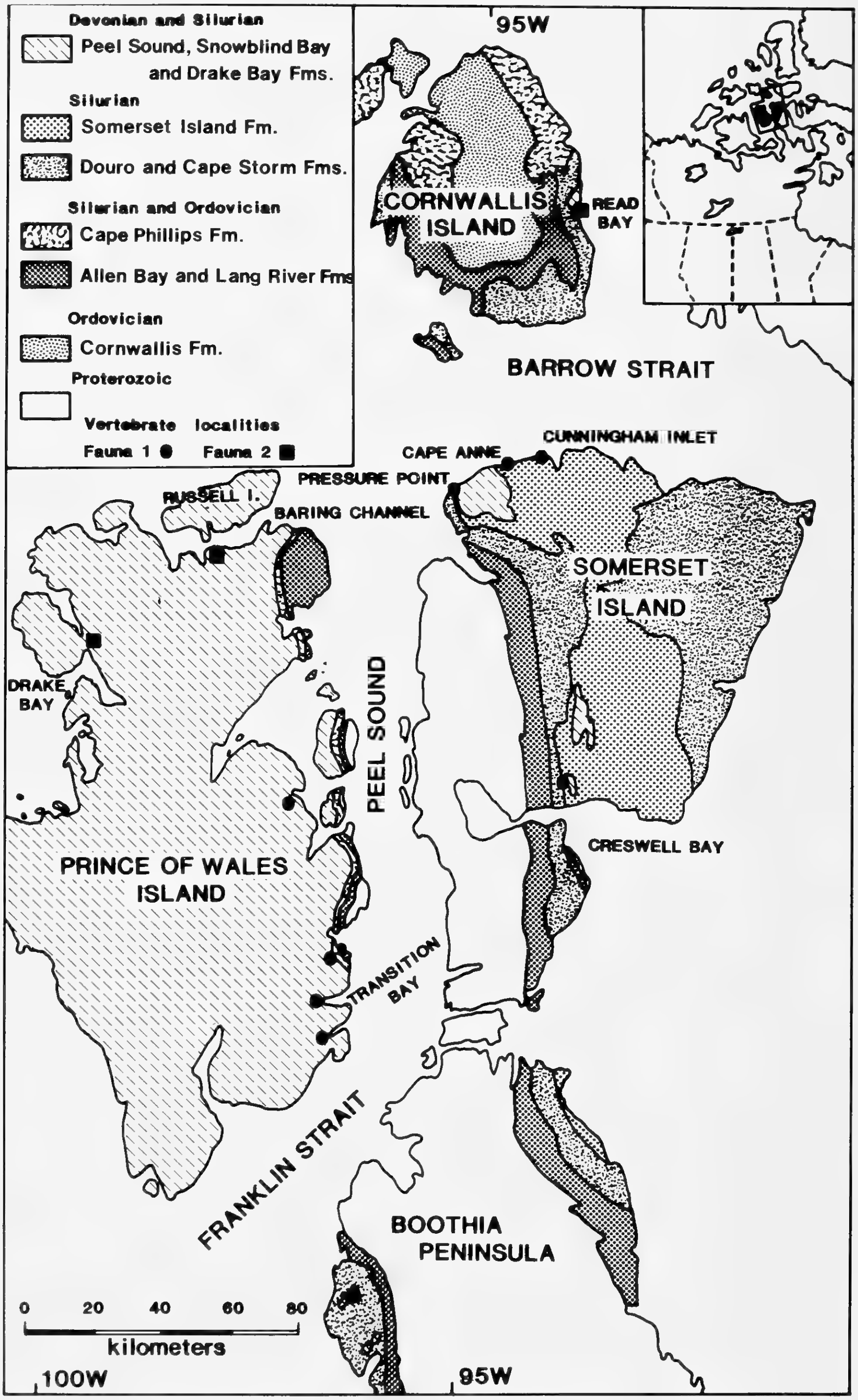

Fig. 1. Map showing collecting localities and geology of Prince of Wales, Somerset and Cornwallis Islands.

sequences developed in the Anglo-Welsh borders and in Spitsbergen has proved difficult for a number of reasons. It has been shown (Dineley and Loeffler, 1976) that heterostracan faunas in Europe and Canada remained essentially separate until the Early Devonian, when mixing was facilitated by the collision of the two continents. This faunal mixing is thought to have begun at the base of the Pococki zone, thus allowing the reliable use of ostracoderms for correlation of North American and European strata only after this date. Thelodonts have a wide geographical range at an earlier date, a feature attributed by Turner (1973) to a possible marine larval stage.

It also appears that a number of heterostracan groups occurred earlier in the Canadian arctic than elsewhere (Broad and Dineley, 1973). Thorsteinsson (1967) has reported anaspids, cyathaspidids and thelodonts from the Cape Phillips Formation, Cornwallis Island, in strata dated by graptolites as from late Llandoverian or early Wenlockian to early Ludlovian in age, and Broad (1973) has reported the earliest known amphiaspids from Pridolian strata on Ellesmere Island. In addition the ranges of the Canadian arctic faunas have been insufficiently known and hence correlations have been tentative. These factors have resulted in greater reliance being placed on the associated invertebrate faunas to date Silurian and Devonian strata in the Canadian arctic.

New descriptions of some of the fauna (Dineley, 1976; Elliott, 1983; Elliott and Dineley, 1983; Loeffler and Dineley, 1976; Vieth, 1980), together with new information on associated invertebrates (Thorsteinsson, 1980; Uyeno, 1980), and revisions of the Spitsbergen faunas (Blieck, 1982; Blieck and Heintz, 1979), have now made possible a more detailed correlation of some of the Canadian arctic faunas.

STRATIGRAPHY

The faunas come from localities on Boothia Peninsula, and Somerset, Prince of Wales and Cornwallis Islands (Fig. 1), and occur in a thick sequence of Palaeozoic sediments flanking the Boothia Uplift (Kerr and Christie, 1965; Kerr and deVries, 1976). The uplift was caused by the Cornwallis Disturbance (Kerr, 1977), which had its greatest effect on local sedimentation during the Early Devonian. Continental clastic rocks were shed from the uplift during pulses of activity, but largely shallow marine carbonates were deposited when the influence of the uplift was slight. The lower Palaeozoic succession is thus characterized by a series of facies changes radiating from the Boothia Uplift. The succession (Fig. 2) was first described on Cornwallis Island (Thorsteinsson, 1958) where limestones and dolostones of Lower Ordovician to Silurian age are replaced northwards by graptolitic shales.

On Somerset and Prince of Wales Islands the first sequence that need concern us is the Douro Formation (this now replaces Read Bay Formation (Thorsteinsson, 1980)), a series of argillaceous limestones recently redefined by Miall and Kerr (1977). Jones and Dixon (1977) have shown it to be markedly diachronous across Somerset Island, ranging from Ludlovian in the west to Pridolian or younger in the east. On Somerset Island this formation is followed by the Somerset Island Formation (Miall, Kerr and Gibling, 1978). This formation is not found on Prince of Wales Island but is probably laterally equivalent to the lower member of the Peel Sound Formation there (Miall *et al.,* 1978). The formation consists of a lower member containing mottled limestones and dolostone, and red siltstone. The sediments were deposited in intertidal and supratidal environments in succession to the lagoonal and subtidal conditions prevailing in Read Bay times.

The succeeding Peel Sound Formation occurs over much of Prince of Wales Island, and in gentle synclines in the Cape Anne — Pressure Point and Creswell Bay areas of Somerset Island. On Somerset Island it has been redefined (Miall and Kerr,

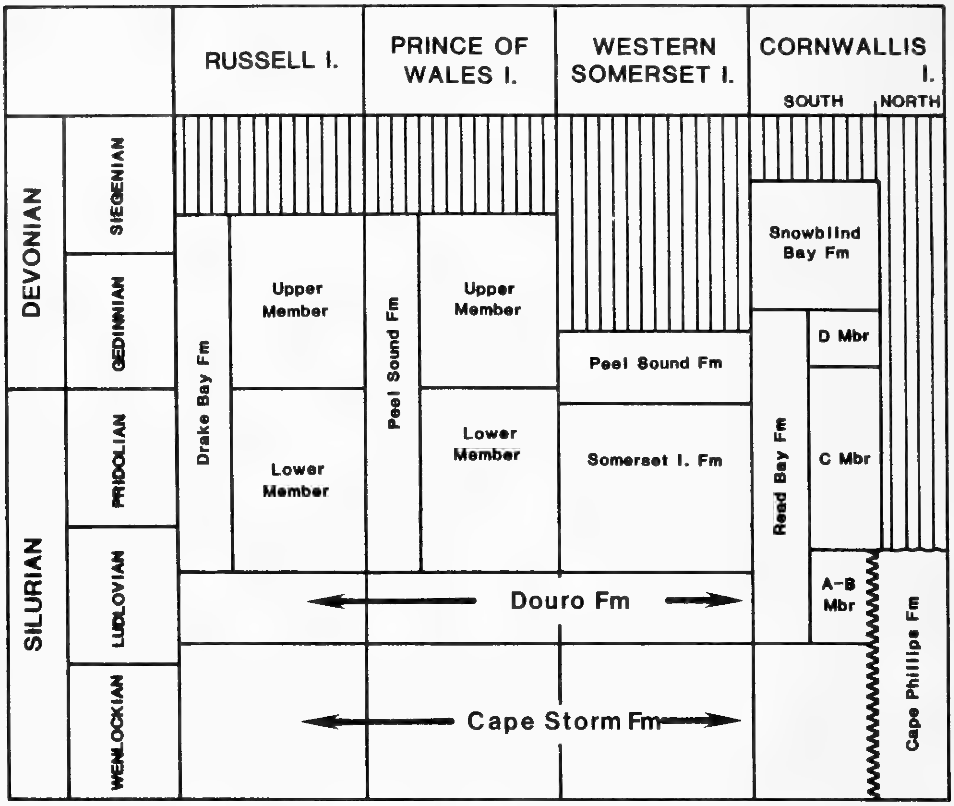

Fig. 2. Correlation of Silurian and Devonian strata in the central Canadian arctic.

1977) to take account of the new Somerset Island Formation, and consists of red sandstones and siltstones grading up into oligomict conglomerates and pebbly sandstones. On Prince of Wales Island the Douro Formation grades upwards into a similar succession, divided by Miall (1970) into a lower member consisting of interbedded limestones, siltstones, sandstones, and oligomict conglomerates, and an upper characterized by the disappearance of virtually all but conglomerate in the succession. Westwards it grades through five distinct facies outcropping as north-south bands. Conglomerate in the east is replaced laterally by conglomerate-sandstone, sandstone, sandstone-carbonate and carbonate facies (Broad, Dineley and Miall, 1968; Miall, 1970). The carbonate facies appears to be laterally equivalent to both members of the Peel Sound Formation nearer the uplift, and these sediments are now designated the Drake Bay Formation (Mayr, 1978).

On Cornwallis Island the Snowblind Bay Formation (Thorsteinsson and Fortier, 1954; Thorsteinsson, 1958) is a lateral equivalent of the Peel Sound Formation (Gibling and Narbonne, 1977). It rests conformably on the Sophia Lake Formation and consists of limestone breccia and conglomerate, siltstone and sandstone.

THE FAUNA OF THE SOMERSET ISLAND FORMATION AND THE LOWER MEMBER OF THE PEEL SOUND FORMATION

This fauna is represented in scattered localities on Somerset and Prince of Wales Islands and Boothia Peninsula (Fig. 1, Fauna 1), but is most completely known from a ravine at Transition Bay on the east coast of Prince of Wales Island which cuts through vertical strata of the Douro and Peel Sound formations (Broad and Dineley, 1973). The vertebrates occur mainly in the sandstones and siltstones of the lower member of the Peel Sound Formation, where they consist of accumulations of disarticulated shields and plates, locally stacked and current aligned. The completeness of the section has allowed a tentative range chart to be produced (Fig. 3).

The fauna from this locality has already been dealt with in a number of publications. Broad has described the amphiaspids (1973), the traquairaspidids (1971), and with Dineley (1973) the cyathaspidid *Torpedaspis*. The pteraspidids have been described by Elliott (1984) and Elliott and Dineley (1983). A faunal replacement of *Traquairaspis* by *Protopteraspis* cannot be seen here as traquairaspidids are found throughout the section and occur with *Protopteraspis* towards the top. However a replacement of the Anchipteraspidinae by *Protopteraspis* can be seen, *Ulutitaspis truncata* and *U. notidana* characterizing the lower part of the section before replacement by *Protopteraspis sartokia* and *P. pygmaea*. *Boothiaspis* is particularly abundant at the base of the sequence but only one species, as yet undescribed, extends up into the section. *Corvaspis* occurs throughout almost the entire section as does *Torpedaspis* and *Poraspis;* however *Pionaspis* appears to be characteristic of the central part only.

This fauna is still incompletely known, as work on the traquairaspidids is still unpublished, and the cyathaspidids are still to be described. However the tentative ranges do provide a framework for local correlation. Localities to the north and south of Transition Bay and on the west coast of Boothia Peninsula have yielded *Protopteraspis pygmaea* (Fig. 1; locs 1,2,10,12 of Elliott and Dineley, 1983), indicating a position in the upper part of the lower member of the Peel Sound Formation. Further south on Prince of Wales Island (loc. 11 of Elliott and Dineley, 1983), the presence of *Protopteraspis siliktokia* with *Corvaspis* probably indicates a similar age.

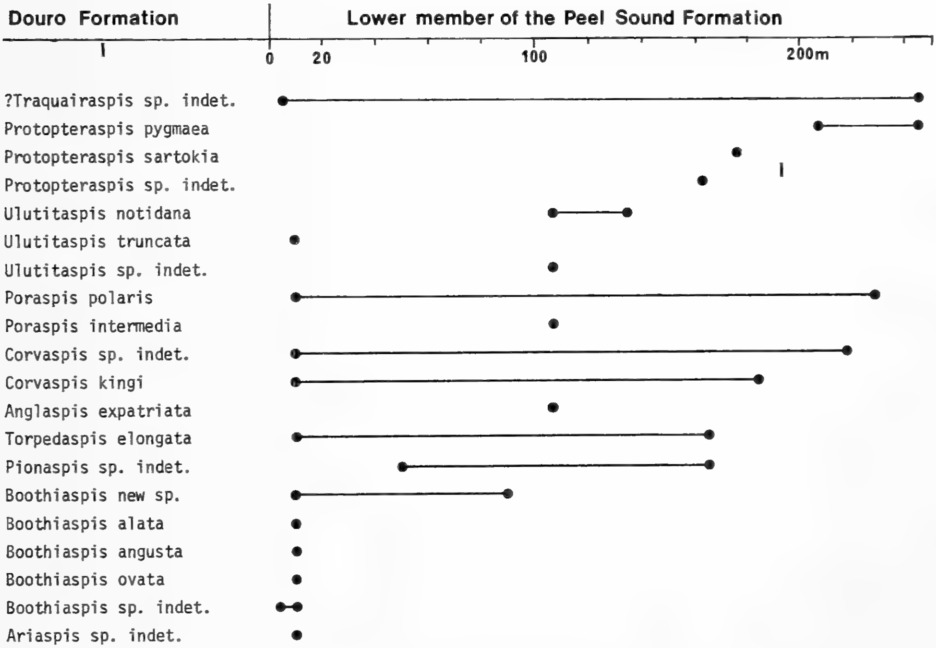

Fig. 3. Ranges of vertebrates in the lower member of the Peel Sound Formation at Transition Bay, Prince of Wales Island. (Some information from Broad and Dineley, 1973).

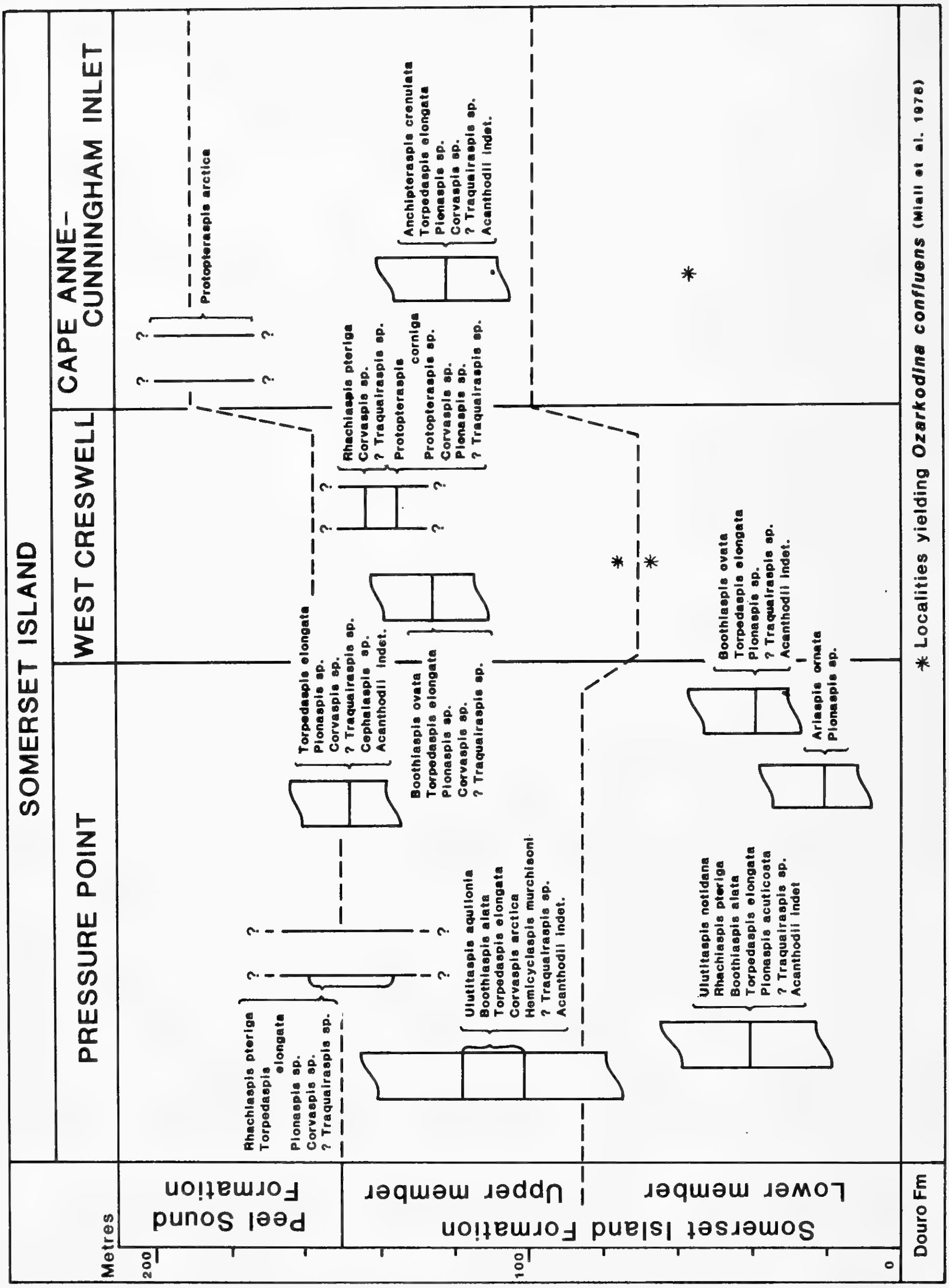

Fig. 4. Correlation of vertebrate horizons in the Somerset Island Formation, Somerset Island. (Some faunal and locality information from Broad, 1973; Broad and Dineley, 1973; Dineley, 1968; Gibling pers. comm.; Loeffler and Dineley, 1976).

To the east of the Boothia Uplift, on Somerset Island, no section through the Somerset Island Formation is as well known faunally as that at Transition Bay. However, a number of vertebrate horizons are sufficiently well known to enable some correlations to be made (Fig. 4). In the Pressure Point area a similar fauna is found, though no *Protopteraspis* is known from the upper part of the sequence. *Ulutitaspis* is again characteristic of the central part of the section, but is replaced in the upper part by *Rhachiaspis*. Several other forms have longer ranges here than on Prince of Wales Island. *Torpedaspis* and *Pionaspis* are present to the top of the formation, and *Boothiaspis alata* extends into the upper member, where it is associated with *Hemicyclaspis murchisoni,* one of the few vertebrates with stratigraphic significance beyond the Canadian arctic. Though *Protopteraspis* is not known at Pressure Point, it is found at Creswell Bay, where *P. corniga* occurs with *Rhachiaspis* in the upper member of the Somerset Island Formation. The exact stratigraphic horizon for this locality is not known, and neither is that for the locality yielding *Protopteraspis arctica* at Cape Anne on the north coast of Somerset Island. On lithological grounds however, both are probably at the top of the Somerset Island Formation.

Though the same species of *Protopteraspis* do not occur on both sides of the uplift, the faunas in the Somerset Island Formation and the lower member of the Peel Sound Formation are sufficiently similar to indicate their stratigraphic equivalence. Traquairaspidids, *Torpedaspis, Pionaspis, Ulutitaspis,* and *Corvaspis* have similar ranges in both, and *Protopteraspis* occurs in the upper part of both. *Boothiaspis* however appears to range higher in the Somerset Island Formation.

AGE OF THE FAUNA

The only truly diagnostic vertebrate in this fauna is *Hemicyclaspis murchisoni,* which occurs 15-18 metres above the base of the upper member of the Somerset Island Formation at Pressure Point. This is regarded as an index fossil for the lowest Downtonian of the Anglo-Welsh succession (White, 1950), now regarded as equivalent to the early Pridolian (Loeffler and Dineley, 1976). This occurrence was originally reported as being in the base of the Peel Sound Formation (Dineley, 1968), and Thorsteinsson (1980) has used this to suggest that the Somerset Island Formation is nowhere younger than late Ludlovian. However, redefinition of the base of the Peel Sound Formation (Miall and Kerr, 1977) would place this occurrence just above the base of the upper member of the Somerset Formation, thus indicating that the upper part of the formation could be younger than late Ludlovian in age. *Boothiaspis alata* occurs in both members of the Somerset Island Formation at Pressure Point, and also in the Devon Island Formation in southern Ellesmere Island. Here it is associated with a monograptid, dated as Pridolian on Cornwallis Island by Thorsteinsson (*in* Broad, 1973), where it occurs below *Monograptus transgrediens* Perner. *Ariaspis ornata,* which occurs in the lower member of the Somerset Island Formation at Pressure Point, has also been reported from Beaver River (Denison, 1963), and the Delorme Formation (Dineley and Loeffler, 1976). This heterostracan could indicate an age range of Wenlockian to Pridolian, as *Monograptus dubius* which occurs above the Beaver River fauna is known to extend from the Llandoverian to the Pridolian (Broad and Lenz, 1972). *Pionaspis acuticosta* which occurs with *Ariaspis ornata* at Pressure Point is otherwise known only from Muncho Lake, British Columbia, in strata considered to be late Downtonian on the presence of a traquairaspidid similar to *T. symondsi,* and a cyathaspidid held by Denison (1964) to be of this age. Dineley and Loeffler (1976) however, consider so precise a date debatable, considering the increase in knowledge of the range and diversity of these groups in the arctic.

Few diagnostic invertebrates are known from these horizons. However Miall *et al.*

(1978) have dated localities in the Somerset Island Formation at Cape Anne and Creswell Bay as Pridolian (Fig. 4), based on the presence of *Ozarkodina confluens* gamma morphotype, and *Pelekysgnathus* sp. Thorsteinsson (1980) considers the base of the formation to be latest Ludlovian (Latialata zone) on Boothia Peninsula, as *Pedavis* sp. aff. *P. thorsteinssoni* occurs there, and is associated with *Pedavis latialata* in the lower part of the Read Bay Formation on Cornwallis Island. On Prince of Wales Island, invertebrate dating of the lower member of the Peel Sound Formation has yielded Late Silurian ages (Bolton and Copeland, *in* Broad and Dineley, 1973; Bolton *pers. comm.*, 1976) for the whole of the sequence. Thorsteinsson (1980) concludes that the age range is late Ludlovian to early Pridolian based mainly on the presence of *Hemiarges bigener* towards the top of the lower member of the Peel Sound Formation. This trilobite is known from widely separate localities in the Canadian arctic, but wherever it can be related to diagnostic fossils it appears to be of Pridolian age (Thorsteinsson, 1980). On balance therefore it appears that both the lower member of the Peel Sound Formation and the Somerset Island Formation range from late Ludlovian to early Pridolian in age.

THE FAUNA OF THE UPPER MEMBER OF THE PEEL SOUND FORMATION AND THE DRAKE BAY AND SNOWBLIND BAY FORMATIONS

This fauna was originally described from the Baring Channel area on the north coast of Prince of Wales Island (Fig. 1), where it occurs in the sandstone-carbonate facies of the upper member of the Peel Sound Formation (Miall, 1970). Collecting at two levels has yielded a varied fauna, normally preserved as dissociated shields and plates, accumulated on bedding planes and showing current alignment, though some complete specimens are known. The arthrodire *Baringaspis dineleyi* Miles (1973) occurs in both horizons, while *Ctenaspis obruchevi* and *C. russelli* Dineley (1976) occurs in the upper and lower respectively. *Stegobranchiaspis baringensis* Elliott (1983) occurs at both horizons, as does a second, as yet undescribed, pteraspidid, and a third, *Escharaspis alata* Elliott (1983), is known from one specimen from the lower horizon. The upper member of the Peel Sound Formation was considered to be the age equivalent of the Snowblind Bay Formation on Cornwallis Island (Thorsteinsson and Tozer, *in* Fortier *et al.*, 1963), and a vertebrate fauna from the base of the formation at Read Bay supports this view. *Stegobranchiaspis baringensis* and the undescribed pteraspidid occur at this locality, and also found in common are *Anglaspis* sp., *Ctenaspis* sp. cf. *C. russelli*, ?*Weigeltaspis* (a primitive psammosteid), and a porolepid. In addition, the pteraspidid *Unarkaspis schultzei* Elliott (1983) occurs here, and suggests correlation with the upper part of the Drake Bay Formation on the east coast of Prince of Wales Island, which has also yielded the undescribed pteraspidid, the same *Anglaspis* sp., and a similar porolepid.

AGE OF THE FAUNA

No elements of this fauna are known from elsewhere in the Canadian arctic, although Vieth (1980) has reported the presence of *Turinia pagei, Gomphonchus sandalensis* and *Nostolepis* sp. at Baring Channel. They were associated with *Pelekysgnathus serratus serratus* (determined by O. H. Walliser; H. P. Schultze, *pers. comm.*, 1976), and other conodonts which closely resemble forms found in upper Lochkovian and lower to middle Pragian (upper Gedinnian-Siegenian) strata elsewhere in the Canadian arctic (Uyeno *in* Gibling and Narbonne, 1977). Thorsteinsson (1980) notes the presence of *Pedavis pesavis pesavis,* an index species of the latest Lochkovian conodont zone, with *Anglaspis* in the Drake Bay Formation. No dates are available for the base of the

Snowblind Bay Formation, but the greatest possible age for this fauna is indicated by a dating of early to possibly middle Lochkovian for the strata directly below it (Thorsteinsson, 1980). It therefore seems probable that this fauna is of late Lochkovian to early or middle Pragian (late Gedinnian to Siegenian) age.

Correlation with European Succession

White (1950, 1956, 1961) and Ball and Dineley (1961) used the heterostracans of the Anglo-Welsh borders to subdivide the Old Red Sandstone succession into the Downtonian, Dittonian and Breconian. Though there have been revisions of this scheme, particularly of the Downtonian-Dittonian boundary (Allen and Tarlo, 1963), the vertebrate succession of the Anglo-Welsh borders is still retained as a standard for correlation.

In Spitsbergen, vertebrates have been used to zone the Lower Devonian Fraenkelryggen and Ben Nevis Formations. Following the stratigraphic correlations of Friend (1961) and Ørvig (1969), the Fraenkelryggen is regarded as encompassing the Pococki and Leathensis zones of the Anglo-Welsh succession (White, 1950), spanning the uppermost Downtonian and lowermost Dittonian equivalents. Ørvig (1969) has shown that the Primaeva horizon of the Fraenkelryggen Formation can be correlated with the upper Symondsi or lowermost Leathensis zones of the Anglo-Welsh succession, while Blieck and Heintz (1979) have correlated the Anglaspis horizon with the upper part of the Leathensis zone, based on the presence of pteraspidids similar to *Protopteraspis leathensis.* In the Ben Nevis Formation the Vogti horizon has been correlated with the lower part of the Crouchi zone by Goujet and Blieck (1977). Though they felt that it showed many similarities with the Leathensis zone, the

SPITZBERGEN VOGTI HORIZON	PODOLIA CZORTKOV HORIZON	ARCTIC CANADA PEEL SOUND, DRAKE BAY, SNOWBLIND BAY FMS.
Protopteraspis vogti		Stegobranchiaspis baringensis
Miltaspis anatirostra – – – – – – – –	Althaspis (Loricopteraspis)	Escharaspis alata
Podolaspis goujeti – – – – – – – – –	Podalaspis podolica – – – – – ? – – –	Unarkaspis schultzei
	Traquairaspis sp. indet.	
Poraspis rostrata		
Homalaspidella nitida		
Irregulareaspis sp. indet. – – – – –	Irregulareaspis stensioi	
Anglaspis sp. indet. – – – – – – – – –	– – – – – – – – – – – – – – – – – –	Anglaspis sp. indet.
Ctenaspis cancellata – – – – – – – –	Ctenaspis sp. indet. – – – – – – – – –	Ctenaspis russelli
Ctenaspis sp. indet.		Ctenaspis obruchevi
		Ctenaspis sp. indet.
Corvaspis sp. indet. – – – – – – – –	Corvaspis sp. indet.	
Weigeltaspis heintzi		Weigeltaspis sp. indet.
Turinia pagei – – – – – – – – – – –	Turinia pagei – – – – – – – – – – –	Turinia pagei
Turinia oervigi	Turinia oervigi	Turinia polita
Apalolepis cf. obruchevi	Apalolepis obruchevi	
Gomphonchus cf. sandalensis – – – –	– – – – – – – – – – – – – – – – – –	Gomphonchus sandalensis
Nostolepis striata – – – – – – – – –	Nostolepis sp. indet. – – – – – – – – –	Nostolepis striata
Nostolepis gracilis		
Lepidaspis sp. indet.		
Osteostraci common – – – – – – – –	Cephalaspis sp. indet. – – – – – – – –	Cephalaspis sp. indet.
	Placoderms – – – – – – – – – – – –	Baringaspis dinelevi

Fig. 5. Correlation of the faunas from the Vogti horizon, Spitsbergen, the Czortkov stage Podolia and the upper member of the Peel Sound. the Drake Bay and Snowblind Bay formations. (Some information from Blieck, 1982; Goujet and Blieck, 1977; Obruchev and Karatajute-Talimaa, 1967; Turner, 1973; Vieth, 1980).

presence of *Benneviaspis* and *Weigeltaspis,* which do not occur in Britain until later, led them to correlate it with the higher zone. The upper part of the Ben Nevis Formation may be equivalent to the upper part of the Crouchi and the Leachi zones, and the presence of *Althaspis*-like forms in both (Ball and Dineley, 1961; White, 1956, 1961) has been used as an argument in favour of this (Blieck and Heintz, 1979).

The lowest Canadian arctic fauna is dated as Ludlovian to Pridolian in age, chiefly on associated invertebrates. The only diagnostic vertebrate is *Hemicyclaspis murchisoni,* from the upper member of the Somerset Island Formation, which is also the index for the lowest zone of the Downtonian in the Anglo-Welsh succession. Few of the other arctic vertebrates can be correlated with those in Spitsbergen and western Europe. *Protopteraspis* and the traquairaspidids are the most diagnostic forms, but in Spitsbergen *Protopteraspis* does not occur until the Plant or possibly the upper part of the Corvaspis horizons (Blieck and Heintz, 1979) of the Fraenkelryggen Formation. Its appearance has been taken as a marker for the Downtonian-Dittonian boundary in the Anglo-Welsh borders. If applied to the arctic fauna, these correlations would be very much at variance both with the invertebrate dating, and with the presence of *Hemicyclaspis murchisoni.* It therefore seems probable that *Protopteraspis* occurs earlier in the Canadian arctic than it does elsewhere (Elliott and Dineley, 1983). The lowest faunal horizon in Spitsbergen, the Psammosteus horizon, does show some faunal similarity to the arctic fauna, as Blieck (*pers. comm.* 1982) has found a form that is probably a member of the Anchipteraspidinae, and *Corvaspis kingi* and traquairaspidids occur in both. It is possible therefore that the upper part of the arctic fauna may range as high as the Pococki zone, which has previously been correlated with the Psammosteus horizon (Fig. 6). However, the lower part of the fauna probably ranges down into the upper Ludlovian, and therefore has no faunal equivalent in Spitsbergen.

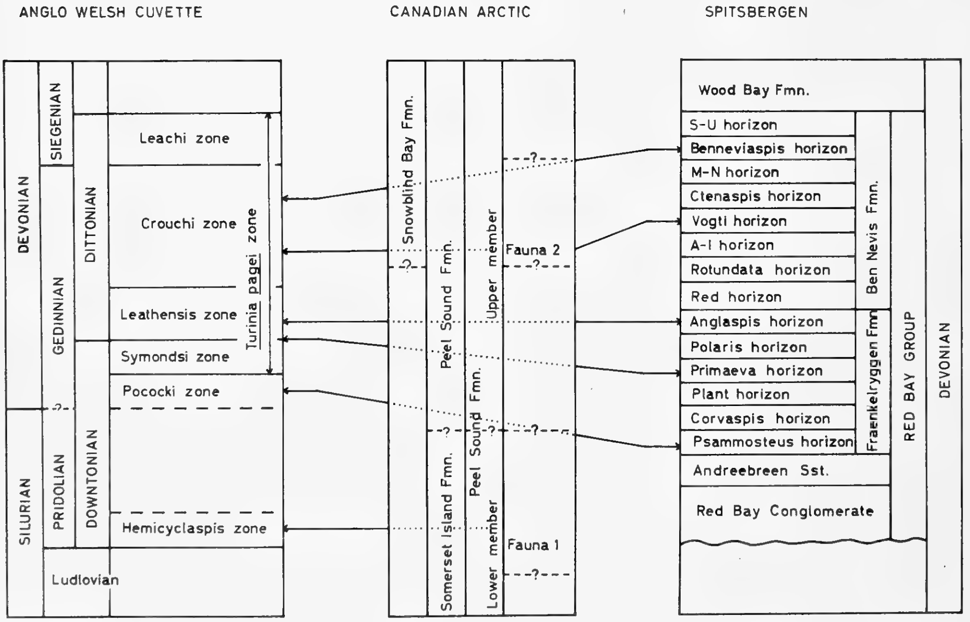

Fig. 6. Correlation of the Canadian arctic vertebrate horizons with the Anglo-Welsh and Spitsbergen successions.

The upper arctic fauna is dated as late Gedinnian to early Siegenian on associated invertebrates, which suggests that this horizon should be correlated somewhere within the Crouchi and Leachi zones of the Anglo-Welsh successions. Blieck and Heintz (1979) have suggested that the Vogti horizon of the Ben Nevis Formation is probably equivalent to the lower Crouchi zone, and the succeeding horizons could be equivalent to the upper Crouchi and Leachi zones.

Though the pteraspidids have been used as the most diagnostic members of the Spitsbergen fauna, and though the same forms do not occur in the Canadian arctic, comparison of the whole fauna does show a distinct similarity between the Vogti fauna and that from the arctic. Goujet and Blieck (1977) pointed out the comparable faunal associations between the Vogti horizon and the Czortkov stage in Podolia, citing the presence of similar pteraspidids of *Althaspis* and *Podolaspis* type, the cyathaspidids *Irregulareaspis* and *Ctenaspis,* and the thelodont *Apalolepis,* a genus considered to be characteristic of the Dittonian in Great Britain (Turner, 1973). Although the same pteraspidids are not present in the Canadian arctic, *Unarkaspis schultzei,* which shows a morphological similarity to *Podolaspis,* may indicate that a similar stage of development had been reached (Elliott, 1983). *Protopteraspis* is found only in Spitsbergen at this time; however *P. vogti* is the last member of this genus, and continued in this area after dying out in the Canadian arctic (Blieck, 1981; Elliott and Dineley, 1983). *Ctenaspis* occurs in all three horizons, and *Anglaspis* and *Weigeltaspis* occur in both the Vogti and Canadian arctic horizons. *Turinia pagei* is found in all three, as is also *Nostolepis*; and *Gomphonchus sandalensis* is common to the Canadian arctic and Vogti horizons. Differences are evident in the fact that *Baringaspis dineleyi* is present in the Canadian arctic fauna, while arthrodires are absent from the Vogti horizon (Goujet and Blieck, 1977; Blieck and Heintz, 1979). However, this may be due to differences in the environment of deposition. It appears possible, therefore, to draw an approximate correlation between the Canadian arctic fauna, that of the Vogti horizon in Spitsbergen, and the Crouchi zone of the Anglo-Welsh succession, already shown (Goujet and Blieck, 1977) to be equivalent in its lower part to the Vogti horizon. However elements of the same fauna extend upwards in the Spitsbergen succession. *Anglaspis* ranges up into the Benneviaspis horizon, as does *Ctenaspis,* and possibly *Miltaspis anatirostra* and *Podolaspis goujeti.* The correlation of this fauna is not clear therefore, and it may in part be correlative with the Leachi zone of the Anglo-Welsh succession, and the Benneviaspis horizon in Spitsbergen.

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Placoderm Interrelationships: a new Interpretation, with a short Review of Placoderm Classifications

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GOUJET, D. F. Placoderm interrelationships: a new interpretation, with a short review of placoderm classifications. *Proc. Linn. Soc. N.S.W.* 107 (3), (1983) 1984: 211-243.

Some of the major classifications of placoderms are briefly reviewed, in their relation to phylogenetic ideas about the group, and the more recent hypotheses of placoderm interrelationships are critically evaluated. Using reinterpreted characters (body armour composition, skull-roof bone pattern, tesserae, number of paranuchal plates, endolymphatic duct, position of nasal capsules, cervical joint, claspers, ornamentation and histology of the dermal bone), a new cladogram, based on 50 synapomorphies, is proposed for all placoderm orders except stensioellids and pseudopetalichthyids, which remain too poorly known. Two main divisions are recognized. In the first branch arthrodires, phyllolepids, petalichthyids and ptyctodontids are characterized by their ventral body armour with an anterior median ventral plate. The second branch groups acanthothoracids, antiarchs and rhenanids on two synapomorphies: a premedian plate, and dorsal nasal capsules. Other synapomorphies (tesserae, structure of the shoulder girdle, and of the cervical joint) require the Acanthothoraci to be dismembered into at least two groups linked respectively to the rhenanids (tesserate forms) or to the antiarchs. The position of *Radotina prima* is also discussed. As a main conclusion, arthrodires and antiarchs are no longer considered as sister-groups. Their elongated body armour is seen as a result of convergent adaptation. The various acanthothoracids share synapomorphies with one or other of the two main divisions, and the Acanthothoraci therefore forms a stem-group of imprecise phylogenetic status.

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A SHORT HISTORY OF PLACODERM CLASSIFICATIONS AND THEIR MEANING

M'Coy (1848) created the name Placodermi to distinguish, among the 'ganoids', a family grouping the genera *Asterolepis, Pterichthys, Bothriolepis, Coccosteus* and *Chelyophorus,* and also the ostracoderm agnathan *Psammosteus.* Since then the definition and classification of placoderm fishes have undergone a number of different versions, as summarized by Obruchev (1964, 1967). My purpose here is to consider only those which represent the major steps in our understanding of the placoderm concept.

During the second half of the nineteenth century and up to 1930 the unity of the group had been rejected by a majority of authors, who followed Cope (1889) and Woodward (1891) in linking ptyctodontids generally to holocephalans, antiarchs to ostracoderm agnathans, and the arthrodires (a name created by Woodward in 1891 for the 'Coccosteans' of previous authors) to the dipnoans. However Dean (1899, 1901) and Hussakof (1905, 1906) recommended keeping apart the arthrodires from lungfishes, and created a separate class, the Arthrognathi.

Since then the unity of Placodermi has been gradually restored, first by Stensiö (1925), who allied petalichthyids, ptyctodontids, and rhenanids to the arthrodires, without erecting a new classification. Later, Stensiö (1931), Gross (1931), and Heintz (1932) returned the antiarchs to the group, Heintz including them in the class

Placodermata as a sub-class equivalent to the Arthrodira, which then comprised only the orders Acanthaspida (Dolichothoraci or Arctolepida), and Coccosteida (= coccosteids + pachyosteids).

Among the classifications of the first half of this century, the following, by Gross (1937), was most influential, and formed a basis for a number of works, some fairly recent (e.g. Denison, 1958; Miles, 1967):

Phylum Elasmobranchi
    Class: Placodermi
    1st Group: Antiarchi
    2nd Group: Arthrodira
        Order 1: Euarthrodira
            Suborder: Acanthaspida (= Arctolepida)
            Suborder: Brachythoraci
        Order 2: Phyllolepida
        Order 3: Petalichthyida
        Order 4: Ptyctodontida
    3rd Group: Rhenanida
    4th Group: Stegoselachii

This classification thus included all major groups except the Acanthothoraci (= Palaeacanthaspida), which was defined later by Stensiö (1944). In it, Gross expressed the gradual evolution of the body armour. He assumed that the long armour of antiarch or dolichothoracid type was a primitive state, and the short armour was specialized. This derived from a progressive reduction in length of the flanks of the body armour observed in arthrodires, from the 'Acanthaspida' (Dolichothoraci) of the Early Devonian, to the Late Devonian Pachyosteomorphi. Gross then transposed such a model to the Placodermi as a whole.

Westoll (1945) interpreted the evolution of the group according to similar processes, but proposed a different grouping: the Arthrodira, Petalichthyida (uniting the Macropetalichthyida and Rhenanida), and Antiarcha (sic) were ranked as separate orders in the class Placodermi. If phylogeny is considered to represent the sequence of formation of monophyletic groups, these classifications are not really phyletic. They do not express the assumed relationships between various members of the class Placodermi, but only a gradual morphological transformation series of one character, the body armour.

Stensiö's classifications (1944, 1959, 1963, 1969) were built on the same general principle, but on a different basic assumption. He organized the Placodermi according to their relative degree of fin concentration and the length of the endoskeletal pectoral articulation. Fin evolution was considered to reflect the ontogenetic development of the paired fins in selachians, according to the fin-fold theory of Gegenbaur and Goodrich (1909). An initially long based fin, and a body armour devoid of spinal plate (as in the 'Pachyosteomorph arthrodires'), supposedly gave rise to a highly concentrated fin, as exemplified by the antiarchs. In the last of Stensiö's classifications, the placoderms (named Arthrodira) are distributed in two major groups: Euarthrodira and Antiarchi. The first group includes two super-orders: the 'primitive' Aspinothoracidi, lacking a spinal plate and showing a long-based pectoral fin, and the 'more advanced' Spinothoracidi, possessing a spinal plate, which supposedly developed by fusion of the anterior fin radials, and a 'concentrated' pectoral fin. Stensiö proposed (1969: 153) that the spinothoracid arthrodires 'should have evolved partly from early primitive prearthrodires, and partly from some Aspinothoracidi'. The groups are, in that case, evidently founded on parallelism or convergence.

Under this classification, the subsets may not correspond to natural (monophyletic) groups, and euarthrodire families are kept apart which, in view of their shared specializations, should be grouped together. The morphological basis for this classification is also undermined because some of the so-called Aspinothoracidi possess a spinal plate (Mark-Kurik, 1963; Heintz, 1968). Stensiö (1969: 53) evaded this problem by considering in these cases that it represented a 'pseudo-spinal' plate, not homologous to the true spinal, even if it occupied the same position, with the same basic function of fixing together dorsal and ventral halves of the armour and covering the endoskeletal scapulo-coracoid.

But the major drawback of Stensiö's classification is the confusion caused by using the same terminology as other authors to qualify different taxa. Under the name Arthrodira are grouped all the placoderms of the other authors; the term Placodermata (sic) then designates the set composed of the Arthrodira and the Holocephali, which are supposed to be ptyctodontid descendants (Ørvig, 1962). The name Euarthrodira, also kept by Stensiö, designates all the non-antiarch placoderms of the other authors.

A different attitude was expressed in the classifications of Romer (1966) and Miles (1969). The practical aspect was emphasized, to give an organized list of clearly defined orders, which may or may not be monophyletic. No supra-ordinal groupings were proposed, so there is no real hierarchical classing. Although not expressing any ideas on the interrelationships of the groups of placoderms, such classifications have the advantage of flexibility in permitting the possible affinities between groups to be worked out without remodelling all taxonomic ranks and the associated nomenclature.

However it is still necessary to go beyond such a state of our knowledge, and to build up a phylogenetic hypothesis of relationships which, by initiating new research, can enrich our information on all the placoderm groups. In our present state of knowledge any attempt of that sort cannot claim to be more than a working hypothesis. To remain in the realm of scientific enquiry, in the sense of Popper (1973), the hypothesis must be testable. For this it must meet certain methodological requirements, but most importantly, it must be as explicit and comprehensive as possible to permit corroboration or refutation.

PLACODERM INTERRELATIONSHIPS: SOME RECENT HYPOTHESES

Although different, the hypotheses of placoderm interrelationships proposed by Denison (1975, 1978) on the one hand, and by Miles (1973), Miles and Young (1977), and Young (1980) on the other, adhere to such principles. These schemes are my initial working hypotheses to grapple with the problems of placoderm interrelationships. Both schemes are based on characters of the body armour and associated structures like the dermal cervical joint. Denison takes also into account other criteria like the pattern of dermal bones in the skull, and the nature of the superficial skeletal tissue of the dermal bone.

The proposals of these authors will be discussed here using characters deduced from the study of the skull-roof and endocranium, and a revision of the supposed homologous structures in the body armour. However, to avoid doubtful interpretations of material rather badly known and hard to analyse, I will not include the Stensioellidae and the Pseudopetalichthyidae. These occupy an important position in Denison's phylogeny, as models for the primitive condition of many characters. I will also initially assume that the various placoderm orders (arthrodires, antiarchs, phyllolepids, rhenanids, acanthothoracids, ptyctodontids, and petalichthyids) are monophyletic groups in the sense of Hennig (1966).

Denison's phylogeny scheme (Fig. 1) differs from that of Miles and Young (1977) both in its initial assumptions, and in the methodology used to reconstruct phylogenies.

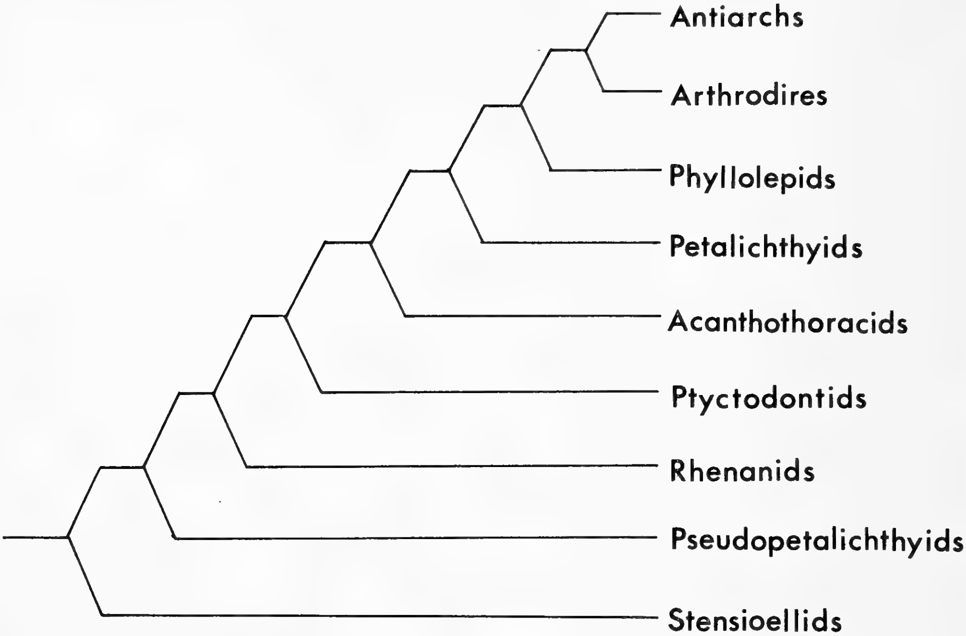

Fig. 1. Denison's phylogeny of placoderms (after Denison, 1978: fig. 10).

Miles and Young adopt a strictly cladistic attitude, but Denison admits, as a methodological principle, the search for ancestor-descendant relationships. Thus, he classifies monophyletic groups with others which are not, causing confusion in the composition, understanding, and definition of higher ranked groups. This applies mainly to the arthrodires, and actinolepid arthrodires are a 'grade' group, from which the other arthrodires, phyllolepids, and the antiarchs are thought to arise.

Another initial assumption is that Denison apparently shares Schaeffer's opinion (1975) that placoderms are the sister-group of all other gnathostomes. He assumes that a short body armour is the primitive condition of placoderms, and that distinctive specializations in the various groups can be used as the foundations of a phylogenetic classification. He proposes a number of primitive characters based on the morphology of stensioellids, pseudopetalichthyids, and ptyctodontids, but he also refers to acanthothoracids and rhenanids. Among the 18 primitive characters listed by Denison (1975), the following 15 can be discussed as relevant to this study:

1) The ventral shoulder girdle consists of a single pair of plates homologous either to the interolaterals or the anterior ventrolaterals of the Arthrodira; between them, a median plate has been identified only in Ptyctodontida.

2) The lateral shoulder girdle consists only of anterior laterals and anterior dorsolateral plates, except in some Acanthothoraci where posterolaterals and posterior dorsolaterals are also present.

3) The spinal plates are absent, or small and doubtfully distinct, except in acanthothoracids and ptyctodontids.

4) A medial dorsal is probably absent in stensioellids and pseudopetalichthyids.

5) Pectoral fins are narrow-based, even in rhenanids where the fins are much expanded distally.

6) There is no exoskeletal cervical joint, except in ptyctodontids where it is developed differently from arthrodires and antiarchs.

7) The anterior vertebrae are fused to form a synarcual which articulates with the occipital region of the neurocranium (not known in Acanthothoraci).

8) The neurocranium is long and slender with a long occipital region, except in ptyctodontids where it must have been short.

9) The dermal cranial roof bone pattern may be variable and unstable with relationships between bones and sensory canals not firmly established, except in ptyctodontids.

10) Dermal cranial roof bones may be small, and part of the roof may be covered with thin, superficial tesserae in acanthothoracids and rhenanids; much of the skull in stensioellids is covered with denticles or tesserae; the central part of the cranial roof of pseudopetalichthyids is covered with small dermal bones, but there may have been denticles or tesserae elsewhere. Denticles and tesserae are unknown in ptyctodontids, but may have covered the snout and cheek where dermal bones are largely absent.

11) The jaws, where known, are more or less transverse and lack large dermal elements, except in ptyctodontids.

12) Gill covers (submarginals) may be present, though their dermal bones are small in ptyctodontids.

13) The orbits are small and lateral in stensioellids and most acanthothoracids, large and dorsolateral in ptyctodontids, and dorsal in pseudopetalichthyids, rhenanids, and one late genus of acanthothoracid; the last condition is surely specialized.

14) The nostrils are known only in rhenanids and acanthothoracids where they are usually dorsal, a condition that is surely specialized. In stensioellids, pseudopetalichthyids and primitive acanthothoracids, they are presumed to be anterior or anteroventral; there are no clues of their position in ptyctodontids.

15) Pelvic fins are long-based and semicircular in rhenanids, stensioellids and pseudopetalichthyids; they are specialized by the development of claspers in male ptyctodontids.

On eight of these charactlers (1-4, 8-10, 12), of which they temporarily accepted the validity, Miles and Young (1977: 128) listed nine unparsimonious consequences of Denison's phylogeny. However some of these criticisms follow from a particular interpretation by Miles and Young of Denison's scheme. For example they claim that the loss of the dermal neck-joint in phyllolepids involves a reversal in evolution, but Denison (1975) regarded phyllolepids as more closely related to actinolepids than to the other arthrodires and the antiarchs, and the loss of the neck-joint was therefore not implied. The anterior dorsolateral plate in *Phyllolepis* demonstrates the presence of a sliding dermal neck-joint very similar to that of actinolepid arthrodires (see Stensiö, 1936: pl. 14, fig. 2; Young, 1980: 69).

Miles and Young's (1977) alternative scheme (Fig. 2), is mainly built on features of the body armour. From the distribution of its component bones among the various groups of placoderms, they suggest a hypothetical ancestral morphotype of the armour made up of the following plates: a single median dorsal, paired anterior dorsolaterals, posterior dorsolaterals, anterior laterals, interolaterals, anterior ventrolaterals, and an anterior median ventral. This morphotype also assumes certain homology conventions and postulates which will be discussed later.

Two other characters used are the presence or absence of tesserae, and the number of paranuchal plates (one versus two). The potential phylogenetic importance of these characters had been suggested earlier by Westoll (1967). Miles and Young attempted to elucidate their phylogenetic meaning by analysing the alternative hypothesis, but were unable to select a preferred solution using a parsimony criterion. They concluded

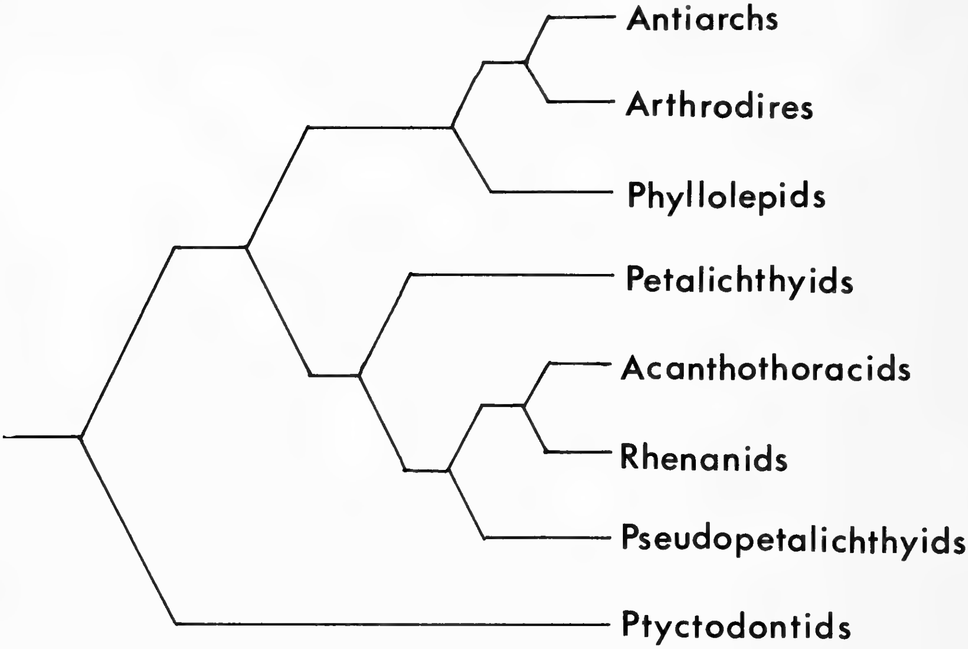

Fig. 2. Miles and Young's phylogeny of placoderms (after Miles and Young, 1977: fig. 5).

that presence of tesserae does not define any important group, because within a supposed monophyletic group (the Acanthothoraci), some members have tesserae and some do not. However they proposed the presence of two paranuchal plates as a synapomorphy uniting petalichthyids, acanthothoracids, rhenanids, and pseudopetalichthyids, but were unable to present strong supporting arguments. In their own words, they admit this character as a valid synapomorphy 'simply on the ground that trial and error has shown it to be the more useful hypothesis for (their) work' (Miles and Young, 1977: 133). In other words, it does not contradict their conclusions based on their trunk armour analysis, and thus might be seen as an 'a priori' statement.

On the other hand, there is no unequivocal evidence of two paranuchal plates in rhenanids (gemuendinids of Miles and Young, 1977), in spite of Westoll's account (1967: fig. 3). In known Acanthothoraci, the homologies of the supposed paranuchal plates are not easily established, and the plate interpreted as a medial paranuchal by Ørvig (1975) in *Romundina* is interpreted as a posterior central by Denison (1978) and Young (1980).

In their final diagram, Miles and Young group the non-ptyctodontid placoderms in two distinct lineages. Arthrodires (Fig. 3**A, B**) and antiarchs (Fig. 3**C, D**) are united on the presence of posterior ventrolateral, posterior median ventral and posterolateral plates; in other words, they possesss a long body armour. The phyllolepids (Fig. 5**B**) are the only other placoderms supposed to possess a true posterior ventrolateral; this is interpreted as a synapomorphy linking them to the arthrodires and antiarchs. The second lineage groups the petalichthyids (Fig. 7**D**), acanthothoracids (Figs 8, 9), rhenanids (Fig. 7**I**) and pseudopetalichthyids. The supposed uniquely derived shared characters of these groups are two pairs of paranuchals, and a long occipital region of

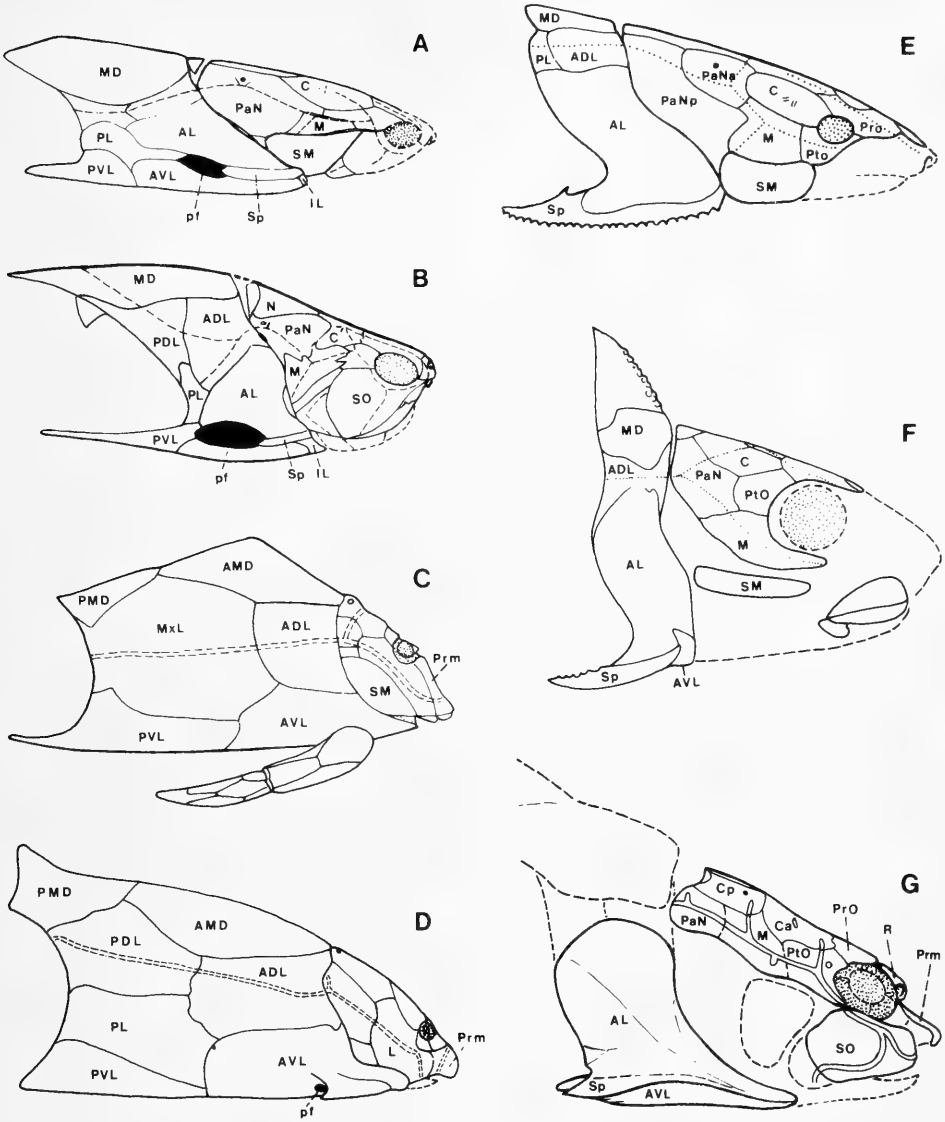

Fig. 3. Lateral view of the dermal armour in representatives of the various placoderm groups. **A**, actinolepid arthrodire: *Sigaspis lepidophora,* from Goujet (1973). × 0.6. **B**, brachythoracid arthrodire: *Coccosteus cuspidatus,* from Miles and Westoll (1968). × 0.4. **C**, asterolepid antiarch: *Pterichthyodes milleri*, from Traquair (1914). × 0.4. **D**, yunnanolepid antiarch: *Yunnanolepis parvus,* from Zhang (1978). × 2.4. **E**, petalichthyid: *Lunaspis heroldi,* simplified from Stensiö (1963). × 0.5. **F**, ptyctodontid, *Rhamphodopsis threiplandi,* from Miles (1967). × 2.4. **G**, acanthothoracid: *Romundina stellina*, slightly modified from Ørvig (1975). × 2.3.

the skull. Acanthothoracids and rhenanids are also assessed as sister-groups on one common specialization: the dorsal position of the nasal apertures (Fig. 10**A**, **B**, **D**). A premedian plate may be linked to this character, but Miles and Young note that this plate had not been clearly demonstrated in rhenanids. They conclude that the premedian plate in acanthothoracids and antiarchs has originated independently, but this contradicts the rule of bone regression they advocate as a low level evolutionary law. According to this rule, they claim to have been more ready to accept the multiple loss of bones than their multiple origin.

The dorsal position of the nasal apertures back from the rostral margin is in my opinion a major feature which influenced the whole development of the front part of the endocranium and the morphology of the brain cavity. This feature appears underestimated by Miles and Young, and if it could be shown that the resemblances of the body armour are less important than they propose, the nasal position would suggest a closer relationship between antiarchs and acanthothoracids.

To place ptyctodontids within their phylogenetic scheme Miles and Young use a primary sexual character: the pelvic and prepelvic claspers. This appeal to structures otherwise known only in elasmobranch fishes implies that they consider placoderms to be elasmobranchiomorphs.

REANALYSIS OF PHYLOGENETICALLY IMPORTANT CHARACTERS

Miles and Young's hypothesis appears more parsimonious than Denison's, but it is built on preliminary choices and assumptions about the significance of paranuchal plates and the body armour composition which call for discussion. This discussion will be the source of different ideas from which a new hypothesis of placoderm interrelationships will be proposed.

THE BODY ARMOUR (Figs 3, 4, 5)

The primitive composition of the body armour proposed by Miles and Young presupposes several hypotheses about the homology of various plates. Thus they suggest the term 'anterior ventrolateral', and not 'interolateral', for the single paired plate in the anterior ventral position of ptyctodontids (Fig. 5**C**) and rhenanids (Fig. 5**G, H**); 'median dorsal' for the anterior median dorsal plate of antiarchs (AMD, Fig. 3**C, D**; the posterior median dorsal is supposed to be secondarily incorporated from behind); and 'posterior median ventral' for the median ventral plate of antiarchs (MV, Fig. 5**F**).

These homologies have been retained here, and I also accept that a true spinal is present in rhenanids (Figs 5**G, 7I**), even if it is fragmented or covered with tesserae.

On the other hand, I will not follow Miles and Young's suggestions on the following five points:

i) the supposed absence of posterolateral plates in Acanthothoraci (Fig. 4**A, B**). This plate has not been recovered in any acanthothoracid, but its existence or the presence of a topographically equivalent element is witnessed by a clear contact face on the posterior part of the anterior lateral plate in *Palaeacanthaspis* (Fig. 4**B**; Stensiö, 1944: fig. 4B) or *Weejasperaspis* (White, 1978: fig. 5), and an overlapped area on the posterior dorsolateral plate of *Kosoraspis* (Fig. 4**A**; Gross, 1959: fig. 8). In other forms, it is supposed to be missing (*Romundina,* Ørvig, 1975). Where it has been observed, the overlapped area suggests a very small 'posterolateral' plate, indicating that it may have been a modified scale incorporated in the body armour. In primitive placoderms, as implied by some arthrodires (e.g. *Sigaspis,* Goujet, 1973) and antiarchs (Lyarskaya, 1981: fig. 36), the tail may have been covered with large scales.

ii) the distribution of posterior ventrolateral plates. According to Miles and Young these are present only in arthrodires, antiarchs and phyllolepids (PVL, Fig. 5**A, B, F**), suggesting a common ancestry for the three groups. They deny that a true posterior ventrolateral exists in petalichthyids, rhenanids and acanthothoracids, all groups in which such a plate can be assumed on positive evidence.

In petalichthyids, Miles and Young (1977: 130) interpret the plates situated just behind the anterior ventrolateral plates in *Lunaspis* (Fig. 5**D**) as modified scales like

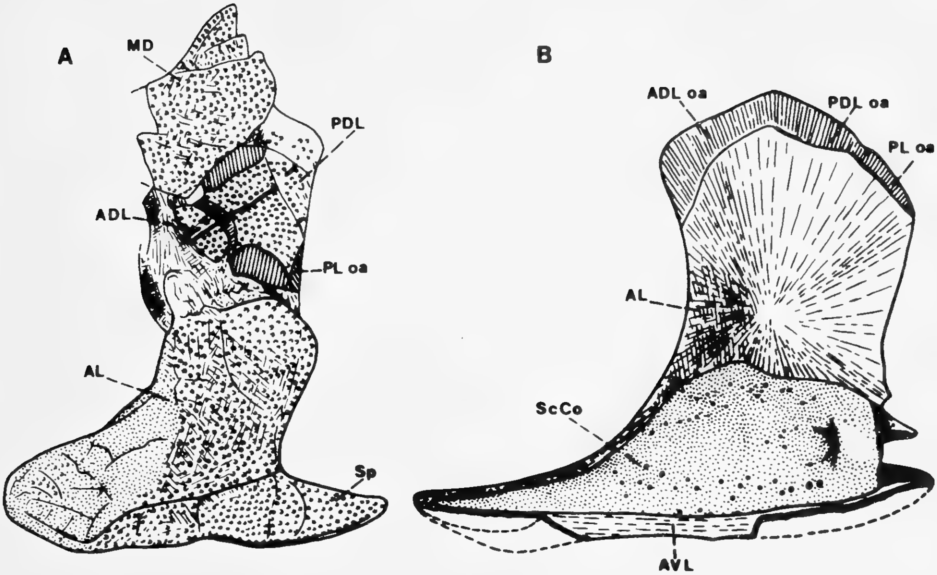

Fig. 4. **A**, *Kosoraspis peckai*, lateral view of the body armour, from Gross (1959). × 0.6. **B**, *Palaeacanthaspis vasta*, inner view of the endoskeletal shoulder girdle and its dermal cover, from Stensiö (1944). × 1.5.

those behind the trunk armour in *Sigaspis* (Goujet, 1973: fig. 2). This raises the question of how a 'true' posterior ventrolateral plate may be characterized. Miles and Young argue that there is also no posterior median ventral plate in *Lunaspis,* but in the only specimen (Fig. 5**D**) showing the ventral part of the body armour, the area of the posterior median ventral is apparently imperfectly prepared (Gross, 1961: pl. 5), or badly preserved. In *Wijdeaspis,* the visceral surface of the anterior ventrolateral plate (Heintz, 1937: pl. 1, fig. 5) clearly shows fine radiating striations around the mesial bone margins characteristic of overlap areas, including the zones corresponding to those for the posterior median ventral and posterior ventrolateral in arthrodires. Either the posterior median ventral plate was present in petalichthyids, or the corresponding space in *Lunaspis* was open, or covered by scales. But both these alternatives seem very unlikely, as these conditions are not known in other placoderms. The possibility that *Lunaspis* had a median ventral opening in the trunk armour is also contradicted by the high degree of ossification of the dermal armour in this genus.

Regarding the lack of data on a posterior ventrolateral plate in other petalichthyids, I point out that complete articulated individuals are known only in *Lunaspis. Macropetalichthys* from North America and China (Stensiö, 1925; Pan, Wang and Liu, 1975), and *Wijdeaspis* from Spitsbergen (Heintz, 1937) and USSR (Obruchev, 1964: pl. 1, figs 1, 2, 4) are only known from disarticulated elements. Among the *Macropetalichthys* material I have examined in various North American collections, the proportion of body plates to the number of skulls is very low. This may be the result of selecting out the most spectacular specimens, during the sporadic discoveries of the 19th century. Only the anterior ventrolateral, spinal and anterior lateral plates are common in museum collections.

As a conclusion, I accept Gross's (1961) interpretation of *Lunaspis* (Fig. 5**D**) as a model for petalichthyids. The plate named posterior ventrolateral (PVL) is a strict homologue of the one in arthrodires and phyllolepids. It even presents the peculiar S-shaped suture between the right and left plate which characterizes this contact in some arthrodires (*Arctolepis,* Fig. 5**A**; *Tiaraspis,* Gross, 1962a). This interpretation has been argued by Young (1980: 63) who reaches almost the same conclusion.

However, I do not follow either Gross's or Young's interpretation of the small paired plate situated immediately behind the posterior ventrolateral plate. Gross (1961: fig. 5) calls it a 'posterior ventral' plate, and considers it as an exclusive feature of petalichthyids (or of *Lunaspis*). Young (1980: 64) considers it to be the posterior part of the posterior ventrolateral; he interprets the transverse linear feature on the specimen not as a suture, but as the external expression of an inner transverse ridge inferred to encircle the body armour as in antiarchs and dolichothoracids (*Dicksonosteus,* Goujet, 1975). In my opinion, this small plate is not strictly part of the body armour; by comparison with *Sigaspis* (Goujet, 1973: fig. 1), it would seem to represent a dermal cover for the pelvic girdle.

Thus, the only differences between the posterior ventrolateral plate in *Lunaspis* and in arthrodires and antiarchs seem to be its smaller size, and an apparent lack of a lateral ascending lamina forming part of the side of the armour. It is relevant to note that the posterior ventrolateral plate in phyllolepids also lacks a lateral lamina, and I suggest that its absence is a plesiomorphic state, a proposal supported by the interpretation of the body armour of rhenanids and acanthothoracids.

In rhenanids, Miles and Young (1977) also concluded that a posterior ventrolateral was absent (cf. Stensiö, 1959, 1969). Miles and Young refer to *Gemuendina* (Fig. 5**G**), which has been interpreted in two different ways. Posterior ventrolateral plates were reconstructed by Stensiö (1959: figs 13, 14, 16) but this was not accepted by Gross (1963: 58). *Gemuendina,* like all the material from the Hunsrück shales, remains extremely difficult to interpret, and the question cannot be answered with such material. However, in *Jagorina* (Fig. 5**H**) there is clearly a separate plate in the same position as the posterior ventrolateral plate on the only specimen known (Stensiö, 1959: fig. 60), which cannot be confused with a bony process of the anterior ventrolateral as in the case of *Gemuendina.* This plate is very small, compared to its homologue in arthrodires or antiarchs. Moreover, there is no midline contact between the left and right plates, and the ventral side of the trunk armour is widely embayed from behind. Nevertheless, I interpret this plate as a posterior ventrolateral homologous to that in arthrodires, antiarchs, phyllolepids, and petalichthyids.

The posterior ventrolateral plate in acanthothoracids was not considered by Miles and Young, but the anterior ventrolateral of *Romundina* has a clear overlap area (PVLoa, Fig. 5**E**; Ørvig, 1975:pl. 4, figs 2, 4) which suggests a plate in the same situation as the posterior ventrolateral of *Jagorina.* More complete acanthothoracid material is needed to confirm the size and shape of this plate, but in my opinion the evidence of the overlap area is sufficient to demonstrate its existence in this group.

iii) On the distribution of the interolateral plate among placoderms, Miles and Young (1977: 130, table 1) accept its presence in five groups (arthrodires, phyllolepids, petalichthyids, acanthothoracids and pseudopetalichthyids). In the last three groups, however, the presence of such a plate is questionable. The pseudopetalichthyids are too

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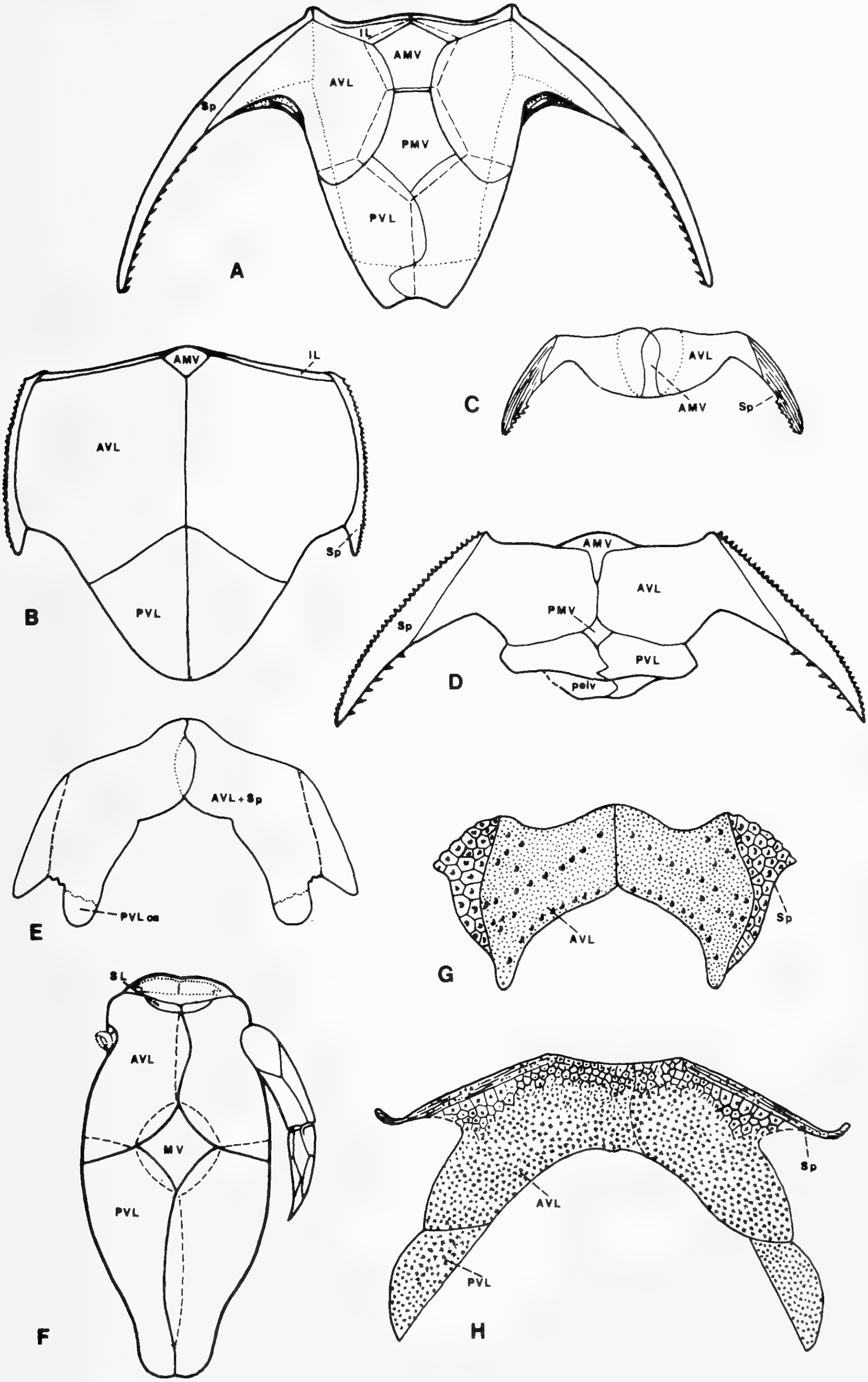
Fig. 5. Ventral view of the trunk shield in representatives of the various placoderm groups. **A,** phlyctaeniid arthrodire: *Arctolepis decipiens.* × 0.45. **B,** phyllolepid: *Phyllolepis orvini,* from Stensiö (1959). × 0.4. **C,** ptyctodontid: *Rhamphodopsis threiplandi,* from Miles (1967). × 2.3. **D,** petalichthyid: *Lunaspis broilii,* from Gross (1961). × 0.4. **E,** acanthothoracid: *Romundina stellina,* modified from Ørvig (1975). × 2.2. **F,** antiarch: *Asterolepis maxima,* from Traquair (1914). × 0.2. **G,** rhenanid: *Gemuendina stuertzi,* from Gross (1963). × 0.6. **H,** rhenanid: *Jagorina pandora,* redrawn from Stensiö (1959). × 0.6.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poorly preserved for meaningful discussion, but there is better evidence regarding petalichthyids.

In *Lunaspis,* Gross (1961) made a point of delineating the interolateral plate with dotted lines, and this plate has never been identified in any other petalichthyid, even in those specimens where the anterior ventrolateral plate remains in close association with the spinal plate. Thus, I consider that the interolateral plate is absent in petalichthyids.

In Acanthothoraci, the same plate has been reconstructed in *Palaeacanthaspis* by Stensiö (1944: fig. 4B), in *Romundina* by Ørvig (1975: fig. 4A), and in *Brindabellaspis* by Young (1980: fig. 21). These three authors have again delimited the plate by dotted lines, the area supposed to correspond to the interolateral plate being indistinguishable from the anterior ventrolateral. In the absence of clear evidence I do not admit a separate interolateral plate in Acanthothoraci.

To summarize, only in arthrodires (Fig. 5**A**) and phyllolepids (Fig. 5**B**) is the interolateral a definite separate plate, with its own centre of radiation. This plate can also be characterized by the presence of a wide transverse groove on its ventral surface.

iv) The plate classically called anterior ventrolateral in antiarchs includes, in my opinion, an anterolateral component which dorsally encloses the pectoral fenestra (Jollie, 1962: fig. 6-70). In fact, the antiarchs seem to possess a single plate covering the scapulo-coracoid, whether it is called an anterior ventrolateral, or considered as an integrated complex including spinal and anterolateral elements. In no antiarch are these components clearly delimited, even if, in yunnanolepids (Fig. 3**D**; Zhang, 1978) a spinal process is present.

This single unit, with no sutures between the plates covering the endoskeletal shoulder girdle, seems to be an exclusive feature of the antiarchs, and can be retained as a good apomorphy for the group.

In some respects, a similar situation is met with in Acanthothoraci, although the spinal, anterolateral and anterior ventrolateral plates still remain as distinct components. In *Palaeacanthaspis* (Stensiö, 1944), the sutures between the spinal and both other plates can be drawn from the change in orientation of the radiating internal tubules of the bone. In *Weejasperaspis* (White, 1978), they are suggested by the distribution of ornamental ridges or rows of tubercles. In forms where the ornament is evenly distributed, the sutures are more difficult to set out. In *Brindabellaspis* (Young, 1980) only the posterior end of the suture between the spinal and the anterolateral has been clearly seen. In *Romundina,* the suture between the spinal and anterior ventrolateral plates can be observed on a single specimen (Ørvig, 1975: pl. 5, fig. 6), thanks to the wear of the bone surface. Therefore, at first sight, the 'pectoral cover' in *Romundina* and *Brindabellaspis* might be regarded as a single plate, as in antiarchs (see also Mark-Kurik, 1974: fig. 8). It differs mainly in its large post-branchial lamina, which is absent in antiarchs. More typically, the pectoral cover appears to be composed of two elements (*Weejasperaspis, Palaeacanthaspis, Kosoraspis;* Gross, 1959: fig. 8, and possibly *Radotina kosorensis*), the anterolateral area being divided from the ventral shield (spinal and anterior ventrolateral plates) by a distinct suture.

If a high cohesion of the pectoral cover is a seemingly common feature amongst Acanthothoraci, it does occur also to a lesser extent in forms where the plates exist as separate units. In such cases they remain articulated when fossilized. This is the case in actinolepid arthrodires (see Stensiö, 1944: fig. 15), ptyctodontids, petalichthyids, and rhenanids. As in some Acanthothoraci, the anterolateral plate often separates more easily than the components of the ventral unit, namely the spinal, anterior ventrolateral, interolateral (when present) and anteroventral plates (the last in actinolepid arthrodires only).

I consider the cohesion of the ventral unit as a character which may correspond to

	MD	ADL	AVL	AL	Sp	PVL	PDL	PL	AMV	PMV	IL	AV	dermal pectoral unit
ACANTHOTHORACI	1	1	1	1	1	1	1	1	?	0	0	0	1,0
ANTIARCHS	1	1	1	0	1,0	1	1	1	0	1	0	0	1
ARTHRODIRES	1	1	1	1	1	1	1	1	1	1	1	1,0	0
PETALICHTHYIDS	1	1	1	1	1	1	1	0	1	1	0	0	0
PHYLLOLEPIDS	1	1	1	1	1	1	0	0	1	0,?	1	0	0
PTYCTODONTIDS	1	1	1	1	1	0	0	0	1	0	0	0	0
RHENANIDS	1	1	1	1	1	1	0	0	?	0	0	0	0

Fig. 6. Distribution of plates in the armour of individual placoderm groups.

the primitive condition in the placoderms, but the firm relationship between the anterolateral plate and the ventral unit, with partly synostosed sutures as seen in *Brindabellaspis* or *Romundina,* is likely to be a secondary specialization.

v) The anterior median ventral was regarded by Miles and Young (1977) as a primitive component of the placoderm trunk armour, but this plate has never been found in Acanthothoraci, although an articulated body armour is not known in this group, and the overlap area seen medially on the anterior ventrolateral might be for this element. In rhenanids, an anterior median ventral has been included by Stensiö (1959: fig. 60) in *Jagorina,* as an element fused with the right anterior ventrolateral. However an anterior median ventral is lacking in *Gemuendina,* and given the available data on *Jagorina,* the presence of such a plate in this group is uncertain.

Relevant here is the interpretation of the semilunar plate of antiarchs, and whether it is homologous with the anterior median ventral of arthrodires, as assumed by Miles and Young (1977). On morphological grounds, there are no striking differences between this plate and the unpaired semilunar of bothriolepid antiarchs. However, an unpaired semilunar is restricted to bothriolepids and a few asterolepiforms (e.g. *Gerdalepis*) amongst the antiarchs. This condition can therefore be interpreted as derived, relative to the paired semilunars of other asterolepiforms, sinolepids, and yunnanolepiforms, where they are rather large plates (see Zhang, 1978: fig. 1). In this case, the primitive antiarch condition shows that homology with the anterior median ventral cannot be accepted. The alternatives are that the semilunar is either homologous with the interolateral of arthrodires (Stensiö, 1969: 517), or is a special plate restricted to the antiarchs. I do not accept the first alternative for morphological reasons (the semilunar has no postbranchial lamina), and I provisionally suggest therefore that the semilunar plate is a special apomorphy of antiarchs.

The discussion on these five points just presented leads to a reconsideration of Miles and Young's (1977) table of the distribution of the homologous plates in the body armour of the various placoderm orders. My conclusions are summarized in Fig. 6.

From this table, the primitive morphotype of the body armour may be inferred as a pair of composite bones (with an anterolateral, spinal, and anterior ventrolateral) covering the endoskeletal shoulder girdle, associated with a single median dorsal, paired anterior and posterior dorsolateral, and paired posterior ventrolateral plates. The flanks were open behind the pectoral fin articulation. The posterolateral plate exists in antiarchs and arthrodires, but also in Acanthothoraci. It cannot be kept as a synapomorphy of the two former groups, and could also be a component in the ancestral state of the armour. If so, the absence of a posterolateral in phyllolepids, petalichthyids, ptyctodontids, and rhenanids, would be secondary.

The pectoral fenestra is unique to antiarchs and arthrodires, but the surrounding plates are different, so it cannot be regarded as homologous between the two groups. The posterior ventrolateral plate which accompanies the closure of the flanks of the armour behind the pectoral fenestra has been considered by Miles and Young and Denison as a shared specialization of antiarchs and arthrodires, but the presence of such a plate in some Acanthothoraci and rhenanids devalues this character.

The presence of an interolateral as a separate unit only in arthrodires and phyllolepids suggests a closer relationship between them. Otherwise, the body armour composition provides little evidence on the interrelationships of the other groups. However, the fused dermal pectoral unit in *Brindabellaspis* and *Romundina* would support a closer relationship of these acanthothoracids with the antiarchs.

THE SKULL ROOF PATTERN

At first glance, the characters concerned with the skull roof are more difficult to use than those of the body armour. The analysis of the significance of tesserae and paranuchal plates given by Miles and Young (1977) well illustrates this difficulty; on neither point could a preferred hypothesis be demonstrated by these authors.

Regarding the skull roof dermal bone pattern (Fig. 7), I agree with Denison that this feature should be used with caution in assessing relationships. In fact, our present knowledge of placoderms shows that a fixed bone pattern in one group can only be easily interpreted with reference to that of another by invoking fusion-fragmentation processes, or intermediate states, as numerous as are necessary to effect the required transformation. This is hardly a testable procedure.

Yet, as Denison has noted, the absence of fixed relationships between the skull roof bones and to the sensory canal pattern might be a plesiomorphy in placoderms. In other words, the primitive condition of the skull roof would correspond to an unstable bone pattern. The best examples of such a labile state can be found in the tesserate forms, mainly the Acanthothoraci. By comparing the known skull roofs of *Radotina* (Gross, 1958, 1959) or *Kosoraspis* (Gross, 1959) it is clear that almost all show, in a similar skull roof pattern, a different extent of plates and tesserate areas. These observations have led me to reconsider two problems already analysed by Miles and Young (1977), namely the phyletic significance of tesserae, and of the number of paranuchal plates.

Considering first the meaning of tesserae, one point needs clarification; 'tesserae' *sensu stricto* are superficial elements superimposed on the dermal plates (Gross, 1959; Westoll, 1967), as in *Kimaspis* (Mark-Kurik, 1973). They should not be confused with dermal plates of small size. This important distinction could be analysed further to resolve much misunderstanding, but this is beyond the scope of the present study. Here, I use the term tesserae in the sense of Gross (1959) and Stensiö (1963, 1969). As Miles and Young (1977) have pointed out, if tesserae are interpreted as secondary structures, a reversal in the evolution of some groups towards a supposed micromeric ancestral state must be considered. If, on the contrary, tesserae are considered as a plesiomorph state, this implies their disappearance at least in three groups of macromeric placoderms: arthrodires, antiarchs, and some acanthoracids. In the last group, tesserae are absent in *Romundina* (Fig. 8C; Ørvig, 1975), *Palaeacanthaspis* (Stensiö, 1944), and *Radotina prima* (Fig. 9; Gross, 1958).

The parsimony principle does not permit a reasonable choice between these hypotheses, yet Miles and Young favoured the first, that tesserae are a secondary feature. They noted that the body armour in most placoderms is made of large plates, and the thoracic tesserae which occur only in rhenanids can thus be seen as secondary,

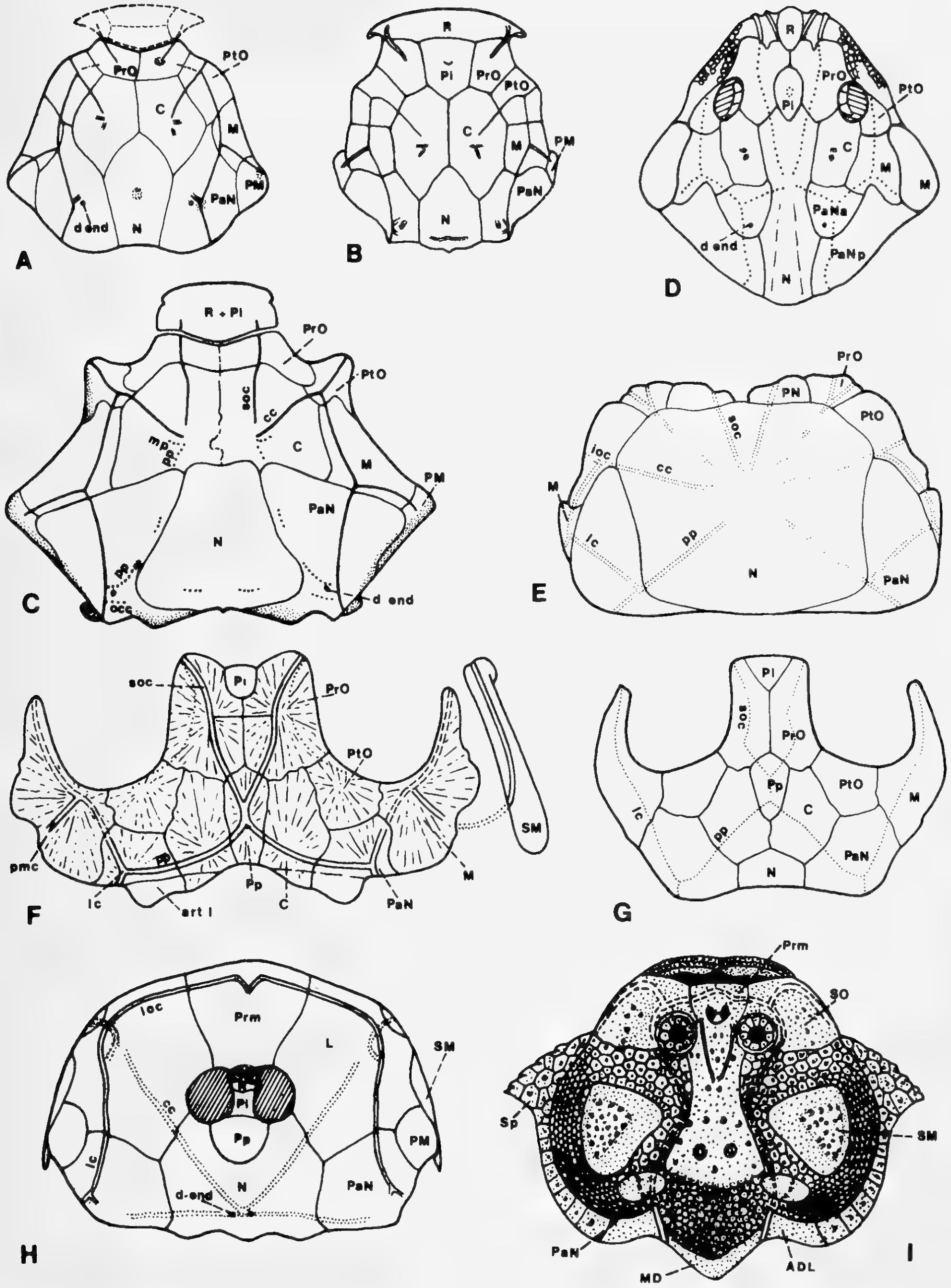


Fig. 7. Cranial shield of various placoderms, dorsal view. **A,** actinolepid arthrodire: *Kujdanowiaspis* sp., modified from Denison (1958). × 0.6. **B,** phlyctaeniid arthrodire: *Arctolepis decipiens,* from Goujet (1975). × 0.6. **C,** brachythoracid arthrodire: *Buchanosteus confertituberculatus,* from White and Toombs (1972). × 0.35. **D,** petalichthyid: *Lunaspis broilii,* slightly modified from Gross (1961). × 0.5. **E,** phyllolepid: *Phyllolepis orvini,* from Stensiö (1936). × 0.15. **F,** ptyctodontid: *Ctenurella gladbachensis,* from Ørvig (1962). × 2.3. **G,** ptyctodontid: *Rhamphodopsis threiplandi,* from Miles (1967). × 5. **H,** antiarch: *Bothriolepis canadensis,* from Denison (1978). × 0.8. **I,** rhenanid: *Gemuendina stuertzi,* from Gross (1963). × 0.6.

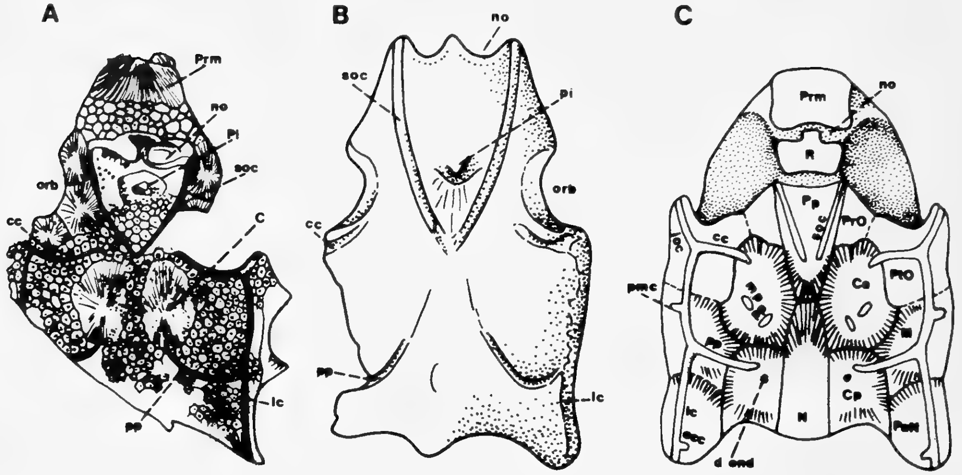


Fig. 8. Skulls of acanthothoracids, dorsal view. **A,** dermal shield of *Radotina kosorensis,* from Gross (1959). ×0.6. **B,** upper surface of the endocranium of *Radotina prima,* redrawn from von Koenen (1895). ×1.3. **C,** cranial shield of *Romundina stellina,* from Ørvig (1975). ×3.

and as a synapomorphy uniting members of this last group. The fact that the pattern of distribution of tesserae on the skull roof is rather similar in gemuendinids and acanthothoracids (Westoll, 1967) reinforces this suggestion.

Accepting this solution would imply that within the Acanthothoraci the tesserate forms would be more closely related to rhenanids than to the non-tesserate acanthothoracids. Thus, this proposal would dismember the Acanthothoraci into two diverging sets.

Also to be considered is the possible presence of tesserae in the petalichthyid *Lunaspis* (Fig. 7**D**). In this fish, a series of platelets covers the anterior part of the cheek, in the position of the suborbital plate of other placoderms. These platelets have been interpreted as tesserae on morphological grounds (Stensiö, 1969; Denison, 1978: 12), but they may not be homologous to the tesserae as they occur in acanthothoracids and rhenanids. Concerning the tesserate acanthothoracids we lack any information on this part of the skull, but in rhenanids (*Gemuendina*; Fig. 7**I**), one of the areas conspicuously devoid of tesserae is the suborbital region. This is covered by a large dermal plate associated with the palatoquadrate (Gross, 1963), as is the suborbital plate of other placoderms. Whereas the distribution pattern of tesserae on the skull of acanthothoracids and rhenanids is rather similar, it differs entirely from that in petalichthyids, as exemplified by *Lunaspis.* I therefore do not consider the suborbital tesserae of *Lunaspis* as any indication of a closer relationship of this fish with the tesserate acanthothoracids and rhenanids, notwithstanding the general similarity of these platelets.

Turning now to the number of paranuchal plates in the skull, the proposal (Westoll, 1967; Miles and Young, 1977) that this depended on the length of the occipital region has not provided conclusive results. It can be noted however that, except for the petalichthyids, more than one paranuchal plate is generally encountered among forms lacking a stabilized skull roof pattern. If these features were considered to be linked, and a variable skull roof pattern is accepted as a plesiomorphy, it follows that two paranuchals is also likely to be the primitive condition.

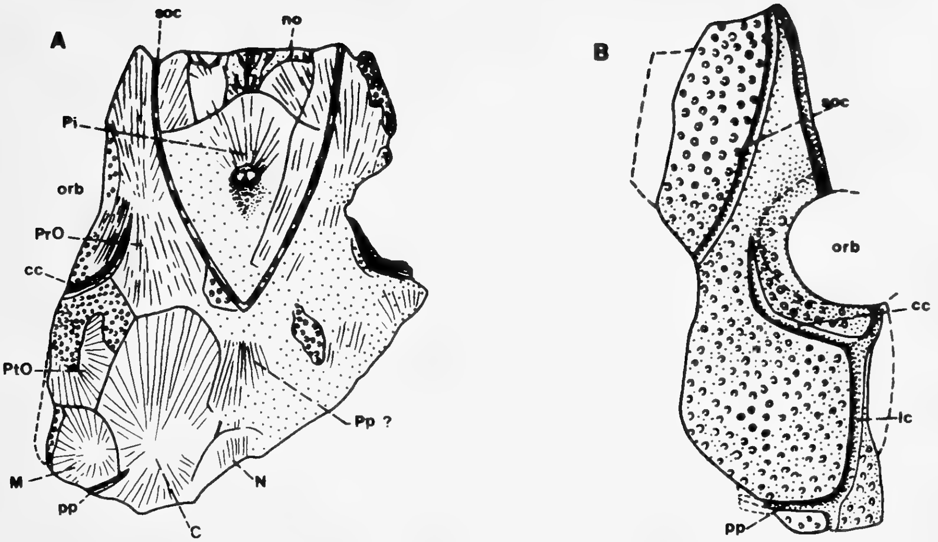


Fig. 9. **A**, *Radotina prima,* incomplete skull with part of the dermal bone preserved. × 1.5. **B**, *Radotina* sp., positive cast of the anterior half of a skull, from Gross (1958). × 0.75.

In petalichthyids, the primitive feature of two paranuchals has persisted, but on the anterior paranuchal three special structures are associated: the posterior pit-line, the main lateral line, and their junction in front of the endolymphatic foramen. This association on the same paranuchal plate is found elsewhere only in the arthrodires (on the single paranuchal plate), and I suggest that this is a special shared feature of the two groups.

Considering in more detail the position of the endolymphatic opening, two main patterns occur in placoderms:

a) The external foramen may be almost directly above the endocranial opening. This means the dermal part of the endolymphatic canal is short, and both internal and external openings are close to the mid-line of the skull. This condition occurs in antiarchs (e.g. *Bothriolepis,* Fig. 7**H**; Stensiö, 1948: figs 9, 12; *Asterolepis,* Karatajute-Talimaa, 1963: figs 2, 7), acanthothoracids (*Romundina,* Fig. 8**C**; Ørvig, 1975: pl. 1, figs 1, 3; *Brindabellaspis,* Young, 1980: figs 1, 2; *Kosoraspis,* Gross, 1959: fig. 6B, D-F), and petalichthyids (*Macropetalichthys,* Stensiö, 1969: figs 21, 130 A, B).

b) The dermal endolymphatic duct is a long oblique tube running in the thickened dermal bone, from the mesially placed endocranial opening to the external foramen, situated far postero-laterally. This occurs only in arthrodires. In all their subgroups the external foramen opens at the radiation centre of the paranuchal plate, behind the distal division of the posterior pit-line, and in front of the occipital line, where these join the main lateral line (Fig. 7**A-C**).

Since this second condition is an exclusive feature of arthrodires, it can be proposed as a synapomorphy supporting the monophyly of the group. By comparison, the first pattern can be regarded as plesiomorphic. Outside the placoderms, in the Osteostraci on the one hand (see Wangsjo, 1952; Janvier, 1980), or in the elasmobranchs on the other, the endolymphatic duct opens near the mid-line, or even by a single median foramen, which supports this interpretation.

I regard an external foramen for the endolymphatic duct as an ancestral primitive character. No trace of such a foramen is shown in ptyctodontids (Ørvig, 1971: 30), and there is also no indication of an endocranial opening. In rhenanids, on the contrary, the internal foramen exists, but no external opening has been noted. From the position of the internal foramen, and if we suppose the duct to be vertical, it should open within the small transverse groove called the 'middle pit-line' in *Jagorina* and *Asterosteus* (Stensiö, 1969: figs 92, 98).

THE POSITION OF THE NASAL CAPSULES, AND THE PREMEDIAN PLATE

Generally open to the front, the endoskeletal nasal capsules in placoderms are covered by a rostral plate which usually bears a medial process separating the incurrent nostrils (see Denison, 1978). They occupy one of the three following positions relative to the orbital cavity:

1) at the extremity of a well-developed endocranial ethmoidal region, far in front of the pineal pit. This is the condition in petalichthyids (Stensiö, 1969), the acanthothoracid *Radotina prima* (Figs 8**B**, 9**A**; von Koenen, 1895: pl. 4, fig. 2; Gross, 1958: fig. 6, pl. 1, fig. 3), and *Radotina* sp. (Fig. 9**B**; Gross, 1958: fig. 6, pl. 3, figs 5, 6).

2) at the end of a short ethmoidal region, where they open ventrally and are covered by a wide rostral plate (arthrodires, Fig. 10**C**).

3) in a posterodorsal position on a well-developed ethmoidal region, and at the anterior limit of the orbital cavity. In this position they open to the front in *Romundina* (Fig. 10**B**) and the antiarchs (Fig. 10**A**), or to the front and slightly upwards in *Radotina kosorensis* (Fig. 8**A**) and rhenanids (Fig. 10**D**).

Where a well-developed endocranial 'rostrum' is present, its dermal cover varies. In case 1 it is composed of a small and more or less elongated rostral plate (*Lunaspis,* Fig. 7**D,** or *Wijdeaspis,* see Heintz, 1937; Obruchev, 1964:pl. 1, fig. 1). In case 3 there is a prerostral plate — called a premedian, after the antiarch terminology — which is generally short in acanthothoracids (*Romundina,* Fig. 10**B**; Ørvig, 1975: pl. 3, fig. 4; *Radotina kosorensis,* Fig. 8**A**; Gross, 1958: fig. 1) and in most early antiarchs (see Janvier and Pan, 1982), but longer in bothriolepids (see Stensiö, 1948; Long, 1983). In his original description of *Radotina kosorensis* Gross interpreted the plate in a prerostral position as a rostral; this interpretation was followed by Denison (1975: fig. 3), but the plate was renamed a premedian by Denison (1978).

Three morphological transformation sequences can be proposed to account for these three conditions:

Hypothesis A: Anteriorly-placed nasal capsules, opening to the front (state 1 above) was the ancestral condition, and states 2 and 3 represent diverging specializations.

Hypothesis B: State 2, with the nostrils opening downwards, was ancestral. The nostrils opening to the front (state 1) was an intermediate state, and posteriorly-situated nasal capsules (state 3), was the ultimate specialization.

Hypothesis C: Posteriorly-situated nasal capsules (state 3) was ancestral, terminal capsules (state 1) was an intermediate condition, and nostrils opening ventrally (state 2), was the most specialized condition.

By reference to the most general condition in gnathostomes, we may test which of these three solutions is most parsimonious, which does not mean of course that it is correct, but only the most reasonable preliminary proposal. Tests to falsify these hypotheses must be inferred from other combinations of characters exhibited by other forms, and using parsimony as a strict methodological principle. Accordingly, I apply the same 'rule' as Miles and Young: I will be more inclined to accept a multiple independent loss of a bone than its multiple origin.

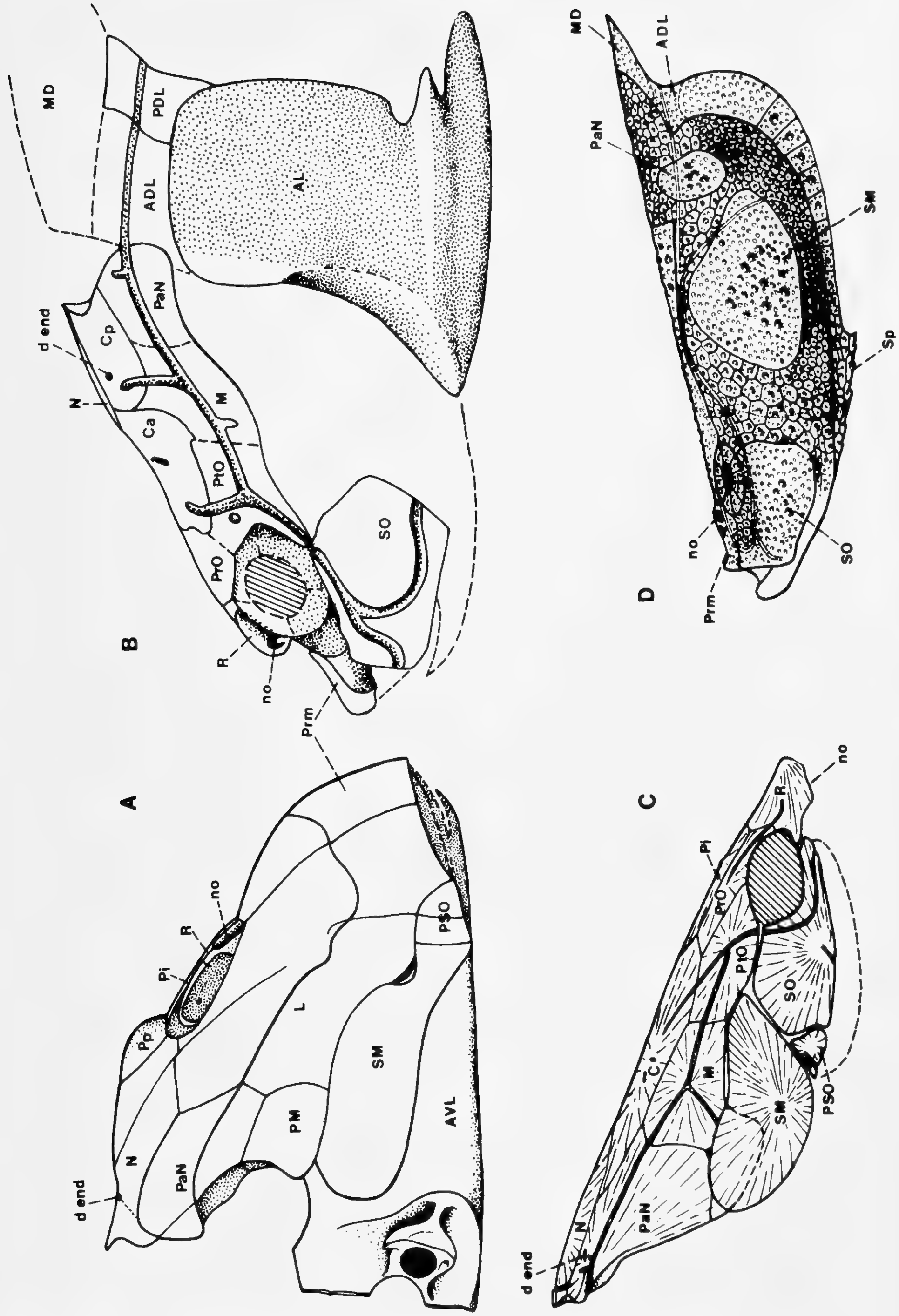


Fig. 10. Lateral view of the skull. **A,** antiarch: *Bothriolepis canadensis,* from Stensiö (1948). × 1. **B,** acanthothoracid: *Romundina stellina,* after Ørvig (1975). × 2.8. **C,** arthrodire: *Arctolepis decipiens,* from Goujet (1972). × 1.2. **D,** rhenanid: *Gemuendina stuertzi,* modified from Stensiö (1969). × 0.35.

Given these conditions, hypothesis B is less parsimonious. It requires a development of the subnasal shelf of the endocranium, then the backward regression of the nasal capsules, and the formation of a new plate, the premedian, to cover the dorsal face of the ethmoidal subnasal shelf.

Hypotheses A and C are equally parsimonious insofar as they imply only bone regression. However I dismiss hypothesis C because dorsal or anterodorsal nasal capsules is an extremely rare occurrence among gnathostomes, even if it is a general case in osteostracans. Moreover, there is no indication of a premedian plate in state 1 above (terminal nasal capsules on an endocranial 'rostrum'), even if Denison (1978: fig. 22C) has reconstructed such a plate in *Radotina prima* (but see Figs 8**B**, 9).

It could be objected that a prerostral ('premedian') plate exists in arthrodires, where it is called the internasal plate (see *Coccosteus,* Miles and Westoll, 1968). However, to my knowledge, this plate is absent in nearly all dolichothoracids and a number of brachythoracids, and therefore may have arisen within the group.

I conclude that hypothesis A is the preferred solution. It supposes two diverging specializations from an ancestral state with an endocranial 'rostrum' and terminal nasal capsules opening to the front. The implication that the ventral nostrils in arthrodires is specialized is supported by the fact that the ethmoidal region of the endocranium in actinolepid arthrodires (see *Kujdanowiaspis*, Stensiö, 1963: fig. 14) or some primitive brachythoracids (*Buchanosteus*, White and Toombs, 1972; Young, 1979: fig. 2) has a rather long subnasal shelf. A trend toward shortening of this region can be deduced from the evolution of several lineages inside the group. This is well illustrated by *Dicksonosteus* (Goujet, 1975: fig. 4), in which the internasal wall is covered ventrally by a narrow internasal lamina which represents the most anterior point of the ethmoidal endocranial region, notched laterally by the ventral nostrils.

The dorsal position of the nostrils in rhenanids could be considered a result of the 'pseudobatoid' adaptation which characterizes the group. However, the antiarchs and the species of *Radotina* which share this character do not show this specialization in body shape, and their high armour and lateral eyes do not seem particularly well adapted for life on the bottom. This supports the hypothesis that a large premedian plate and the backward shifting of the rostral plate is a special synapomorphy for a group composed of the antiarchs, rhenanids and acanthothoracids with the exception, among the latter, of *Radotina prima,* a form which also lacks tesserae. Thus, the contradiction already noted regarding the significance of tesserae applies again. If we accept posterodorsal nasal capsules and the premedian plate as synapomorphies, this again implies that the Acanthothoraci is not a monophyletic group.

To summarize, by combining the various characters already discussed (tesserae, premedian plate, position of the nasal capsule), three groups can be distinguished within the Acanthothoraci, characterized as follows:

Group 1: no tesserae, a long preorbital region of the skull with terminal nostrils, but no premedian plate. This is the case in *Radotina prima* only.

Group 2: no tesserae, a long preorbital region of the skull covered by a premedian plate, and nasal capsules in a posterior position (just in front of or between the orbits). Examples are *Romundina, Palaeacanthaspis, Brindabellaspis*(?).

Group 3: tesserae, a long preorbital region of the skull covered by a premedian plate, and nasal capsules posteriorly placed. Examples are *Radotina tessellata, R. kosorensis, Kosoraspis peckai, Kimaspis*(?).

The interpretation as synapomorphies of the characters discussed above implies that members of group 3 are related to the rhenanids, which share the same three characteristics, but with tesserae as their only synapomorphy. Group 2 may be more closely related to the antiarchs; the presence of a transverse groove on the posterior part of the premedian of *Romundina,* similar to the preorbital depression of early antiarchs (Janvier and Pan, 1982: fig. 8), is proposed as a synapomorphy supporting this sister-group relationship. This leaves Group 1, which is characterized only by primitive features, and for which no precise relationship can be proposed to other groups of placoderms.

THE CERVICAL JOINT

The dermal cervical joint, its variations, and their phylogenetic implications, were discussed by Miles and Young (1977: 138-139). They concluded that the ginglymoid joint in phlyctaenioid arthrodires (phlyctaeniids and brachythoracids), ptyctodontids, and antiarchs, were independently acquired. They also supposed that 'primitive' arthrodires, as in several other placoderm groups, had no dermal joint, and that the 'sliding joint' and the ginglymoid joint developed within this group as diverging specializations (Miles, 1973). This is contrary to Denison's (1975) view that the ginglymoid joint was possibly derived from the sliding joint.

The dermal cervical joint has been identified, in one form or another, in arthrodires, phyllolepids, antiarchs, ptyctodontids, and petalichthyids. On the other hand, it has not been demonstrated in rhenanids, most acanthothoracids, stensioellids, and pseudopetalichthyids. For the reasons advanced above (p.213) I will not consider the last two groups.

In rhenanids, the probable absence of a cervical joint may be a secondary state, related to the extension of tesserated areas, since the presence of a joint presupposes a certain rigidity of the back of the skull. In *Gemuendina* (Figs 7**I**, 10**D**; Gross, 1963: fig. 1) one or two rows of tesserae lay between the anterior dorsolateral plate and the small plate supposed to represent the paranuchal. If the tesserae are the result of a secondary bone fragmentation, then the lack of a joint would also be the result of a regressive process. This might be confirmed by looking at the condition in the groups supposed to be most closely related to rhenanids. Under Miles and Young's (1977) and Young's (1980) hypotheses, the Acanthothoraci are this sister-group, but if tesserae are regarded as a uniquely derived character, only tesserate forms can be members of this sister-group, namely *Radotina kosorensis, R. tessellata, Kosoraspis,* and (?) *Kimaspis.* The material of these forms (Gross, 1958, 1959; Mark-Kurik, 1973) provides no evidence of the structure of the cervical joint. It can be noted however that in the Acanthothoraci, the paranuchal projects backwards, and the posterior skull roof margin is embayed. This has been considered a possible synapomorphy of the group (Young, 1980: 67). In *Romundina* (Ørvig, 1975: pl. 1, fig. 3), the visceral surface of the posterior expansion of the paranuchal shows a rough surface which indicates an articular contact with the anterior dorsolateral plate. This plate is unknown in this form, but we can suppose the presence of an articular lamina on the body armour. This point needs clarification with new material, but I consider the cribrosal surface on the paranuchal plate as a positive argument supporting the hypothesis of a sliding articulation in *Romundina.* In other Acanthothoraci, *Brindabellaspis* shows an articular facet on the posterior endocranial expansion of the skull ('craniospinal process', Young, 1980: figs 7-9) covered dorsally by the paranuchal plate. This is evidence of a lateral articulation. Other evidence is provided by an anterior dorsolateral plate from Kotelny Island assigned by Mark-Kurik (1974: fig. 9a,b) to an undetermined 'arctolepid', because of a supposed articular condyle. But this 'condyle' differs from that of typical arctolepids by a remarkable character: its concave dorsal surface. Moreover, the bone bears an ornamentation of stellate tubercles, a morphological detail mentioned, to date, in Acanthothoraci and rhenanids alone among placoderms. Mark-Kurik (*pers. comm.*) now considers that this plate belongs to an acanthothoracid. Thus, we have another indication of the presence of an articular lamina in this group. This lamina bears a fossa as in antiarchs, and differs from what is seen in actinolepid arthrodires. If we add that a swelling of the articular lamina can be seen on some anterior dorsolateral plates of *Wuttagoonaspis* (Ritchie, *pers. comm.*), it can be concluded that the articular condyle of phlyctaeniid style as well as the armour fossa of antiarchs can evolve from a flange. Consequently, the sliding joint can be regarded as the primitive condition in placoderms.

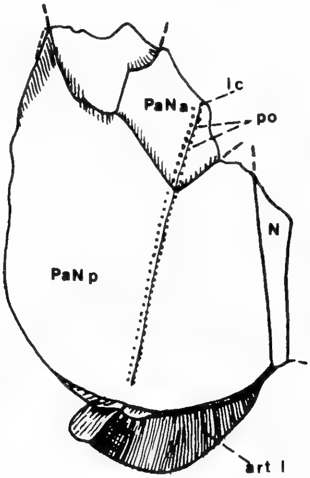


Fig. 11. Macropetalichthys pelmensis, fragmentary skull roof, after Gross (1937). × 0.6.

In petalichthyids, Miles and Young (1977: 138) noted that the cervical joint is hardly understandable due to poor information on the anterior dorsolateral plate. In the Cleveland Museum collections I have studied three anterior dorsolateral plates assigned to *Acantholepis* (BW 3-254, BW 3-238, BW 3-337) showing the articular area. All three have a high articular lamina, exhibiting in front a poorly-developed condyle, which can be interpreted as intermediate between the articular lamina seen commonly in actinolepid arthrodires, and the flat simple condyle of *Wuttagoonaspis*. However, the ascription of these plates to petalichthyids is still controversial. The most interesting phylogenetic information drawn from the cervical joint is given by *Macropetalichthys pelmensis* (Fig. 11; Gross, 1933: pl. 8, fig. 4; 1937: fig. 23B). This form is known by an isolated paranuchal plate which bears a horizontal mesial flange projecting backwards. Such a flange is very similar to the one described in *Ctenurella gladbachensis* (Ørvig, 1960) or *C. gardineri* (Miles and Young, 1977). Although this flange does not carry the articular surface, in both *Macropetalichthys* and *Ctenurella* it forms a posteroventral projection of the thickened posterior margin of the paranuchal plate, which is possibly related to protection of the nuchal gap. This flange may be absent in other petalichthyids, for example *Wijdeaspis warrooensis* (Young, 1978). However this form possesses a dermal cervical joint extremely similar to the one observed in early ptyctodontids (see Mark-Kurik, 1977: fig. 6), particularly in the shape and orientation of the articular fossa, which is longitudinal, contrary to its disposition in arthrodires. Although variation in the cervical joint in petalichthyids needs further investigation, the features recorded above are not seen in other groups to my knowledge, and can be proposed as a synapomorphy of ptyctodontids and petalichthyids. Other shared derived characters of these groups, supporting a sister-group relationship (Fig. 12), are as follows:

1) Their sensory lines are included in tubes which project below the lower surface of the dermal bone, and communicate with the exterior by means of tubules opening on the surface by pores. They also show the same pattern of lines; the supraorbital canal and posterior pit-line canal converge to the centre of the nuchal or 'centronuchal' plate, and the central line is missing (see Ørvig, 1957, 1962, 1971).

Denison (1978: 12, 35) mentions tubular canals and pores in some acanthothoracids (*Kimaspis* and *Kolymaspis*). In *Kimaspis,* the original description (Mark-Kurik, 1973) refers to sensory lines enclosed in the bone tissue, but there is no indication of pores. The structure is very similar to that observed for the main lateral line of the skull in actinolepid and phlyctaeniid arthrodires, where they are represented by a deep groove opening by a narrow slit.

In *Kolymaspis,* Bystrow (1956) does not quote such canals. No precise idea concerning this point is provided by the cast I have studied. However, the widely open supraorbital canal on this skull, and the absence of any indication of pores, suggests that the other sensory lines are presumably not like those in ptyctodontids and petalichthyids. Thus, I consider that tubular canals with superficial pores have not been proved to exist outside these two groups of placoderms. This feature can be kept as a valuable synapomorphy.

2) Ptyctodontids and petalichthyids are the only placoderms where the suborbital and postsuborbital plates are absent, or represented by tiny plates sometimes interpreted as tesserae.

THE PELVIC AND PREPELVIC CLASPERS

Since these organs have been identified only in ptyctodontids they should be of little or no importance for the study of interrelationships inside the placoderms. However Miles and Young referred to them, for they identified only primitive characters or autapomorphies in ptyctodontids, from which it was difficult to build a defensible hypothesis of relationships. They also used the pelvic and prepelvic claspers when comparing the placoderms to other gnathostomes. Their most parsimonious solution, according to the other assumptions of their phylogenetic model, was that ptyctodontids may represent the sister-group of all other placoderms, because they retain the pelvic and prepelvic claspers assumed to have been present in the common ancestor of placoderms and chondrichthyans. Since both categories of claspers have been found only in ptyctodontids and holocephalans, and chondrichthyans are considered to be a monophyletic group, the most parsimonious solution is that the prepelvic claspers have independently disappeared in non-ptyctodontid placoderms and in elasmobranchs. This solution, which explains in the simplest way the clasper distribution, assumes however that pelvic and prepelvic claspers in ptyctodontids and holocephalans are homologous structures. The morphological grounds for this need reexamination.

The pelvic claspers in ptyctodontids are best known. They comprise an exoskeletal plate which covered the copulatory organ, developed, as in chondrichthyans, from the mesial part of the male pelvic fin. This clasper plate has been recovered, in a remarkable state of preservation, in *Rhamphodopsis* (Miles, 1967: fig. 16; pl. 6, fig. 3) and *Ctenurella gardineri* (Miles and Young, 1977: fig. 35). Its ventral position relative to the fin evokes more the elasmobranch condition rather than that of holocephalans (Miles, 1967: 113). This anatomical feature, implying a similar complex reproductive biology, is one of the arguments set out to group placoderms and chondrichthyans as elasmobranchiomorphs (see Miles and Young, 1977; Goujet, 1982). However no sign of such a clasper has ever been found in the other placoderms, and the possibility of their separate origin in ptyctodontids and elasmobranchs, where they show a somewhat different morphology, cannot be excluded. Nevertheless, their possible homology is retained here.

The prepelvic claspers, as interpreted by Ørvig (1960, 1962) and Miles (1967), are represented by a pair of small plates lying in front of the pelvic fin. In *Rhamphodopsis,* where they are best known, each clasper is an elongate dermal plate attached to an endoskeletal ossification. Compared to the prepelvic clasper of holocephalans, however, two important details undermine their possible homology:

i) the prepelvic clasper in holocephalans is an elongated organ, mainly cartilaginous, and normally hidden in a cutaneous pocket. When extracted, it forms a rod bearing on its internal side a series of tiny discrete hooks supposed to be used by the male in grasping and maintaining the female during copulation.

In *Ctenurella gardineri,* Miles and Young (1977: 193) mention a bony plate bearing hooked denticles, which they interpret as a possible prepelvic clasper, although the precise position of this plate on the body is unclear. Supporting their interpretation is the hooked superficial ornament, which evokes the discrete spiny scales of the holocephalan prepelvic clasper. However, both the exoskeletal plate of the male pelvic fin in *Rhamphodopsis* (see Miles, 1967: fig. 19), and the posterior element of the pelvic clasper in *Ctenurella gardineri* (Miles and Young, 1977: fig. 35C, pl. 5A) also bear such hooked denticles. Thus, the ornament in itself cannot be sufficient to retain Miles and Young's suggestion without doubt. Moreover, the small dermal spine interpreted as a prepelvic clasper in *Ctenurella gladbachensis,* as reconstructed by Ørvig (1960: 327, fig. 5), apparently has a rather different morphology. *Rhamphodopsis* is the only form in which the position of the supposed prepelvic clasper is clear, but in this form it is a simple plate of dermal bone showing the same ornamentation as the plates of the armour (see Miles, 1967). If these bones were situated rather deep in the skin, as indicated by the loss of superficial ornament in ptyctodontids, it is impossible to imagine for this 'clasper' the same function of grasping the female during copulation.

ii) The plate supposed to represent a prepelvic clasper in the male is also present in female *Rhamphodopsis,* and was labelled by Miles (1967: fig. 13) as a 'dermal plate lying ventral to the pelvic girdle', a definition which applies also to the male element.

Hence both basic criteria which define the prepelvic clasper in holocephalans are not met in ptyctodontids, where the so-called prepelvic clasper is neither a grasping organ nor restricted to the males. I therefore propose a return to Watson's interpretation (1934, 1938) that these structures simply represent the pelvic girdle. This interpretation, rejected by Miles (1967: 112), implies that the pelvic girdle included a dermal element associated with the endoskeleton. This is contrary to the condition in *Coccosteus* (Miles and Westoll, 1968), and the large majority of gnathostomes, where the pelvic girdle is exclusively endoskeletal. However, an association between the pelvic endoskeletal girdle and a dermal plate has been described in several other placoderm groups, particularly those known by articulated individuals, as in the arthrodires (*Sigaspis,* Goujet, 1973: fig. 2), rhenanids (*Gemuendina,* Gross, 1963: fig. 4), stensioellids (Gross, 1962b: fig. 4), and petalichthyids.

To conclude, I assume that the ptyctodontid 'prepelvic clasper' is only the dermal cover of the pelvic girdle. This exoskeleton may be a primitive condition in placoderms for both pelvic and pectoral girdles. This interpretation is supported by the remarkable fact that all the taxa in which a pelvic exoskeleton has been identified also have a highly-developed scale covering. The lack of a pelvic exoskeleton in *Coccosteus* for example may thus be a secondary condition due to regression of the dermal cover and squamation.

DERMAL BONE HISTOLOGY AND ORNAMENTATION

In placoderms, the dermal plates are composed essentially of two types of hard tissue: bone and semidentine. The bone, which may be either laminar or with primary osteons, makes up the basal and middle layers of the dermal plates. The semidentine is restricted to the superficial layer where it forms the tubercular ornament. This semidentine, containing typical unipolar cell cavities with a long centrifugal apical tubule, is an exclusive feature of placoderms, and a good synapomorphy for the group (Goujet, 1982). However it is largely absent in groups showing regression of the superficial ornament, namely antiarchs (Gross, 1931: fig. 2, pl. 1), phyllolepids (Bystrow, 1957: fig. 25), and some arthrodires (mainly pachyosteomorphs).

Although information is lacking on the histology of many important forms (e.g. ptyctodontids, early antiarchs, *Brindabellaspis*), the available evidence suggests a correlation between the histology of the superficial hard tissue, and the nature of the ornament, which may be of phylogenetic significance. Amongst placoderms the various types of superficial dermal ornament may be organized into five main categories:

1) stellate tubercles showing acute crests, sometimes denticulate, which are separated by deep valleys (Acanthothoraci; see Gross, 1958, 1959; Ørvig, 1975).

2) closely-set flattened tubercles of irregular shape *(Brindabellaspis;* Young, 1980).

3) clear-cut tubercles with either a rounded tip or a 'crown' of dense hard tissue, bearing fine radiating ridges (arthrodires, petalichthyids; see Gross, 1957, 1961, 1962a; Ørvig, 1957, 1971; and possibly *Radotina prima;* Gross, 1958).

4) ridges, either concentric (phyllolepids), radiating, or in an irregular pattern of low ridges and/or blunt tubercles (antiarchs; see Stensiö, 1948; Karatajute-Talimaa, 1963).

5) a smooth or irregular surface, with numerous pores of the vascular canals (ptyctodontids, pachyosteomorph arthrodires).

The histology of the stellate tubercles (category 1), as described by Gross (1973) and Ørvig (1975, 1979), consists of a massive semidentine with few basal vascular canals. Ørvig (1979) calls it orthosemidentine. It has been demonstrated in rhenanids (*Asterosteus = Ohioaspis,* Gross, 1973) and in acanthothoracids (*Romundina,* Ørvig, 1975, 1979). In *Romundina,* this semidentine presents a mixture of unipolar odontocytes and more irregular cavities resembling the sclerocytes of some kind of mesodentine, a common hard tissue outside the placoderms. This tissue can be interpreted in its organization as a semidentine which has kept some characters of a preceding mesodentinous state. From this, we can infer that the thick semidentine present in *Romundina* and the rhenanids may represent a primitive condition.

The histology of *Brindabellaspis* dermal bone is still unknown, but from the massive aspect of the irregular superficial tubercles, it may be predicted that it is probably made of the same type of semidentine as that in the Acanthothoraci.

The ornament of category 3 is more common among placoderms. Its histology shows a semidentine restricted to the peripheral layer at the tip of the tubercles, and surrounding the ascending vascular canals which occupy the core of each tubercle. Ørvig (1979: 234) calls this pallial semidentine, and it seems to be specific to this third type of ornament.

In the ornament of categories 4 and 5, there is only bone tissue. The semidentine has disappeared from the shield plates, but may be retained in the jaw bone.

The phylogenetic significance of the ornament and histology in the placoderms can be analysed as follows. The orthosemidentine and stellate tubercles may be assumed to be the primitive condition, as indicated by the histology observed in *Romundina.* This plesiomorphous state only occurs in acanthothoracids and rhenanids. The pallial semidentine may be seen as a uniquely specialized condition, associated with the crowned tubercles met with in petalichthyids and arthrodires. The same histological structure may also occur in the tubercles of early ptyctodontids (*Tollodus,* Mark-Kurik, 1977), and on the post-branchial lamina of unornamented ptyctodontids, where well-defined tubercles persist (see Miles and Young, 1977: pls 2F, 4A). To date, the histology of these has not been described.

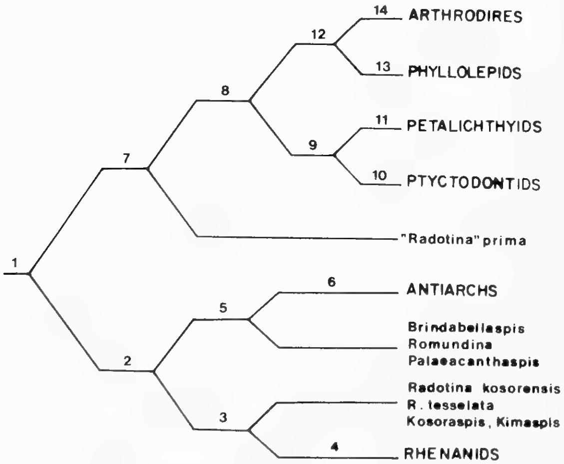
The bony nature of the ornament in a majority of antiarchs, some arthrodires, and phyllolepids, is a secondary regression of the superficial hard tissue, presumably due to a deeper situation of the plates in the skin. This is clearly the case in arthrodires (Stensiö, 1969), and in the antiarchs, where the early forms show an ornamentation of well-defined closely-set tubercles (yunnanolepiforms, Zhang, 1978: pls 4, 5, 8). I suggest that this regressive process has probably occurred independently in each group. Thus it has a low phylogenetic value in the present context.

PLACODERM INTERRELATIONSHIPS: A NEW SCHEME

Using the characters discussed above, the cladogram of Fig. 12 has been set up. It gives a view of placoderm interrelationships which differs to a large extent from those proposed by Denison (Fig. 1) and Miles and Young (Fig. 2).

The placoderm orders are distributed in two major clusters. One groups the arthrodires, phyllolepids, petalichthyids, and ptyctodontids, which share anterior and posterior median ventral plates, and the association, on the same paranuchal, of the endolymphatic foramen and the confluence of the posterior pit-line with the main lateral line (8, Fig. 12). The second cluster groups the rhenanids and antiarchs as major units, which share one uniquely derived character (2, Fig. 12): the dorsal position of the nasal capsules and the presence of a large premedian plate covering the ethmoidal expansion of the endocranium.

This grouping contradicts both Denison's and Miles and Young's phylogenetic schemes, in which the arthrodires and antiarchs are considered as sister-groups using a different synapomorphy (the long body armour with closed flanks behind the pectoral fenestra). This supposed synapomorphy is based on a different appreciation of the distribution of homologous body plates amongst the various placoderm orders. My analysis of these plates, summarized in Fig. 6, shows that most of these plates are present in a majority of the groups taken into account. This assessment is unlikely to change if stensioellids and pseudopetalichthyids were included. Currently these cannot be investigated to the same degree as the other groups.



When applying the parsimony principle, the only plate which can seriously question the proposed cladogram is the median ventral plate of antiarchs, considered as the homologue of the posterior median ventral plate of arthrodires. It is the only plate for which a separate origin must be supposed in antiarchs on one side, and in the most recent common ancestor of arthrodires, phyllolepids, petalichthyids, and ptyctodontids on the other.

The problem may be seen as an opposition between two conflicting synapomorphies: premedian plate and dorsal nostrils *versus* posterior median ventral plate. The first alternative has been preferred here, because in my opinion the multiple origin of the median ventral plate is more likely than the independent occurrence of the competing character. Given the numerous variations in size and form of the median

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Fig. 12. New cladogram for the major placoderm groups (excluding stensioellids and pseudopetalichthyids).

Characters assumed to be basic placoderm apomorphies (1) are: body armour forming a complete ring surrounding the pectoral girdle, and composed of median dorsal, anterior and posterior dorsolateral, anterolateral, spinal, anterior ventrolateral, small posterior ventrolateral and very small posterolateral plates; pelvic girdle covered with a dermal plate; double cervical joint with an endoskeletal component (between occipital condyles and a synarcual) and a dermal component (the posterolateral part of the skull overlapping the front margin of the anterior dorsolateral plate); ornamented layer of the dermal bone made of orthosemidentine; omega-shaped palatoquadrate closely associated with the anterior cheek-plates (suborbital and post-suborbital), with the adductor mandibulae muscle attached on the ventral face of the metapterygoid and the medial face of the suborbital plate; close association between the dorsal hyoid arch elements and the dermal operculum, with the epihyal modified into a simple rod fused to the visceral surface of the submarginal plate, and playing the role of an opercular process joining the dermal cheek to the skull; endocranium composed of two ossifications (rhinocapsular and postethmo-occipital) separated by a fissure, unless secondarily fused; long ethmoid region of the endocranium with terminal nasal capsules and a long subnasal shelf; lateral orbits; variable skull pattern with numerous plates; cheek covered by three plates, including a large submarginal.

Apomorphies acquired at the following numbered stages are: 2, premedian plate, and backward shifting of the nasal capsules, with nostrils opening at the level of, or just in front of, the orbits; 3, tesserae on the skull roof, particularly in the pineal and orbital regions; 4 (rhenanid apomorphies), pseudobatoid body shape with very flattened skull, loss of the dermal cervical joint, fragmented (or tessellated) anterolateral and spinal plates, strong reduction in body armour length, and loss of the posterior dorsolateral and posterolateral plates; 5, large premedian plate with a preorbital depression, dermal cervical joint with a fossa on the articular flange of the anterior dorsolateral plate, external endolymphatic pore placed medially relative to the endocranial opening, and strong cohesion of the plates covering the endoskeletal shoulder girdle to form a pectoral unit (anterolateral, spinal, anterior ventrolateral plates); 6 (antiarchan apomorphies), a second (posterior) median dorsal plate incorporated in the body armour, pectoral unit represented by a single plate (anterior ventrolateral) enclosing the small pectoral fenestra, pectoral fin modified into a slender appendage covered by plates derived from modified scales, antiarch skull roof pattern with the orbits laterally enclosed by large lateral plates, and semilunar plates present; 7, dermal bone ornamented with evenly distributed tubercles of pallial semidentine; 8, anterior and posterior median ventral plates added to the body armour, and endolymphatic duct opening on the same paranuchal plate as the confluence of the posterior pit-line and the main lateral line of the skull; 9, sensory lines enclosed in tubes projecting below the visceral surface of the dermal skull plates and opening by pores, central sensory line lost, X pattern of the sensory lines on the middle plate of the skull (nuchal or post-pineo-nuchal), fragmentation of the suborbital and post-suborbital plates, and similar structure of the cervical joint; 10 (ptyctodontid apomorphies), loss of rostral plate, endolymphatic duct closed, loss of suborbital and post-suborbital plates, loss of posterior dorsolateral, posterolateral, posterior ventrolateral, posterior median ventral, presence of bony pelvic claspers; 11 (petalichthyid apomorphies), laterodorsal orbits, bounded laterally by pre- and post-orbital plates and medially by the central plate; 12, shortened preorbital region of the skull, and separate interolateral plate with a deep transverse ventral groove; 13 (phyllolepid apomorphies), flattened body, much expanded nuchal plate, loss of rostral plate, loss of posterior dorsolateral and posterolateral plates, and loss of semidentine on the superficial ornament; 14 (arthrodire apomorphies), two pairs of upper tooth plates, large endocranial posterior postorbital processes, wide and short rostral plate, and pectoral fenestra closed posteriorly by the posterolateral and the posterior ventrolateral plates unless secondarily transformed into a deep pectoral emargination in some brachythoracids.

ventral in various antiarch genera (it may even be replaced by several platelets), I regard this plate as an anamestic component of the antiarch body armour, filling the space between the anterior and posterior ventrolateral plates, and arising independently of the posterior median ventral in arthrodires.

The other homologous plates of the body armour in antiarchs and arthrodires were already present in the common ancestor of placoderms, and posterior elongation and/or enlargement of pre-existing elements are the only processes required to obtain the box-like armour. There is then no contradiction in considering the long body armour in both groups as convergently acquired. The differences in its composition in both groups support this view.

The assumed closer relationships between the dolichothoracid arthrodires and antiarchs has certainly been influenced by the ideas developed by Westoll (1945) and retained by Denison (1978: 10) concerning the derivation of the pectoral appendage in antiarchs from a long spinal plate similar to that of the Dolichothoraci. However the discovery of a distinct spinal process in the Yunnanolepiformes (Zhang, 1978), together with a pectoral derivation of this appendage from a spinal plate. On the contrary, it confirms its nature as a modified fin. In any case, as a modified spinal, one may ask why its origin was sought among the Dolichothoraci, since the petalichthyids also have long and stout spinals. Presumably, the reason was the general similarity of the box-like body armour in arthrodires and antiarchs.

The new phylogenetic scheme presented here implies also the following convergences in the evolution of the body armour: the posterior dorsolateral plate has been lost independently in rhenanids, ptyctodontids, and phyllolepids, and the same applies to the posterolateral plate in rhenanids and the common ancestor of ptyctodontids and petalichthyids.

My last remark on the body armour is to stress that its initial composition — as deduced from the matrix of Fig. 6 — is identical to that of the Acanthothoraci, insofar as this is currently known. In addition, the other apomorphic characters of the proposed scheme, and the groupings they lead to, require a partition of the Acanthothoraci, which was initially considered a monophyletic group on the basis of one uniquely-derived character: the shape of the occipital margin of the skull with posteriorly-projecting paranuchals. By retaining the monophyly of the Acanthothoraci, the apomorphies and assumed monophyly of some of the best-founded groups of placoderms (e.g. the antiarchs) would have to be dismissed. Either the initially accepted monophyly of the Acanthothoraci, or the monophyly of all the other groups, must be rejected, and I have chosen the first alternative. I suggest that the Acanthothoraci play in the phylogeny the role of a stem-group, its members being scattered as sister-groups of several major placoderm orders. This solution was earlier proposed by Obruchev (1964, 1967), but in the present case is not put forward by reason of their geological antiquity (which has since been proven false; Westoll, 1967), but strictly on the distribution of homologous characters shared with other placoderms. Nevertheless the Acanthothoraci can still be distinguished by their general morphology from the other placoderms, as is often the case with paraphyletic groups.

One evident weakness in the proposed cladogram is the position of *Radotina prima*. This form has terminal nasal capsules and a well developed 'rostrum', but neither a premedian plate nor tesserae. In brief, it exhibits only (assumed) primitive characters. However, its dermal bone bears closely set tubercles, apparently non-stellate, even if this detail is not mentioned by Gross (1958: 21). This taxon could be placed in a multiple branching of the base of the cladogram (if the available information on its morphology were considered insufficient), but the position proposed in Fig. 12 is based on the assumption that the ornament of *Radotina prima* is made of pallial semidentine, a detail which remains to be confirmed. This position in the cladogram raises the taxonomic question of membership in the genus *Radotina*. The available data on all other species of the genus indicate that *R. prima* does not belong here, and until the type material is redescribed I propose to mention *'R. prima'* between quotation marks as in the present cladogram.

Other weaknesses in this new scheme follow mainly from the absence of adequate outgroup comparison at the proper level to test the phylogenetic significance of some of the basic characters of placoderms (e.g. the initial state of the dermal skeleton). However the scheme forms a basis for future research, when precise tests can be worked out to attempt to falsify the interrelationships proposed. I guess the best tests will come from studies of the 'Acanthothoraci', a group of central importance for our problem. I am confident that some of the keys to understanding placoderm phylogeny will come from investigations of this group.

My final remark is to stress the difficulties in building a practical classification from a cladogram which includes a stem-group, as is the case in the present example. We meet the same problems as encountered when classifying fossils with extant groups: the terminal taxa rule the system. However I see no real objection to abandoning the group 'Acanthothoraci' in a formal cladistic classification, should further studies confirm it as a non-monophyletic group. It can then be retained for its practical use as a vernacular term.

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LIST OF ABBREVIATIONS

ADL — anterior dorsolateral plate
ADL oa — overlap area for the anterior dorsolateral plate
AL — anterolateral plate
AMD — anterior median dorsal plate
AMV — anterior median ventral plate
art 1 — articular lamina of the paranuchal plate
C — central plate
Ca — anterior central plate
Cp — posterior central plate
cc — central sensory line
d end — external foramen for the endolymphatic duct
IL — interolateral plate
L — lateral plate
lc — main lateral line of the head
M — marginal plate
MD — median dorsal plate
mp — middle pit-line of the skull
MV — median ventral plate
MxL — mixilateral plate
N — nuchal plate
no — anterior nostril
occ — occipital sensory line
PaN — paranuchal plate
PaNa — anterior paranuchal plate
PaNp — posterior paranuchal plate
PDL — posterior dorsolateral plate
PDL oa — overlap area for the posterior dorsolateral plate
pelv — pelvic dermal plate
pf — pectoral fenestra
Pi — pineal plate
pi — pineal pit
PL — posterolateral plate
PL oa — overlapping area for the posterolateral plate
pmc — postmarginal sensory line
PMD — posterior median dorsal plate
PMV — posterior median ventral plate
PN — post-nasal plate
po — pores of the sensory tubes
Pp — post-pineal plate
pp — posterior pit-line
PrO — preorbital plate
Prm — premedian plate
PSO — post-suborbital plate
PtO — postorbital plate
PVL — posterior ventrolateral plate

PVL oa — overlapping area for the posterior ventrolateral plate
ScCo — endoskeletal shoulder girdle
SL — semilunar plate
SM — submarginal plate
SO — suborbital plate
soc — supra orbital sensory line
Sp — spinal plate
R — rostral plate.

A Comparison of the developing Dentition of *Neoceratodus forsteri* and *Callorhynchus milii*

A. KEMP

(Communicated by A. RITCHIE)

KEMP, A. A comparison of the developing dentition of *Neoceratodus forsteri* and *Callorhynchus milii*. *Proc. Linn. Soc. N.S.W.* 107 (3), (1983) 1984: 245-262.

The histological structures and growth patterns of the tooth plates of *Neoceratodus forsteri* (Dipnoi) and *Callorhynchus milii* (Holocephali) are compared. The tooth plates share a similar growth pattern, and the dentinal tissues of the tooth plate are based on trabeculae of cellular bone. An enamel-like substance containing a protein that does not have the staining reactions characteristic of collagen, covers the dentinal tissues and extends over part of the trabeculae. Despite extensive similarities between living dipnoans and holocephalans, there are many differences in details of the histological structure of the dental tissues and of the growth pattern. Similarities are likely to be related to a similar diet, and have no bearing on vertebrate phylogeny.

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INTRODUCTION

A hard tissue of unusual fine structure has been described from diverse groups of primitive vertebrates. The term pleromin has been used for this tissue in the dermal skeleton of psammosteid heterostracans (Ørvig, 1976a) and in the tooth plates of holocephalans, dipnoans (Ørvig, 1976b) and ptyctodont arthrodires (Ørvig, 1980), but the terms petrodentine (Lison, 1941; Smith, 1979b), tubular dentine (Denison, 1974) and central columnar dentine (Kemp, 1979) have been used for the same tissue in the tooth plates of dipnoans. Comparison of this material has largely been based on ground polished sections and scanning electron micrographs of fossil specimens or of fully grown tooth plates (Ørvig, 1976a,b, and Smith, 1979b). Several studies have related soft tissue and dentine structures in adults of the recent members of the Holocephali (Bargmann, 1933; Brettnacher, 1939). Other studies have included analysis of developmental processes of the dentition, either in recent holocephalans (Schauinsland, 1903), in fossil dipnoans (Lund, 1970, 1973), or in recent dipnoans (Lison, 1941; Semon, 1899; Kemp, 1977, 1979). Similarities in the hard tissue found in fossil psammosteids and ptyctodonts, and in fossil and recent holocephalans and dipnoans are immediately apparent, but other characters, such as the early growth patterns in young larvae, appear to differ. Schauinsland (1903) found that each tooth plate of the recent holocephalan *Callorhynchus milii* develops from a single mesodermal template, but the superficially similar tooth plate of the recent dipnoan *Neoceratodus forsteri* develops by the fusion of isolated denticles (Semon, 1899).

This paper compares structures in the soft and hard tissues of developing dentitions of *Callorhynchus milii* and of *Neoceratodus forsteri* at the level of the light microscope, and suggests that the resemblance in structures, at least in the recent dipnoans and holocephalans, extends beyond the single hard tissue called pleromin in both groups by Ørvig (1976b). In both species, the tooth plates are based on trabeculae containing enclosed cells, consist of at least two forms of dentine, and are sheathed in an enamel-like substance that contains a protein which does not have the staining reactions characteristic of collagen. The mode of growth of the tooth plates in the two groups is also similar in several respects.

MATERIALS AND METHODS

Juveniles of *N. forsteri* were reared in the laboratory (Kemp, 1981) from eggs collected in the Brisbane River or Enoggera Reservoir. One series was fixed in 10% neutral buffered formalin, embedded in paraffin and sectioned at 10μm. The sections were stained in sirius red (Constantin and Mowry, 1968) Mallory's phosphotungstic acid and haematoxylin (Pearse, 1968) or Masson's trichrome. A duplicate series was fixed in paraformaldehyde/glutaraldehyde fixative (Binnington, 1978), embedded in methacrylate resin and sectioned at 1μm. These sections were stained in 1% toluidine blue in phosphate buffered saline at pH 7.4 or in Heidenhains's iron haematoxylin. Stages of development are described in Kemp (1982b).

Juveniles of *C. milii* were reared in the laboratory from eggs collected off the coast of New Zealand, near Otago. Specimens were fixed in 10% neutral buffered formalin and embedded in paraffin. Sections were cut at 10μm and stained with Heidenhains's Azan (Pearse, 1968), sirius red or toluidine blue in buffer.

TERMINOLOGY

Terminology has become a source of confusion in the field of hard tissue histology. This is partly because some authors recognize more tissues in the tooth plate than do others [compare Denison (1974) and Kemp (1979) with Ørvig (1976b)]. More problems arise when the same term is used for two different tissues e.g. the

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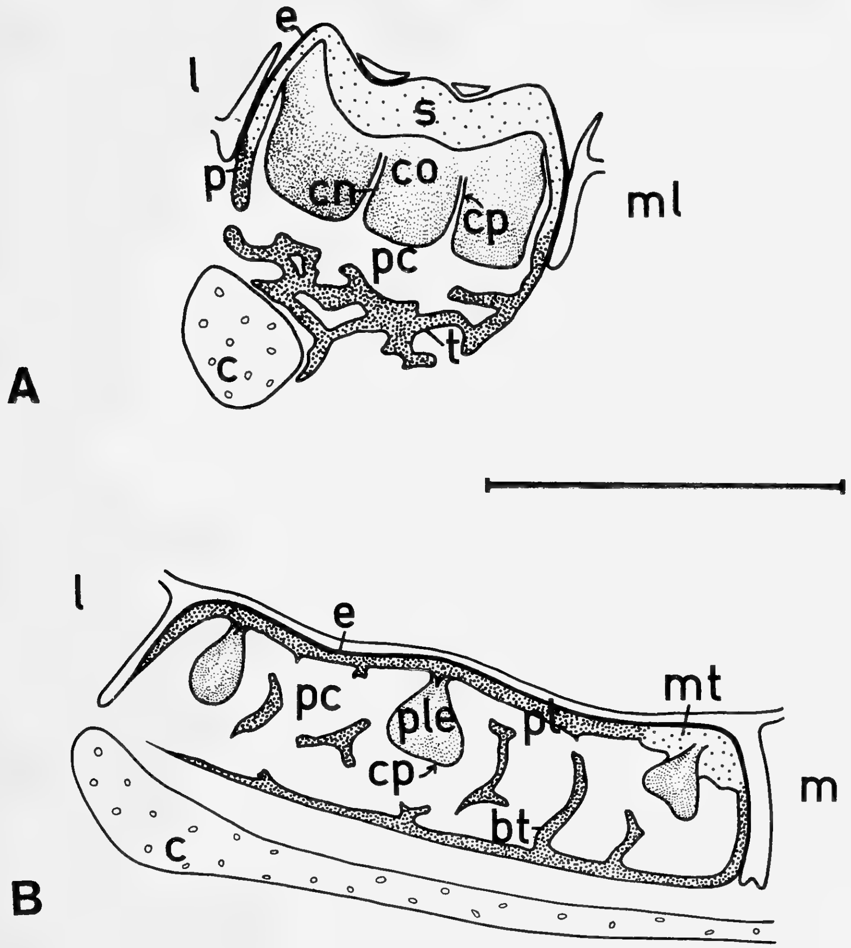
Fig. 1. Terminology used for the hard tissue of *N. forsteri* and *C. milii*.
b.t. basal trabeculae
c cartilage
cn pulp canals Denison (1974) and Smith (1979)
  = pseudohaversian canals Lison (1941)
  = vascular canals Ørvig (1976b, 1980)
co columnar dentine
  = petrodentine Lison (1941) and Smith (1979b)
  = tubular dentine Denison (1974)
  = central columnar dentine Kemp (1979)
  = interstitial dentine Campbell and Barwick (1983)
cp circumpulpal dentine Smith (1979b) and Campbell and Barwick (1983)
  = osteodentine Lison (1941)
  = tertiary columns Kemp (1979)
e enamel-like substance
  = enameloid Parker (1892) and Kemp (1979)
  = enamel Kerr (1903, 1910); Brettnacher (1939); Smith (1979a)
  = vitrodentine Bargmann (1933); Semon (1899)
mt modified trabeculae Ørvig (1967)
  = interstitial substance between osteons Ørvig (1976b)
p pedestal Kemp (1979)
pc pulp cavity Kemp (1979)
  = pulp chamber Denison (1974)
  = soft corium tissue Ørvig (1976b)
  = subdentinal space Campbell and Barwick (1983)
ple pleromin Ørvig (1976b)
  = dentine Schauinsland (1903)
pt primary trabeculae
s secondary mesenchymal matrix Kemp (1979)
  = new dentine Denison (1974)
  = trabecular dentine and pleromic dentine Smith (1979b)
t trabeculae Ørvig (1976b); Kemp (1979).
A. *N. forsteri*
B. *C. milii*
Scale line = 1 mm, 1 = labial face, ml = mediolingual face and m = medial face.



osteodentine of Lison (1941: fig. 3) is not the osteodentine of Ørvig (1976b) but is the circumpulpal dentine of Campbell and Barwick (1983) and Smith (1979). A summary of the terminology used for the tooth plates of *N. forsteri* and *C. milii* is given in Fig. 1, with a list of synonymous terms used by other authors.

The tooth plates of both species are based in bony trabeculae attached to cartilage by collagenous connective tissue fibres. The trabeculae of *N. forsteri* are surmounted by a narrow pedestal of bone surrounding the tooth plate and joining trabeculae and tooth tissue. In *C. milii,* trabeculae form a major part of the tooth plate. Near the occlusal surface, the trabeculae become modified (Ørvig, 1976b). Modified trabeculae consist of layers of matrix with a staining reaction typical of collagen, but denser and less regularly arranged than the primary trabeculae forming the original template of the tooth (compare Fig. 2**A**, **B** and Fig. 2**C**, **D**). Basal trabeculae are found closest to the cartilage at the base of the tooth plate. The tooth plates of both species are coated in an enamel-like substance associated with the cells of the inner dental epithelium. Within the tooth plate, and enclosed by the enamel like substance in *N. forsteri* are two types of hard tissue. The outer fringe is secondary mesenchymal matrix and the central material is columnar dentine (Kemp, 1979), a hard tissue traversed at intervals by

TABLE 1

Staining reactions of hard tissues of the tooth plates of N. forsteri *and* C. milii

a) *N. forsteri*	Sirius red	Toluidine blue in buffer	PTAH*	Masson's trichrome
trabeculae	red	blue = orthochromatic	pink	blue
pedestal	red	’’	’’	’’
secondary mesenchymal matrix	red	’’	’’	’’
columnar dentine	mostly unstained with fine red fibres	’’	’’	mostly unstained with fine blue fibres
circumpulpal dentine	red		’’	blue
enamel-like substance	unstained initially	pink = metachromatic later unstained	blue	unstained

b) *C. milii*	Sirius red	Toluidine blue in buffer	PTAH*	Heidenhain's azan
trabeculae	red	blue = orthochromatic		blue
modified trabeculae	red	’’		’’
pleromin	unstained	pale blue		unstained
circumpulpal dentine	red	blue		blue
enamel-like substance	unstained	pale blue		unstained
c) collagen	red		red-brown	blue with either stain

*PTAH — Mallory's phosphotungstic acid and haematoxylin.

Fig. 2. Photomicrographs of sections of tooth plates of *Callorhynchus milii* embryos. Scale lines = 0.1 mm.

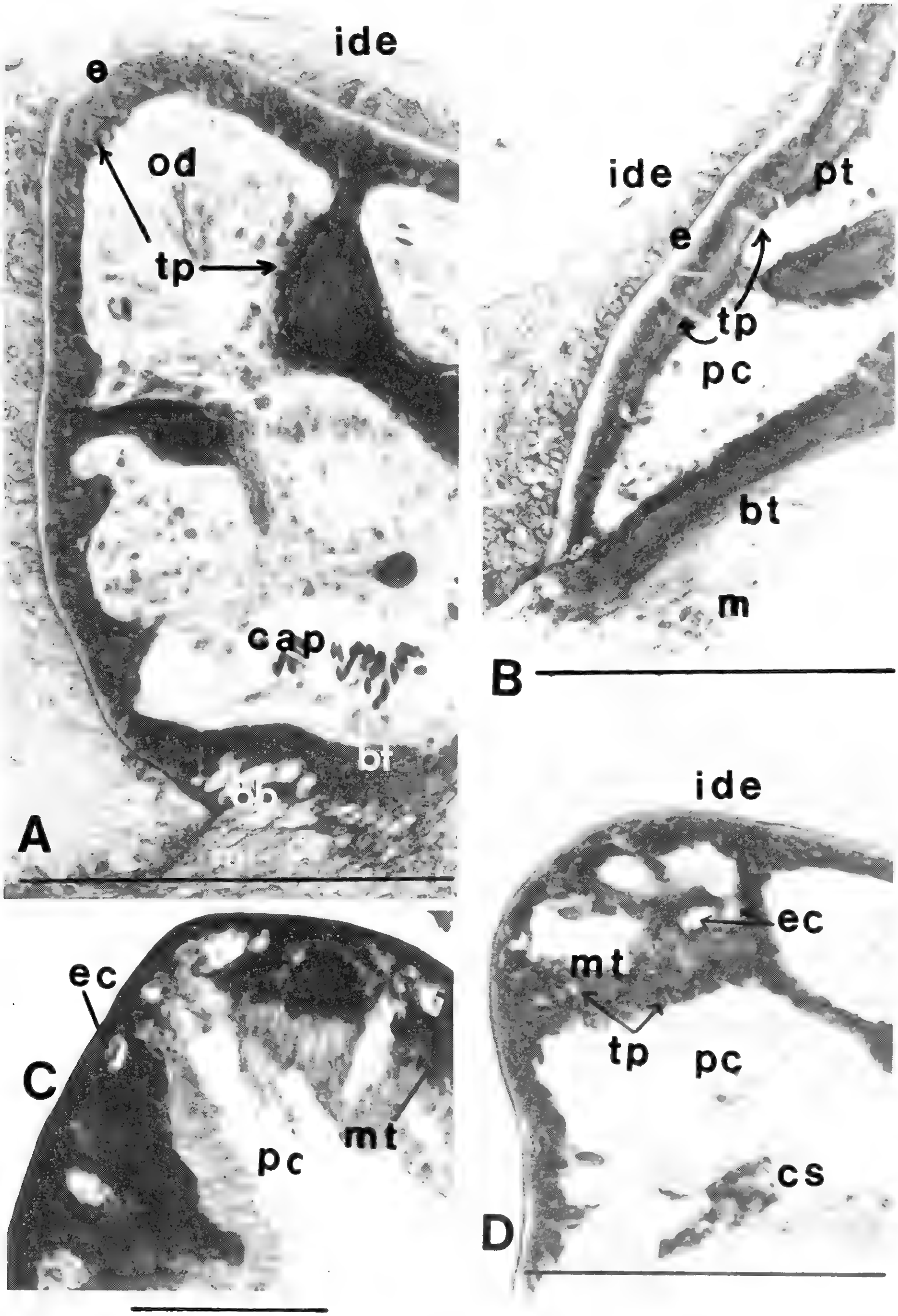
A. Vertical section through the medial face of the right upper tooth plate of an embryo of 75 mm (equivalent to level **B** of Fig. 5). The specimen was embedded in paraffin and the section stained with Heidenhain's azan.

B. Vertical section through the labial face of the left lower tooth plate of the same embryo as in Fig. 2**A**, in a position equivalent to level **A** of Fig. 5, showing active mesenchyme cells and new collagen strands outside the pulp cavity. The enamel-like substance is unstained.

C. Vertical section through the developing modified trabeculae in the medial face of an upper tooth of an embryo of 98 mm (behind the developing column of Fig. 3**B**). Osteocytes and clusters of associated mesenchyme cells in the pulp cavity are present.

D. Vertical section through the developing modified trabeculae of an embryo of 75 mm, showing enclosed cells and Tomes processes.

bt — basal trabeculae, cap — capillaries, cs — collagen strands, e — enamel like substance, ide — inner dental epithelium, m — mesenchyme, ob — osteoblasts, ec — enclosed cells, od — odontoblasts, pc — pulp cavity, pt — primary trabeculae, tp — Tomes processes.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perpendicular canals containing cells and lined by a dense fibrous material, the circumpulpal dentine. The developmental role of the secondary mesenchymal matrix in the tooth plates of *C. milii* is taken by the modified trabeculae near the occlusal surface. Solid rods of pleromin (Ørvig, 1976b) run the length of each tooth plate. This dentine is surrounded by a fibrous layer (equivalent to the circumpulpar dentine) and by cells.

In both species the pulp cavity is extensive, and is rich in cells and capillaries. Most cells are active odontoblasts or osteoblasts. Enclosed in the trabeculae and pedestal are cells, some of which appear to be active with large nuclei and some inactive with crenated nuclei.

DESCRIPTION

The basal trabeculae of *C. milii* tooth plates, and the trabeculae and pedestal of *N. forsteri,* have the accepted characteristics of cellular bone. They contain osteocytes within an organic matrix which is mineralized with calcium phosphate. The matrix gives staining reactions typical of collagen in both species (Table 1). Basal trabeculae have enclosed cells, single or in groups (Fig. 2**A, B**) but no Tomes processes. They grade into primary trabeculae of the tooth plate which have Tomes processes (Fig. 2**A, B**) seen as short branching canals reaching into the trabeculae from the pulp cavity. In *N. forsteri* the trabeculae consist of fine fibres (Fig. 4**A, D**), and are clearly differentiated from the secondary mesenchymal matrix (Fig. 4**D**).

The tooth plates of both species are coated in an enamel-like substance which is associated with the cells of the inner dental epithelium. These cells remain active in growing parts of the tooth plate throughout the life of the animal in both species (Figs 2, 4). The enamel-like substance is shiny in external appearance and the layer is thin. In *C. milii* it covers pleromin, basal trabeculae and modified trabeculae prior to abrasion at the occlusal surface (Figs 2, 5); similarly in *N. forsteri* it covers columnar dentine and secondary mesenchymal matrix before abrasion, and extends down over the pedestal and trabeculae (Fig. 6). Histologically, in both species, it does not stain for collagen with sirius red or Mallory's phosphotungstic acid and haematoxylin (Table 1), but gives a reaction more typical of other proteins (Pearse, 1968). In *C. milii,* the material grades into the underlying trabeculae (Fig. 2); in *N. forsteri* it forms a distinct layer (Fig. 4**B**) which is metachromatic with toluidine blue when it first forms (Fig. 4**B, C**) and stains lightly later (Fig. 4**B**). In decalcified material the lightly stained substance is absent (Fig. 4). The enamel-like substance is the first tooth tissue to appear in *C. milii* (Schauinsland, 1903) and in *N. forsteri* (Semon, 1899; Kemp, 1979), and other tooth tissues develop within the shell it forms. In both species, it appears to be associated with the cells of the inner dental epithelium.

Actively growing trabeculae form a major part of the tooth plate in *C. milii,* and become modified later in life in the occlusal regions of the tooth plate (Fig. 2**C, D**; Ørvig, 1976b). Primary trabeculae form a loose network in the pulp cavity, and appear to be in contact with the enamel-like substance below the inner dental epithelium. Short branching Tomes processes of regular arrangement extend into the trabeculae from the pulp cavity. Modified trabeculae are thicker than the primary trabeculae of the tooth plate, and have coarser fibres and less regularly arranged branching canals (Tomes processes) (compare Fig. 2**A, B** and Fig. 2**C, D**). They retain the staining characteristics of collagen, and cells are enclosed. The place of modified trabeculae in *N. forsteri* is taken by secondary mesenchymal matrix, also collagen rich, with coarse randomly arranged fibres, mineralized with calcium phosphate and actively growing but lacking enclosed cells (Fig. 4). Tomes processes extend into the mineralized matrix from the odontoblasts (Fig. 4**A, D**). Long irregular branching pulp canals extend into the secondary mesenchymal matrix, and areas where the columnar dentine is growing

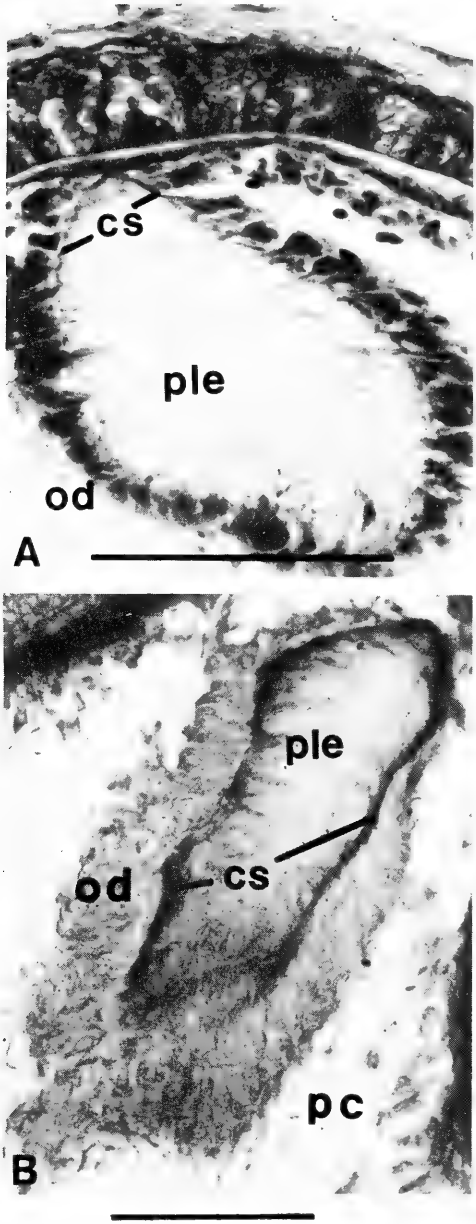

Fig. 3. Photomicrographs of sections of tooth plates of *Callorhynchus milii* embryos. Scale lines = 0.1 mm.
A. Vertical section through developing pleromin in the upper tooth plate of an embryo of 75 mm showing long cell processes entering the pleromin and an early stage in the secretion of circumpulpal dentine.
B. Pleromin in the upper tooth plate of an embryo of 98 mm. Centrally the matrix is unstained and contains branching cell processes; between cells and unstained matrix is circumpulpal dentine, staining for collagen.
Labelling as in Fig. 2, with ple — pleromin.

over the secondary mesenchymal matrix can be seen in the pulp cavity (Fig. 4). This is not a conversion of secondary mesenchymal matrix into columnar dentine, but represents growth of columnar dentine over secondary mesenchymal matrix (see also Kemp, 1979).

The central region of the tooth plates of both species is occupied by an unusual hard tissue having similar properties, called pleromin in *C. milii* and columnar dentine in *N. forsteri.* Centrally, the columnar dentine in *N. forsteri* consists of sparse, fine fibres staining like collagen or reticulin (Table 1) and heavily mineralized with calcium phosphate (Kemp, in preparation). This dentine does not change in relative content of organic and inorganic material as it grows older. It has the same appearance in the light microscope from the time of its first appearance in stage 49 (Kemp, 1979: fig. 3D) throughout development (Kemp, 1979: fig. 10; this paper Fig. **4A, C**) and in the fully formed tooth plate — a highly mineralized matrix containing very fine fibres which stain with sirius red or toluidine blue (Table 1) and become birefringent. Pleromin in the developing tooth plates of *C. milii* has a similar appearance — sparse fibres with a staining reaction characteristic of collagen in an unstained matrix, and similarly, there is no reduction in the collagen content as it grows older.

Surrounding the pleromin in *C. milii,* and lining the pulp cavity and pulp canals in *N. forsteri* are cells which send processes into the tissue, long in *C. milii* and short in *N. forsteri* (Figs 3, **4A**). The cell processes are unbranched in *N. forsteri* (Fig. **4A**) and may branch in *C. milii* (Fig. 3). The collagen fibres that form the circumpulpal dentine increase in quantity as the tooth plate develops (for *Callorhynchus milii,* see Fig. 2**E, F**; and for *N. forsteri* compare Fig. **4A, B** with Kemp, 1979: fig. 10A, B and fig. 11A, B). Circumpulpal dentine is absent in the pulp cavity of *N. forsteri,* where the odontoblasts are in direct contact with the forming columnar dentine, and appears to form within the pulp canals; while in *C. milii* circumpulpar dentine forms within the pulp cavity and develops until it surrounds the rod of pleromin (compare Fig. 3**A** and Fig. 3**B**).

Circumpulpal dentine consists of collagen — fine loose fibres in *C. milii* and a dense mat of fine fibres in *N. forsteri.*

In none of the specimens examined is there any sign of resorption of trabecular or dentinal material from the pulp cavity within the tooth plate (Figs 2, 3, 4). External erosion of the tooth plate is absent in *C. milii;* erosion of the mediolingual face of the tooth plate is found in *N. forsteri,* but is usually above the actively growing part of the inner dental epithelium, and involves both the thin layer of secondary mesenchymal

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Fig. 4. Photomicrographs of sections of tooth plates of *Neoceratodus forsteri* larvae. Scale lines = 0.1 mm.

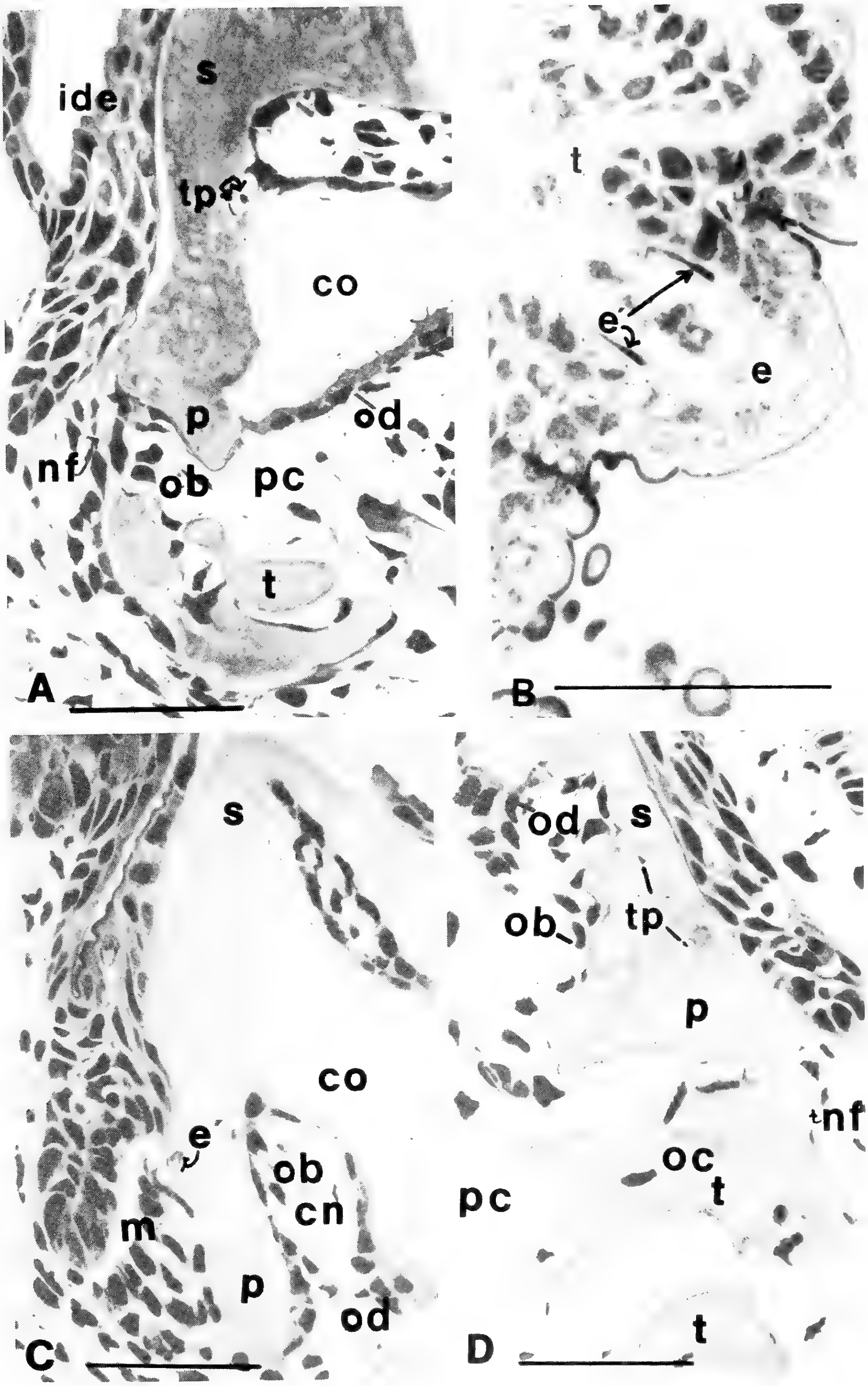
A. Vertical section through the labial extremity of ridge 2 of a lower jaw tooth plate of a larva of stage 54 (Kemp, 1982b). The specimen was decalcified and embedded in glycol methacrylate and the sections were stained with Heidenhain's iron haematoxylin to show fibres.

B. Vertical section through a cusp of a lower jaw tooth plate of a larva of stage 46 showing the change in staining reaction as the enamel-like substance ages. The specimen was not decalcified and was embedded in glycol methacrylate and sections were stained with Toluidine blue in buffer.

C. Vertical section through the labial extremity of ridge 2 of a lower jaw tooth plate of a larva of stage 54 showing the beginnings of the formation of a new cusp with new metachromatic enamel-like substance and active cells in the mesenchyme, pulp cavity and inner dental epithelium. The specimen was decalcified, embedded in glycol methacrylate and stained with Toluidine blue in buffer.

D. Vertical section through the medial region of a lower jaw tooth plate of a larva of stage 54 showing the distinction between pedestal and secondary mesenchymal matrix, with the pedestal associated with active mesenchymal cells on the outside of the tooth plate. Same specimen as Fig. **4A.**

cn — pulp canals, co — columnar dentine, e — older, lightly stained orthochromatic enamel-like substance, e' — newer, metachromatic enamel-like substance, ide — inner dental epithelium, m — active mesenchyme cells, nf — new fibrous material, ob — osteoblasts, oc — osteocytes, od — odontoblasts, p — pedestal, pc — pulp cavity, s — secondary mesenchymal matrix, t — trabeculae, tp — Tomes processes.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matrix and the columnar dentine. The phenomenon becomes progressively more severe as the fish ages, being virtually unknown in tooth plates less than 15 mm, but commonplace in tooth plates of 20-30 mm in length (Kemp, 1977, 1979). This erosion is confined to the outer mediolingual face of the tooth plates.

A distinct line separates the pedestal and the secondary mesenchymal matrix in the *N. forsteri* tooth plate illustrated in Fig. 4**D.** This is above the growing area, irregular in conformation, and under the inner dental epithelium and the enamel-like substance (prior to decalcification). The distinction between the pedestal and the secondary mesenchymal matrix is not always so obvious (compare Fig. 4**A** and **C**).

There are active cells in the region of the pedestal on the external surface of the tooth plate in *N. forsteri* (Fig. 4) and in equivalent positions in *C. milii* (Fig. 2). This corresponds to an area of active production of the epithelial and mesenchymal contributions of new tooth material and is equivalent to the 'resorption surface' described by Smith (1979a) from scanning electron micrographs of *Lepidosiren paradoxa* tooth plates. However, in *N. forsteri* and *C. milii* fibres of new matrix can be seen at the level of the light microscope and the appearance is not one of resorption (Figs 2**A, B**, 4**A, D**).

Active cells capable of secreting new dentine, trabeculae, pedestal, modified trabeculae, secondary mesenchymal matrix and enamel-like substance can be found in similar areas of the tooth plates of both species. In *N. forsteri,* the cells associated with the secondary mesenchymal matrix and columnar dentine have large granular nuclei, irregular shapes and a small quantity of homogeneous cytoplasm (Fig. 4**C, D**). Cells of the inner dental epithelium have large elongated or roughly oblong granular nuclei (depending on position) and relatively little homogeneous cytoplasm (Fig. 4). Cells enclosed within the trabeculae or pedestal may have an appearance similar to that of the cells within the pulp cavity, or may have shrunken cytoplasm and dark pycnotic nuclei. Cells of the pulp cavity of *C. milii* and cells associated with the pleromin resemble fibroblasts with large granular nuclei, and are numerous (Fig. 2). Cells of the inner dental epithelium, and cells enclosed within the trabeculae also have large granular nuclei (Fig. 2).

The pattern of growth of the tooth plates of *C. milii* is shown in Fig. 5 and of *N. forsteri* in Fig. 6. There is a posterior area (postero-medial in upper plates of *C. milii*) where new tissues of all types are laid down. In *N. forsteri* new ridges are added here (Kemp, 1977); in *C. milii* the rods of pleromin are extended and fresh enameloid and trabeculae laid down (Figs 2, 5). There is continuous growth of the trabecular network below and around the dentinal tissue in both species. Secondary mesenchymal matrix grows from within the pulp cavity of *N. forsteri* and columnar dentine grows over the secondary mesenchymal matrix as the tooth plate expands in area (Fig. 4**C** and Kemp, 1979). Active odontoblasts in both species continue to form columnar dentine or pleromin in the pulp cavity, and the inner dental epithelium produces enamel-like substance, including a cusp in *N. forsteri* and without a cusp in *C. milii.* These processes result in growth in area and in depth in the whole tooth plate at the same time as hard tissue is abraded from its occlusal surface.

DISCUSSION

Superficially, the morphology of lungfish and holocephalan tooth plates is similar, and extends beyond the possession of crushing plates — found after all in many other teleostome and elasmobranch fishes. If the transient marginal row of denticles found in the lower jaws of larvae of *N. forsteri* (Kemp, 1977) is not considered, the number and distribution of the plates is the same — two large occluding molariform plates in each jaw, and two incisiform teeth in the upper jaw. The vomers of *C. milii* are opposed by

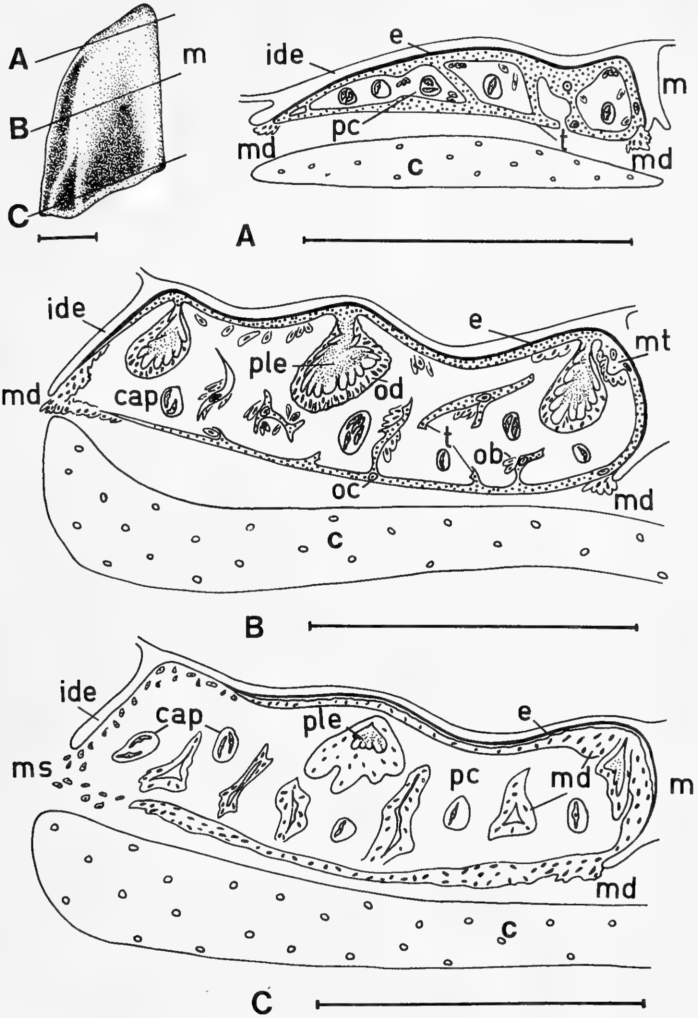

Fig. 5. Diagrams of the left lower tooth plate of a 75 mm embryo of *C. milii* to show the distribution of hard tissues and active cells. Lettering as in Fig. 1 with the following additions —
cap — capillaries, ide — inner dental epithelium, md — dense mesenchyme, ms — diffuse, scattered mesenchyme, ob — osteoblasts, oc — osteocytes, od — odontoblasts, ple — pleromin. Scale lines = 1 mm. Small drawing — occlusal view of whole tooth.
A, B, C, — vertical sections at successive levels of the tooth plate.

the anterior edge of the lower plates which grows forwards to meet them (Bargmann, 1933); the vomers of *N. forsteri* are unopposed. It can be argued that these morphological similarities are purely adaptive. The two species eat a similar diet including molluscs and crustacea that have to be crushed, and have evolved similar dentitions to match. However, the resemblance between the tooth plates of holocephalans and dipnoans goes much deeper and extends to histological structures and to pattern of growth of the tooth plates. These similarities are present throughout the life of the animals although they are easier to demonstrate in young, actively growing specimens.

A framework of basal trabeculae (including a pedestal in *N. forsteri*) is important in the tooth plates of both groups. The basal trabeculae of juvenile *C. milii* are loose and undifferentiated and have the characteristics of cellular bone, i.e. a mineralized collagenous matrix lacking Tomes processes but having enclosed cells. Cellular bone has not previously been recorded in a holocephalan. In *N. forsteri* a base of trabecular bone with a pedestal, both having a mineralized collagenous matrix and enclosed cells, is also retained.

The secondary mesenchymal matrix which appears early in development (Kemp, 1979) is similar to the pedestal and trabeculae, but lacks enclosed cells, contains long irregular and branching canals, has coarser and more tortuous fibres, and has a slightly different staining reaction when compared with trabeculae or pedestal (Fig. 4**D**). Apart from the lack of enclosed cells, secondary mesenchymal matrix is clearly related to bone, but the cells leave irregular Tomes processes in the matrix, and the structure is best considered under the general heading of osteodentine. The modified dentine of *C. milii* contains both Tomes processes and cells and is even more equivocal in its affinities, enclosed cells being a characteristic of bone but not of dentine, and Tomes processes a feature of dentine but not of bone. To avoid coining yet another term for this matrix, it may be better to regard it also as a form of osteodentine.

Tooth plates of both species contain a similar, central hard tissue within a framework of trabeculae and osteodentine. This is eventually exposed on the occlusal surface of the tooth plate but in young animals is separated from enameloid by a thin layer of collagenous material. The distribution of this hard tissue is different in the two species. In *C. milii* it consists of rods of pleromin arranged parallel to the long axis of the tooth plate and in *N. forsteri* it is a centrally-positioned mass traversed by perpendicular pulp canals filled with cells and lined by circumpulpal dentine. In lepidosirenids a part of the mass of columnar dentine contains no pulp canals with circumpulpar dentine (Lison, 1941; Denison, 1974).

The histological structure of the hard tissue and associated soft tissues in holocephalans and dipnoans is similar. It is rich in inorganic material but relatively poor in organic fibres (Kemp, 1979, and in preparation) — calcium phosphate and fine fibres of collagen respectively.

Lison considers that the petrodentine (columnar dentine) of lungfish teeth contains no collagen but is strongly calcified (Lison, 1941: 295) and that there is a progressive reduction in collagen content of the tissues, with a corresponding increase in mineral content as osteodentine (= circumpulpal dentine) grades into petrodentine across the tooth structure. This is a structural change in collagen content, but not a developmental one, as the petrodentine (or columnar dentine) develops from the pulp cavity before circumpulpal dentine appears. The question of organic content of the petrodentine has been considered by James (1953: 17), who suggests that the small quantity of organic material present in the columnar dentine of *Protopterus* and *Lepidosiren* is reticulin, a protein related to collagen (Pearse, 1968). Kemp (1979) found that the fibres visible in the columnar dentine of *N. forsteri* tooth plates is collagen or reticulin; as the fibres can be stained by toluidine blue or sirius red and become birefringent after such treatment they are probably collagenous (Pearse, 1968). A comparison of successive stages of tooth development in *P. annectens* (Lison, 1941) and *N. forsteri* (Kemp, 1979) shows that there is no change in the collagen content of the columnar dentine — the quantity is low in early and late stages of development. There is no evidence for a reduction in the organic content of the columnar dentine itself as the dentition develops. Similar considerations apply to the pleromin of *C. milii* tooth plates — the collagen content does not change within the pleromin, although the quantity of collagen in the circumpulpal dentine increases (Fig. 3**A, B**).

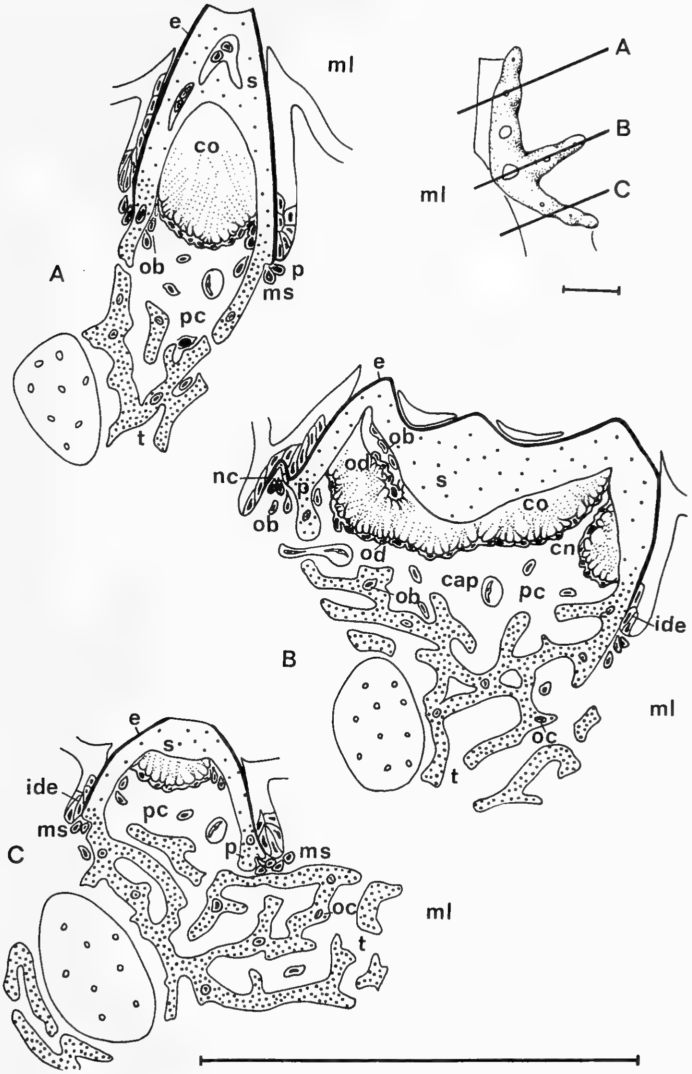

Fig. 6. Diagram of the left lower tooth plate of *N. forsteri* to show the distribution of hard tissues and active cells, based on a larva of stage 54. Lettering as in Fig. 1, with the following additions —
ms — mesenchyme, nc — new cusp, ob — osteoblasts, oc — osteocytes, and od — odontoblasts. Scale lines = 1 mm.
Small drawing — occlusal view of whole tooth.
A, B, C, — vertical sections at successive levels of the tooth plate.

Surrounding the pleromin in *C. milii* and lining the pulp canals in *N. forsteri* there is circumpulpal dentine containing a higher proportion of collagen than the pleromin or columnar dentine. This forms a dense fibrous mat in *N. forsteri,* with openings at intervals for cell processes (Kemp, 1979). In *C. milii* the collagen fibres have a more open structure. The cell processes are short in *N. forsteri,* long irregular and branching in *C. milii.* More pronounced similarities are present in fossil forms (Ørvig 1967, 1976a, b). Collagen content increases in circumpulpal dentine as the tooth plate grows in both groups.

Recent research into development of enamel-like structures in fish has raised some interesting questions about the homologies of this substance (Meinke, 1982; Shellis, 1975; Shellis and Miles, 1974). The structure in Dipnoi, regarded as enameloid by several authors (Kemp, 1979; Kerr, 1903, 1910; Parker, 1982) appears more like an enamel in the scanning electron microscope (Smith, 1979a), but according to this author, should not be considered as homologous with tetrapod enamel. The enamel-like structures of *N. forsteri* and *C. milii,* in common with the enameloid of sharks (Glas, 1962; Garant, 1970) and of *Polypterus* (Meinke, 1982) the enamel of crossopterygii (Smith, 1979a) and the enamel of mammals contains protein other than collagen and is at least in part of epithelial origin. The cells which form the lining of the mouth in Dipnoi come from the endoderm (Kerr, 1903, 1910; Kemp, in preparation) and if such embryonic distinctions have a continuing morphological significance, the definitions of enamel-like structures will need more alterations.

Both *C. milii* and *N. forsteri* retain an inner dental epithelium active in similar positions where new tooth material is forming. This is also the case in *Protopterus annectens* (Parker, 1892). In both groups formation of enamel-like substance, in association with cells of the inner dental epithelium, continues as the tooth plate grows. Also, in *C. milii* and *N. forsteri,* enamel-like substance covers dentinal and trabecular structures.

Although the resemblances in histological structures are interesting, the close similarities in the mode of growth of the tooth plates are more striking. Early growth patterns in dipnoans and holocephalans are not obviously similar. *C. milii* toothplates form a single entity even at the stage of a mesenchymal template (Schauinsland, 1903) with no trace of separate denticles. *N. forsteri* tooth plates form by the fusion of separate denticles (Semon, 1899) in a pattern that closely reflects the shape and structure of the adult tooth plate (Kemp, 1977). The latter method also applies to *L. paradoxa* although the tooth plate forms precociously and has erupted before the larva hatches (Kerr, 1903, 1910) and to several fossil species e.g. *Monongahela* spp. (Lund, 1970, 1973) and *Megapleuron zangleri* (Schultze, 1977). However the mesenchymal template of embryonic *N. forsteri* tooth plates is a single mass with cusp primordia which develop into the isolated denticles of hard matrix; and overlying inner dental epithelium is also a single structure (Kemp, 1977). In both groups, the tooth plates begin to develop as single mesenchymal and epithelial entities, but this may well be a characteristic of the growth of the dentition in many primitive vertebrates, and therefore, not indicative of close relationships between dipnoans and holocephalans.

Increase in size of the tooth plates in both species involves the growth of tooth material, ankylosed bone and underlying cartilage in an integrated fashion. This includes expansion in size as well as changes in shape created by differential growth. Models involving growth in size of the tooth plate alone (e.g. Campbell and Barwick, 1983: fig. 2) do not cover all aspects of the phenomenon, because growth of the supporting structures is not considered.

Wholesale resorption of the tooth plate from within the pulp cavity does not appear to be involved in the growth of the dentition in *N. forsteri* or *C. milii.* There is no evidence that resorption of a part of the tooth plate between tooth and bone occurs to allow expansion, at least at the level of the light microscope, in the areas of the tooth plate that contain active cells. The resorption of material from developing tooth plates of *P. annectens* described by Lison (1941) and from adult tooth plates of *Sagenodus inaequalis* by Smith (1979b) is not labelled in their illustrations, and the extent and position of the resorption is not clear. Further, models involving resorption would result in points of weakness in the tooth plate which is in use throughout the life of the animal. The junction between tooth and bone is not thick in *N. forsteri* or in *C. milii,* and any resorption would result in removal of material from this region. For the tooth plate to grow evenly resorption would have to be extensive all round the tooth plate, and this would make the junction weaker.

The erosion found in the tooth plates of *N. forsteri* (Kemp, 1979, and in preparation) is not sufficient or necessary to explain all the remodelling in the shape of the tooth plate, e.g. reduction in the angles between the ridges and elongation of the tooth plate, as the animal grows (Kemp, 1977). Extensive erosion does not appear until the tooth plate has already completed much of its growth and remodelling. It occurs in parts of the tooth plate remote from the active inner dental epithelium and wears through the secondary mesenchymal matrix into the columnar dentine in non-growing areas of the tooth plate at times when the dentition is in active use (*N. forsteri* does not enter a rest phase at any time of its life cycle). The erosion is always isolated, being found only on the external mediolingual face, and is found in several other species of Australian ceratodonts (Kemp, 1982a, and in preparation).

Shape changes which occur in *N. forsteri* and *C. milii* can be accounted for by a process of differential growth. This alters angles between the ridges and causes the tooth plate to elongate in *N. forsteri.* Erosion roughens the mediolingual face of the tooth plate and removes the 'inner angle' found in juvenile *N. forsteri.* In *C. milii,* much extension on the medial face is unlikely because the tooth plates are so close in this area, but the teeth do change in shape in other parts e.g. the development of the incisiform process on the lower jaw tooth plates to occlude with the vomerine teeth. A fossil bradyodont, *Harpagofututor volsellorhinus,* increases the size of the left hand posterior upper tooth plate in the mid line (Lund, 1982). Growth phenomena are otherwise similar in the tooth plates of Carboniferous bradyodonts (Lund, 1977, 1982).

In the growing tooth plate there are at least five processes going on simultaneously:

a) Extension in length at the back of the tooth plate with additions to all tooth tissues, a process which slows down as the animal grows older (both species)

b) Growth of columnar dentine or pleromin associated with cells in the pulp cavity (both species)

c) Growth of the trabecular network within the pulp cavity in *C. milii,* and below in *N. forsteri,* with growth of the related secondary mesenchymal matrix above the pulp cavity in the latter species. This results in extension of the trabecular network, enlargement of the pulp cavity and areal growth of the tooth plate and associated tissues (both species)

d) Addition of a layer of enamel-like substance to new external surfaces (both species). In *N. forsteri* a cusp is also formed at intervals at the labial extremities of the ridges. This is made up of enamel-like substance and a primary mesenchymal matrix which is eventually incorporated into the pedestal of the tooth plate and ultimately involved with the extending secondary mesenchymal matrix. Cusps are apparently not involved with the growth of *Lepidosiren paradoxa* tooth plates (Denison, 1974: 52-53) but are present in the tooth plates of *Protopterus annectens* (Conant per. com.)

e) The tooth plate wears continually at the occlusal surface (both species).

This model requires the presence of active cells in significant places, in the pulp cavity, in the canals of the columnar dentine in *N. forsteri* and surrounding the column in *C. milii,* around and within the trabeculae and secondary mesenchymal matrix, in the cells of the inner dental epithelium, and around the tooth externally in the mesenchyme below the level of the inner dental epithelium. Such cells are present. There is also evidence of a growth of columnar dentine in areas previously occupied by secondary mesenchymal matrix within the pulp cavity of *N. forsteri,* and of shape changes in the tooth plates of both species if successive stages are examined (Kemp, 1977). The tooth plates of *C. milii* and *N. forsteri* grow in a similar manner that does not appear to involve extensive resorption; what it does involve awaits experimental elucidation.

It is possible to derive most Mesozoic lungfish and all Cainozoic species (those with tooth plates based on radiating ridges with or without cusps) from two stems. Possibly a solid dentinous palate like that of *Dipnorhynchus* developed through stages similar to the dentitions of *Chirodipterus* and *Dipterus* into a tooth plate with radiating ridges and cusps (White, 1965, 1966; Thomson, 1967). Alternatively a stage represented by a lungfish with jaws covered by small denticles became modified by changes in the arrangement and permanence of the denticles (random to radial, shed to fixed) as in *Fleurantia denticulata,* into a tooth plate with radiating ridges and cusps (Denison, 1974; Campbell and Barwick, 1983). Additional evidence for the latter hypothesis is the widespread and ancient habit among larval lungfish of forming a tooth plate by the fusion of initially isolated denticles of primary matrix (Denison, 1969; Lund, 1970, 1973; Schultze, 1977; Kemp, 1977; Kerr, 1903, 1910). Several authors have suggested a similar fusion of isolated elements to form a tooth plate in fossil bradyodonts (Bendix-Almgren, 1970; Lund, 1977) but this fusion, if it occurred, is across a tooth family and not in a radiating pattern; the resemblance may be incidental.

Histological similarities between living dipnoans and holocephalans consist of an enamel-like substance at least in part of epithelial origin and containing some protein that is not collagen, covering a base of trabecular material which encloses a form of osteodentine, and pleromin or columnar dentine with circumpulpal dentine. Like the growth pattern of the tooth plates, none of these structures are the exclusive property of holocephalans and dipnoans. An enamel-like substance related to the inner dental epithelium certainly occurs in sharks and mammals. A dentition ankylosed to a base of cellular bone is not unusual in lower vertebrates (Ørvig, 1967; Peyer, 1968), though it is interesting that cellular bone should be found in the Holocephali. Osteodentines of confusing variety are found in many primitive vertebrates. Petrodentines (pleromin or columnar dentine) occur in the dermal skeleton of psammosteid heterostracans and in the dentition of ptyctodont arthrodires, holocephalans and some of the earliest dipnoans (Campbell and Barwick, 1983; Smith, 1984) as well as more recent lungfish. Also detailed comparison shows that the similarities between holocephalan and dipnoan hard tissues are not really close. Enamel-like substance in *C. milii* grades into the underlying trabeculae; in *N. forsteri* it forms a distinctive layer. *C. milii* has no pedestal. The osteodentine (modified trabeculae) of *C. milii* has enclosed cells and Tomes processes; in *N. forsteri* there are no enclosed cells in the equivalent tissue. Pleromin in *C. milii* is associated with cells with long branching processes; in *N. forsteri* the corresponding cells have short unbranched processes. Circumpulpal dentine has fine fibres forming a dense mat in *N. forsteri;* in *C. milii* this tissue has a more open texture.

These considerations suggest that useful growth patterns and histological structures have been conserved during evolution. They are likely to be found in diverse groups of animals, and the occurrence of a broad similarity in the developing dentitions of the Holocephali and Dipnoi does not necessarily indicate close relationship between the two groups.

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New Phyllolepids from Victoria and the Relationships of the Group

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Two new phyllolepids (Placodermi: Phyllolepidae), *Austrophyllolepis ritchiei,* gen. et sp. nov., and *Austrophyllolepis youngi*, gen. et sp. nov., are described from the Frasnian lacustrine shales near Mt Howitt, Victoria. *Austrophyllolepis* gen. nov. is distinguished from *Phyllolepis* by the presence of a posterior median ventral plate, and by the shape of the marginal plate. *Austrophyllolepis ritchiei,* gen. et sp. nov. is a broad species with a mature armour equally as long as broad whereas *A. youngi* is characterized by having a slender armour, noticeably different from *A. ritchiei* in the proportions of the preorbital, paranuchal, nuchal, median dorsal, anterior lateral, anterior ventrolateral and posterior ventrolateral plates. Both species are represented by individuals in all stages of growth. New anatomical features described for phyllolepids include the visceral surface of the headshield and dorsal endocranial form, gnathalia, parasphenoid, cheek plate, otoliths, axial skeleton, tail and pelvic girdle. It is suggested that the phyllolepids are specialized actinolepidoid euarthrodires because of characters shared in the endocranium, skull roof and trunkshield. The order Phyllolepida (Stensiö, 1934) is made redundant, the family Phyllolepidae (Woodward, 1891) is placed in the infraorder Phyllolepidi of the suborder Actinolepidoidei (Miles and Young, 1977).

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INTRODUCTION

Phyllolepids were dorsoventrally flattened placoderm fishes which have been recorded from continental deposits of Late Devonian age from east Greenland (Heintz, 1930; Stensiö 1934, 1936, 1939), Scotland (Agassiz, 1844; Woodward, 1914, 1920), Belgium (Leriche, 1931), Baltic Russia (Vasilauskas, 1963), North America (Newberry, 1899), Antarctica (Ritchie, 1972), Australia (Hills, 1929, 1932, 1935, 1958b) and Turkey (Dr P. Janvier, pers. comm. 1982). The restricted time range of phyllolepids in the northern hemisphere has made them biostratigraphically useful as zone fossils for part of the Famennian. In Australia phyllolepids are known from Frasnian and Famennian strata (Young, 1974; Fergusson *et al.,* 1979; Long, 1983). Despite the widespread distribution of phyllolepids their structure is known only from a few articulated specimens of *Phyllolepis (P. orvini, P. woodwardi)* and the relationships of the group within the Placodermi have up until now been based only on the features of the dermal armour. Prior to the detailed work of Stensiö phyllolepids were considered by some workers to be agnathans similar to the heterostracan *Drepanaspis* (Woodward, 1914, 1920; Heintz, 1930). The material described in this paper from Mt Howitt, Victoria, reopens the question of phyllolepid relationships within the placoderms in the light of new anatomical observations. Current placement of the phyllolepid placoderms is as a sister group to the antiarchs and euarthrodires (Miles and Young, 1977; Young, 1980; Denison, 1978). Denison (1975, 1978) expresses the opinion that phyllolepids were derived from primitive euarthrodiran stock.

The Mt Howitt fossil site has yielded a diverse fauna of Frasnian freshwater fishes including the placoderms *Bothriolepis gippslandiensis, B. cullodenensis, B. fergusoni, Groenlandaspis* sp. (Long, 1982, 1983a), *Austrophyllolepis ritchiei,* gen. et sp. nov, and *A.*

youngi, gen. et sp. nov; a diplacanthoid acanthodian, *Culmacanthus stewarti* (Long, 1983b), acanthodiform acanthodians similar to *Acanthodes* (Long, 1983c), new genera of dipnoans with bodies resembling *Fleurantia* and *Scaumenacia* (Marsden, 1976), a new genus of palaeoniscoid, and new genera of crossopterygians belonging to both the Osteolepiformes and Porolepiformes. There are no invertebrates from the site although plant remains are common, mostly being lycopsids. The geological setting and taphonomy of the site is discussed by Marsden (1976) and Long (1982b). The age of the locality and correlations with other Late Devonian ichthyofaunas of southeastern Australia was treated by Long (1983a).

The Mt Howitt specimens were prepared both manually and with dilute hydrochloric acid to remove the friable bone so that latex casts could be made. As the respective plates of *Phyllolepis orvini* have been described in detail by Stensiö (1934, 1936) I have omitted lengthy descriptions of each plate of the new material where it is essentially similar to that of *Phyllolepis.* The following descriptions summarize the proportional differences between the species leaving the illustrations to show form and variation of individual plates. This approach has been successfully utilized recently in the series of papers on the Gogo placoderms by Miles and Dennis (1979) and Dennis and Miles (1979, 1980, 1983). The reliability of comparisons with other phyllolepids is shown by the graph (Fig. 24) recording taxa versus material known.

Specimens are housed in the Museum of Victoria, Melbourne. Throughout the text breadth and length are abbreviated as B and L respectively, and plate names are abbreviated in accordance with the text figures.

In Australia phyllolepid plates have been recorded from Taggerty (Hills, 1929) and the South Blue Range in Victoria (Hills, 1936); from Harvey's Range north of Parkes (Hills, 1932) and near Eden in New South Wales (Fergusson *et al.,* 1979); and from the Dulcie Range in the Northern Territory (Hills, 1958). Unpublished finds of phyllolepids from Australia include isolated plates from Freestone Creek, Tatong and Snowy Bluff in Victoria, and from the Jemalong Range, and Khan Yunis in New South Wales. Aside from *Placolepis budawangensis* (Ritchie, 1984) and the Mt Howitt phyllolepids, all other material from Australia is of isolated plates.

HOMOLOGY OF PHYLLOLEPID PLATES

The three anteriormost pairs of headshield plates in phyllolepids have been interpreted in two ways. Before describing the new material systematically it is necessary to clarify the homology of these bones. Criteria for homology used here are outlined by Wiley (1981: 130).

Stensiö (1969) regards the anteromesial pair of headshield plates as true preorbital plates (PRO) whereas Denison (1975, 1978) considers these as possibly being postnasal plates (PN). Both PRO and PN plates carry a section of the supraorbital sensory line groove. I regard this pair of plates as being PRO plates homologous to those of euarthrodires, petalichthyids and some palaeacanthaspidoids because of their situation anterior to the nuchal (or centronuchal; Nu) plate, and their mesial contact. In most euarthrodires, *Wuttagoonaspis,* some petalichthyids and *Kimaspis* the PRO plates are in mesial contact with the central plates (Ce) or centronuchal area posteriorly (Fig. 1). Orbital position is not reliable for identification of the PRO plates as it is a variable feature of most placoderm groups. In euarthrodires the orbit is commonly situated between the PRO and postorbital (PTO) plates, yet in *Actinolepis* (Fig. 1) it is contained by the PTO and PN plates (Mark-Kurik, 1973), and in *Homostius* it is bounded by Ce plates separating the PRO and PTO plates (Obruchev, 1964). In the rhenanid *Brindabellaspis* there is a marginal plate (MG) separating the PRO and PTO plates (Young, 1980). The position of the orbit of phyllolepids is below the anterior half of the PTO

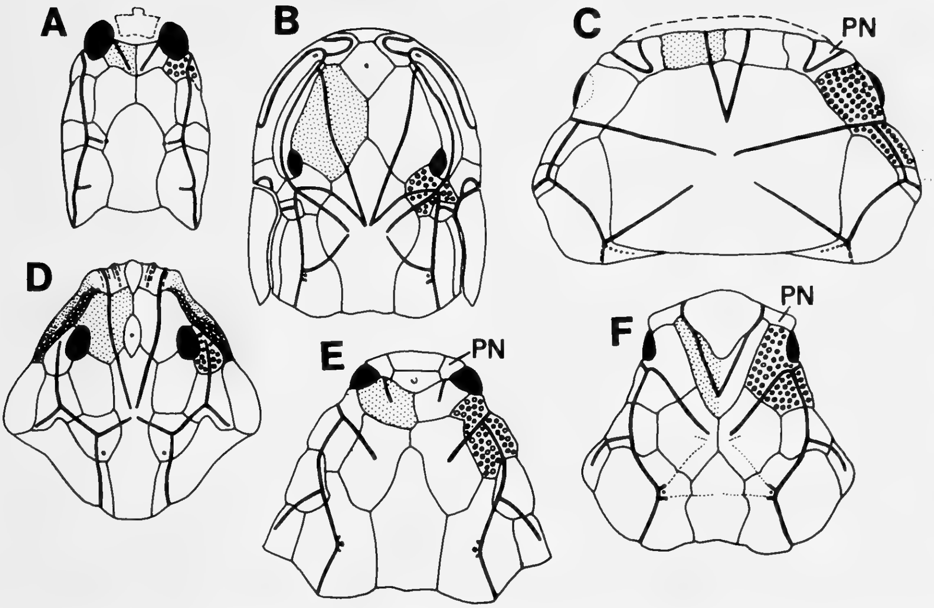


Fig. 1. Homology of the preorbital, postnasal and postorbital plates. Left preorbital plate stippled, right postorbital plate shaded with circles, orbital area in black and postnasal plate labelled PN. **A.** *Kimaspis* (after Mark-Kurik, 1973b). **B.** *Wuttagoonaspis* (after Ritchie, 1973). **C.** *Austrophyllolepis ritchiei* gen. et sp. nov. **D.** *Lunaspis* (after Gross, 1961). **E.** *Kujdanowiaspis* (after Stensiö, 1945). **F.** *Actinolepis* (after Mark-Kurik, 1973a). Note the position of the postnasal plate in *Kujdanowiaspis* and *Actinolepis* and the proposed homology of this plate in *Austrophyllolepis.* The predicted position of the cartilaginous rhinocapsular in *Austrophyllolepis* is represented by a broken line. Not to scale.

plate as indicated by the supraorbital vault described below. As such it is not divided between two plates due to its small size, as also occurs in *Actinolepis.* I conclude that true PRO plates in placoderms are recognized by the presence of a section of the supraorbital sensory line groove, and are situated anterior or anterolateral to the centronuchal area, often in mesial contact with each other or separated by extensions of the pineal, rostropineal or centronuchal plate areas. They most frequently border the anterior or dorsal rim of the orbit, but not always, as in *Actinolepis* and phyllolepids.

The second pair of plates flanking the nuchal plate of phyllolepids have been interpreted as dermosphenotics (or equivalent to the anterior division of the PTO plate of euarthrodires) by Stensiö (1969: 357) and as ?PRO plates by Denison (1978: 41). To evaluate the homology of these plates it is necessary to confirm that the plates contacting them posteriorly are true PTO plates, thus eliminating the first hypothesis. The third pair of marginal plates are regarded as PTO plates because they bear the triple point junction of the central sensory line canal, infraorbital sensory line canal and main lateral line canal, and they possess a supraorbital vault for the optic capsule and have ventral grooves for both the anterior and posterior postorbital endocranial processes. In primitive euarthrodires the PTO plates bear the triple point junction of the sensory line canals, part of the supraorbital vault (or most of it in *Actinolepis*), and have a groove for the anterior postorbital process of the endocranium (*Dicksonosteus,* Goujet, 1975; *Kujdanowiaspis*, Stensiö, 1963). The PTO plate of most placoderms bears the triple point junction of the sensory line canals and part of the orbital border, although relationships to the underlying endocranial processes are variable (see Young, 1980).

Accepting that the third pair of phyllolepid headshield plates are PTO plates (also corroborated by Denison, 1978, and partly by Stensiö, 1969) the second pair of plates situated between the PRO and PTO plates can be interpreted as PN plates by virtue of their position (Fig. 1). PN plates in placoderms are situated lateral to the nasal capsules or their dermal bone cover (rostral plates or rostropineal plates). In several actinolepidoid and phlyctaenioid euarthrodires the rhinocapsular ossification which continued the nasal capsules was independently ossified from the rest of the endocranium, and is often found separated from the post-ethmoid ossification (Jarvik, 1980, vol. 1: 374). Examples of this are *Baringaspis* (Miles, 1973), *Kujdanowiaspis* (Stensiö, 1945), *Simblaspis* (Denison, 1958), *Aggeraspis* (Gross, 1962) and *Gaspeaspis* (Pageau, 1969). From the excellent preservation of the Mt Howitt phyllolepids it is evident that there was not an ossified rhinocapsular bone; instead it was probably cartilaginous like the postethmoid region of the endocranium. The rhinocapsular of phyllolepids would have articulated below the paired preorbital plates, as it does for all euarthrodires with an independent rhinocapsular bone. The PN plates are located on the anterolateral borders of the headshield in phyllolepids and *Actinolepis* (Mark-Kurik, 1973) clearly where the lateral limitations of the rhinocapsular would be expected. The unusual inflexion of a sensory line canal on this plate in phyllolepids is not difficult to explain if the PN plate changes its position from that of primitive euarthrodires, anterior to the PRO plate, to being lateral or anterolateral to the PROs causing a doubling up of the supraorbital canal. Alternatively the looped sensory canal of the PN plate may be a specialization of phyllolepids for increasing the dorsal sensory line length. A similar loop of the sensory line canal in this position is well known in *Chimaera* (Stensiö, 1947: fig. 10).

The remaining plates of the phyllolepid dermal armour are directly homologous with those of other placoderms, and especially similar to those of primitive euarthrodires (Stensiö, 1934, 1936, 1969).

SYSTEMATIC DESCRIPTIONS

Family PHYLLOLEPIDAE Woodward 1891

AUSTROPHYLLOLEPIS gen. nov.

Phyllolepis Marsden, 1976: 122 (from Mt Howitt).
Phyllolepis Long, 1982a: 63 (from Mt Howitt), figs 5D, 6C.
Phyllolepis Long, 1982b: fig. 1 (from Mt Howitt only).
Phyllolepis Long, 1983a: 297, figs 2, 3 (from Mt Howitt only).
Phyllolepid Long, 1983c: 22, fig 7.

Etymology: From the Latin 'australis' southern, combining form for the generic name *Phyllolepis,* pertaining to the Australian location of this phyllolepid.

Diagnosis: Medium-sized phyllolepid placoderms possessing a posterior median ventral plate which is overlapped by the anterior and posterior ventrolateral plates. A small suborbital plate firmly articulates with an ossified process below the postorbital plate. Anterior median ventral plate absent. Marginal plate broad with an external B/L index close to 36. The main lateral line sensory canal enters the paranuchal plate from the marginal plate at a point between 68-72% of the total length of the paranuchal plate. The shape and overlap relationships of the remaining plates are as for *Phyllolepis.*

Type species: Austrophyllolepis ritchiei sp. nov.

Remarks: The new genus is readily distinguished from the two other known phyllolepid genera, *Phyllolepis* and *Placolepis* (Ritchie, 1984), by the presence of a relatively large posterior median ventral plate (PMV). The paranuchal plate (PNu) of *Austrophyllolepis* differs from that of the other two genera by the position of entry of the lateral line canal

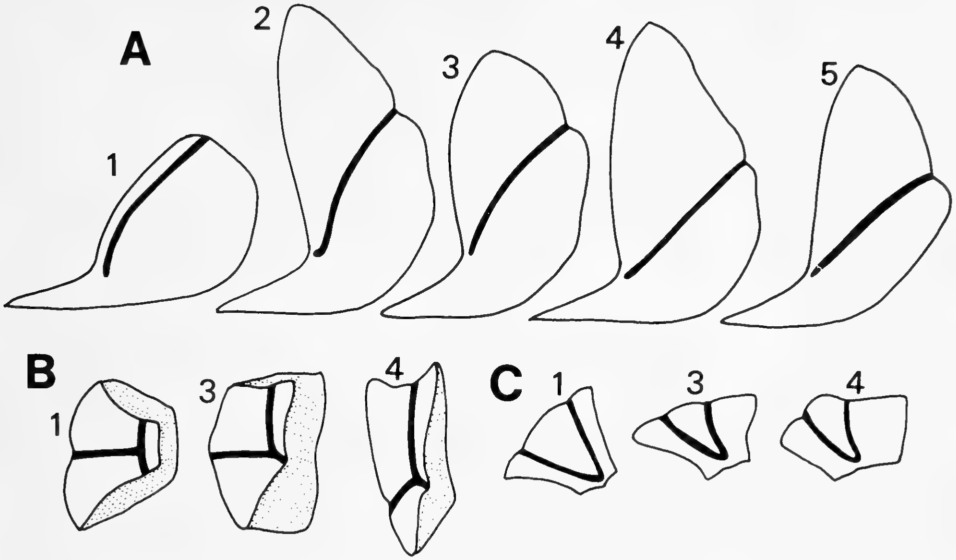


Fig. 2. Differences between the right paranuchal (A), left marginal (B) and left postnasal plates (C) in various phyllolepids. **1.** *Placolepis budawangensis*. **2.** *Austrophyllolepis youngi,* gen. et sp. nov. **3.** *Austrophyllolepis ritchiei* gen. et sp. nov. **4.** *Phyllolepis orvini*. **5.** *Phyllolepis woodwardi*.

which enters the PNu at its anterior extent on *Placolepis* and about midway on *Phyllolepis* (Fig. 2). The anterior median ventral plate (AMV) is known only on *Phyllolepis woodwardi* (Stensiö, 1934) being inferred to be present in *P. orvini* by Stensiö (1936, 1939) despite its absence in the east Greenland material (which I had the opportunity to examine). It is more likely that the AMV plate was variably present in the genus. All the known species of the genus *Phyllolepis* (except for *P. delicatula* Newberry) are represented by anterior ventrolateral plates (AVL) which do not show embayment for a PMV plate. Consequently the presence of a well developed PMV plate in *Austrophyllolepis* separates this genus from both *Phyllolepis* and *Placolepis*. The small 'PX' bones of Stensiö (1936: 15) in *Phyllolepis woodwardi* are too small to be a well formed PMV plate and the posteromesial margin of the AVL plates are not noticeably embayed, only slightly displaced. It is probable that these are fragments of the axial skeleton which have slipped out of a gap in the ventral wall of the trunkshield (compare with the description of the axial skeleton of *Austrophyllolepis* given below).

As the small suborbital plate (SO) of *Austrophyllolepis* has not been observed on other phyllolepids it is retained as a generic feature until further information on the cheek of other species is known. In all other respects the dermal skeleton of *Austrophyllolepis* closely resembles that of *Phyllolepis*.

Austrophyllolepis ritchiei sp. nov.

Figs 1**C**; 2A-**3**, B-**3**, C-**3**; 3-7, 14**A**, **B**; 17; 18**C**; 19**B**, **C**; 23; 25**A**.

Etymology: After Dr Alex Ritchie, Australian Museum, Sydney.

Material: Holotype NMP 160721, a complete individual preserved as a mould of both dorsal and ventral surfaces, lacking the tail. NMP 160722, NMP 160723 imperfect headshields. NMP 160726, complete juvenile armour; NMP 160729 imperfect juvenile armour. NMP 160731, imperfect juvenile in ventral view only. NMP 160736, imperfect median dorsal plate. NMP 160737, headshield with jaws and parasphenoid.

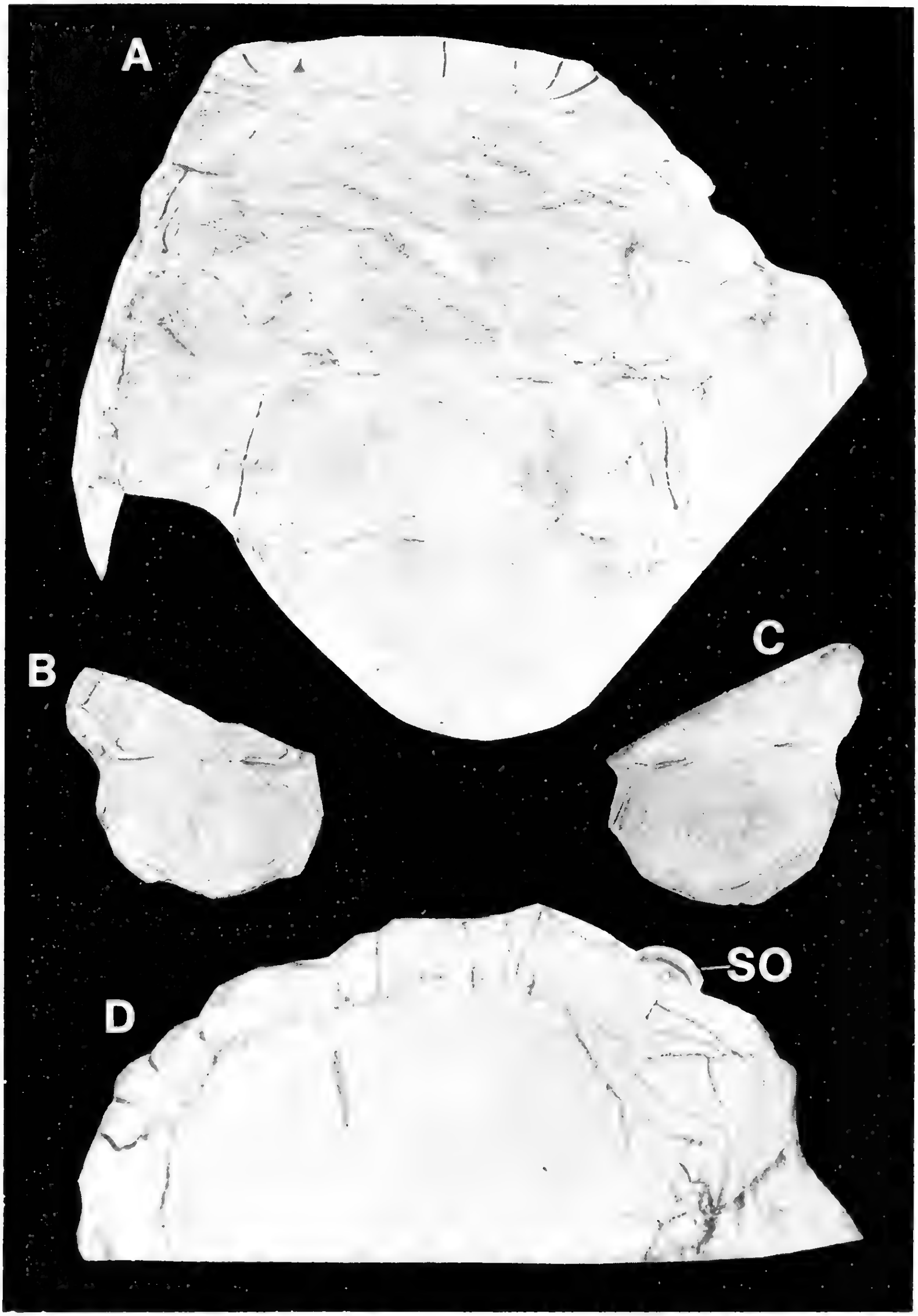


Fig. 3. Austrophyllolepis ritchiei gen. et sp. nov. **A.** Holotype, entire dermal armour in dorsal view, NMP 160721. **B, C.** Imperfect juvenile armour, dorsal view showing the internal mould **(B)** and external cast **(C)**, NMP 160729. **D.** Partial headshield in dorsal view, NMP 160722. All natural size. **A, D** are latex casts, **B** and **C** are actual specimens, all whitened with ammonium chloride. SO, suborbital plate.

NMP 160743, imperfect headshield. NMP 160748, imperfect headshield. NMP 160750, large complete individual with the tail. NMP 160753, disrupted large individual. NMP160756, imperfect headshield. NMP 160759, disrupted headshield. NMP 160763, imperfect ventral trunkshield.

Occurrence and age: From the main quarry in the lower mudstone of the Avon River Group section exposed along the upper Howqua River, Victoria (Marsden, 1976). Frasnian.

Diagnosis: An *Austrophyllolepis* having a maximum mid dorsal armour length around 200 mm. The mature dermal armour is as broad as long, being slighly broader in juveniles. Preorbital plate with an external B/L index close to 200; paranuchal plate has an external B/L index from 58-65; nuchal plates has a B/L index from 126-142; median dorsal plate has a B/L index from 122-145. Anterior ventrolateral plate with an anteromesial angle of 80-83 degrees, anterior division (the area perpendicular to the mesial margin at the anterior limit of the spinal margin) narrow, being close to 10% of the total plate length, overall B/L index around 90. Posterior ventrolateral plate has a B/L index close to 80.

Description: The form and proportions of the dermal armour can be seen in the figures, typified by the holotype (MV P160721; Figs 3**A**, 4**A**, 5). The headshield is characteristically broad with plate relationships similar to *Phyllolepis woodwardi.*

The preorbital plates (PRO) meet medially in an irregular suture. The median division of the PRO plate comprises one third of the total plate surface area. On the ventral surface the thickening below the supraorbital sensory line broadens anteriorly.

The postnasal plates (PN) have lightly convex anterior margins which are over twice the extent of the external posterior margins. As in the PRO plate there is a large thickening on the ventral surface below the V-shaped infraorbital canal groove. The anterior margin has a broad thick region of spongiose bone here, perhaps for attachment of the cartilaginous rhinocapsular. In both the PRO and PN plates there are many small pores close to the anterior margin.

The postorbital plate (PTO) is of the same shape as in *Phyllolepis;* unlike its equivalent in *Placolepis* it contacts the paranuchal plate (PNu). The junction of the infraorbital sensory line canal and the main lateral line canal is closer to the lateral margin of the plate rather than the medial margin as in *Phyllolepis.* Sometimes there is a short profundus sensory line canal present, as in NMP 160723 (Fig. 19**B**, pfc). On the ventral surface of the PTO plate there is a semicircular thickening of bone in the anterior half which I interpret as a supraorbital vault for the optic capsule (Fig 14**A**, sov; see discussion under new anatomical observations). The posterior half of the ventral surface shows a well defined ridge running parallel to the lateral margin of the plate for the posterior postorbital process of the endocranium (pr.ppo). Between this ridge and the supraorbital vault is a central thickening of bone apparently bearing a groove or foramen (it is difficult to determine from latex casts, but is thought to be a foramen in *Placolepis,* Ritchie, 1984). The position of this ridge between the orbit and the posterior postorbital process suggests that it is an ossified extension of the anterior postorbital process of the endocranium. If this is correct then the foramen would have housed the ramus hyomandibularis branch of the seventh cranial nerve, which runs to the epihyal element behind this process in euarthrodires (Goujet, 1975).

The marginal plate (MG) differs from that of *Phyllolepis* only in being slightly broader and proportionately a bit larger (Figs 2, 25). The groove for the posterior postorbital process of the endocranium continues posteriorly onto the MG plate where it terminates, as indicated by a transverse ridge meeting the groove to form a corner which enclosed the tip of the endocranial process.

The paranuchal plate (PNu) differs from that of *Phyllolepis* only in the position of

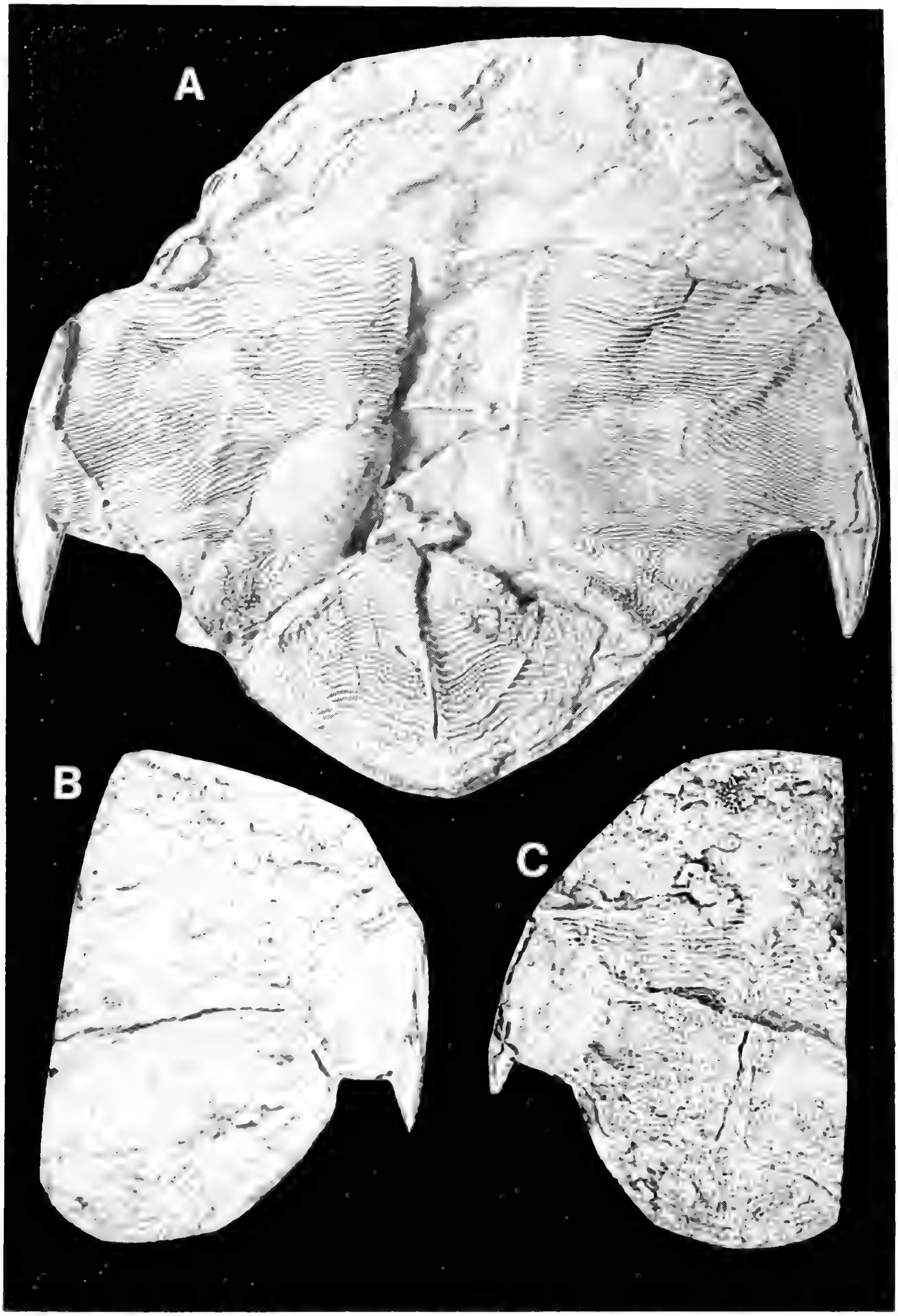


Fig. 4. Austrophyllolepis ritchiei gen. et sp. nov. **A.** Holotype, entire armour in ventral view, NMP 160721, natural size. **B, C.** Juvenile armour in dorsal (**B**) and ventral views (**C**), NMP 160726, × 3. Latex casts whitened with ammonium chloride.

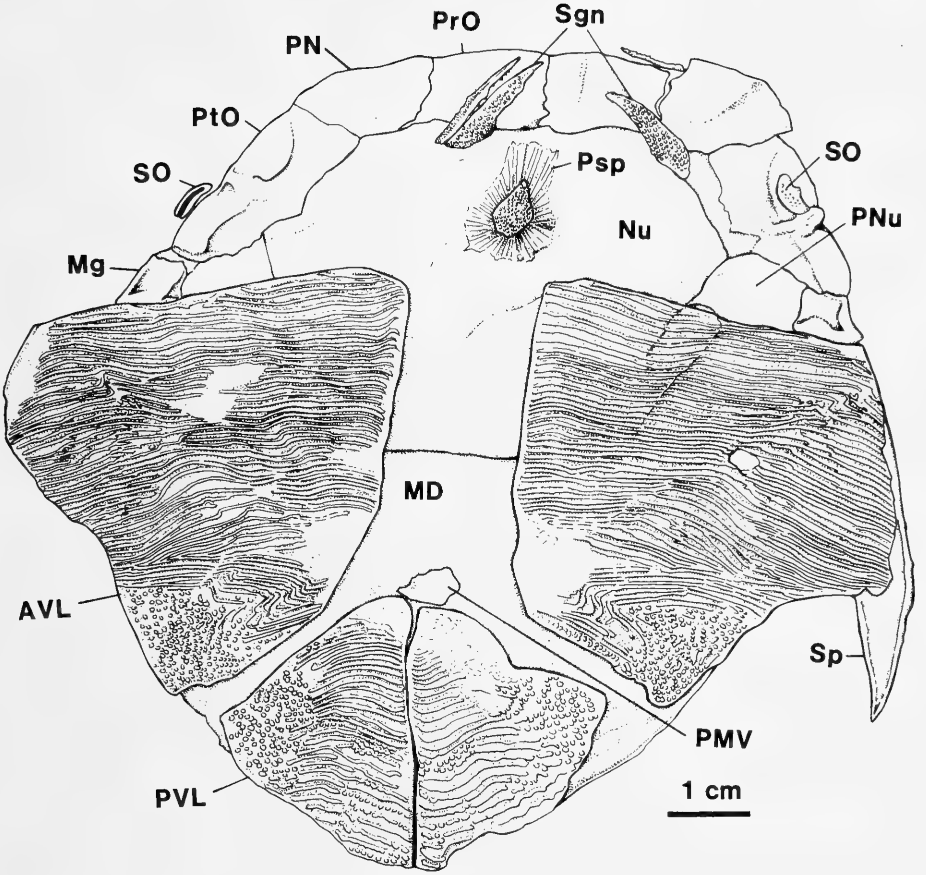


Fig. 5. Austrophyllolepis ritchiei gen. et sp. nov. Holotype in ventral view showing internal surface of head-shield, jaws and parasphenoid. AVL, anterior ventrolateral plate; MD, median dorsal plate; Mg, marginal plate; Nu, nuchal plate; PMV, incomplete posterior median ventral plate; PN, postnasal plate; PNu, paranuchal plate; Pro, preorbital plate; Psp, parasphenoid; PtO, postorbital plate; PVL, posterior ventrolateral plate; Sgn, supragnathals; SO suborbital plate; Sp, spinal plate.

entry of the main lateral line canal as diagnosed above. The ventral surface of the PNu has a prominent crista for the craniospinal process of the endocranium, as in *Phyllolepis orvini* (Stensiö, 1934: pl. 5, fig. 3; noted by Young, 1980).

The nuchal plate (Nu) has similar shape and overlap relations to that of *Phyllolepis*. The anterior margin has a slight median convexity between the supraorbital sensory line canals which meet at a point 72-76% of the total plate length from the posterior margin. External contact margins for the PN, PTO and PNu plates are clearly delineated. Only the supraorbital and central sensory line canals are clearly defined, although the posterior pit line canal may be indistinctly present. The ventral surface of the nuchal plate is slightly depressed centrally without a conspicuous longitudinal median groove as in *Phyllolepis orvini* (Stensiö, 1934: 46), although a broad median depression may sometimes be present (e.g. holotype, Fig. 4**A**).

The median dorsal plate (MD) is broader than long with the posterolateral corners

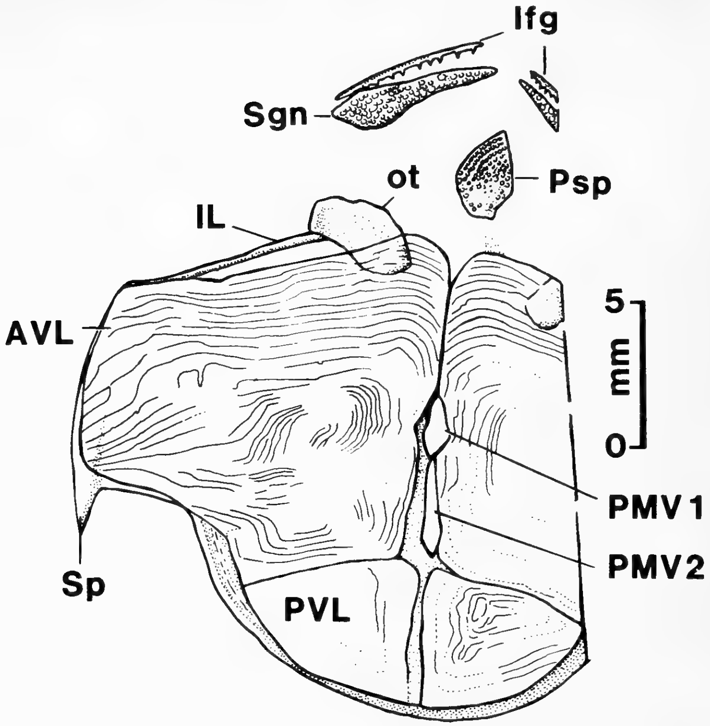


Fig. 6. Austrophyllolepis ritchiei gen. et sp. nov. Juvenile armour in ventral view showing the abnormal development of two median ventral plates. NMP 160726. AVL, anterior ventrolateral plate; Ifg, inferagnathal; IL, interolateral plate; ot, otolith; PMV1,2, posterior median ventral plates; Psp, parasphenoid; PVL, posterior ventrolateral plate; Sgn, supragnathal; Sp, spinal plate.

situated at approximately half the plate length. The anterior margin is straight with the anterolateral margin meeting at an angle of 110 degrees when undistorted. The ventral surface is smooth with a slightly thickened rim, lacking a median groove.

The anterior dorsolateral plate (ADL) is slightly shorter and broader than that of *Phyllolepis*. The anterior face of this plate has a broad flange for the PNu plate, typical of actinolepidoid euarthrodires. The ADL plate is slightly broader than long with the external ornamented surface having a B/L index ca 10 (Fig. 3**B, C**).

The anterior lateral plate (AL) is of similar shape to that of *Phyllolepis*. The proportion of the B:L of the mesial margin is from 85-100, with overall B/L index close to 57. The anteromesial angle is 120°.

The spinal plate (Sp) has small, broad lateral spines. About 25% of the spinal plate extends posterior to the AL plate.

The interolateral plate (IL) is very similar to that of *Phyllolepis orvini* (Stensiö, 1936: 42), differing slightly by the even curvature of the anterior margin. There is a well-defined ridge at the junction of the anterior concave face and the smoothly convex dorsal surface.

The anterior ventrolateral plate (AVL) of *Austrophyllolepis* is characterized by the posteromesial notch for the PMV plate (Figs 5, 7). In *A. ritchiei* there is an anteromesial angle of 80° with a posteromesial angle (extrapolating the margins at the notch for the posterior median ventral plate) of 64°. The lateral margin which meets the spinal plate

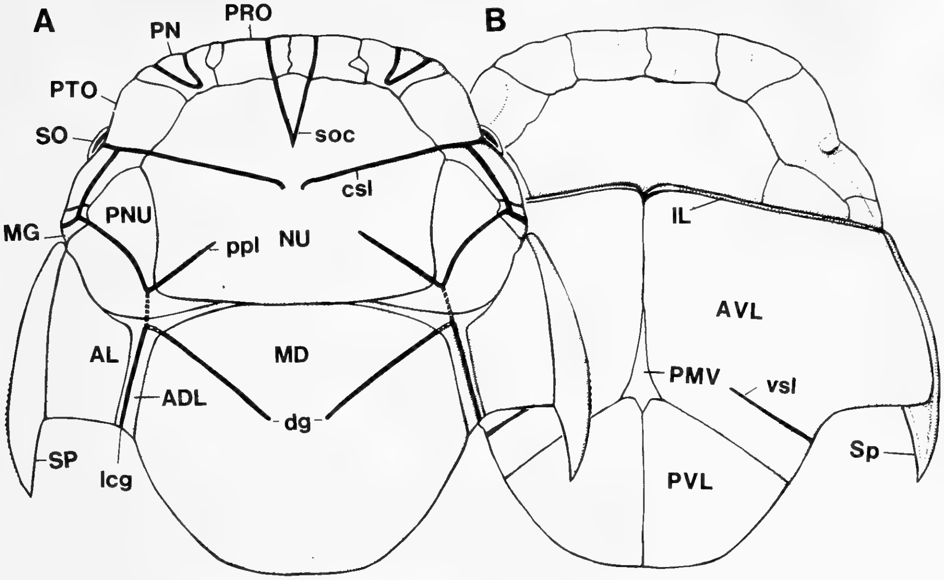


Fig. 7. Austrophyllolepis ritchiei gen. et sp. nov. Restoration of the dermal armour in **A**, dorsal and **B**, ventral views. ADL, anterior dorsolateral plate; AL, anterior lateral plate; AVL, anterior ventrolateral plate; csl, central sensory line canal; dg, dorsal sensory line canal; IL, interolateral plate; lcg, main lateral line canal; MD, median dorsal plate; Mg, marginal plate; Nu, nuchal plate; pmc, postmarginal sensory line canal; PMV, posterior median ventral plate; PN, postnasal plate; PNu, paranuchal plate; ppl, posterior pit-line canal; PRO, preorbital plate; PTO, postorbital plate; PVL, posterior ventrolateral plate; SO, suborbital plate; Sp, spinal plate; vsl, ventral sensory line canal.

is approximately 55% of the plate length. The anterior division of the plate is the area from the anterior limit of the plate to the transverse line crossing the anterolateral corner, perpendicular to the mesial margin. The length of this region is approximately 10% of the plate length. Total B/L index for large AVL plates is ca 90 whereas for juveniles this may be ca 97.

The posterior ventrolateral plate (PVL) is broader than long for juveniles (NMP 160726 B/L index is 124) the mature B/L index is ca 78. The posterior division of the lateral margin is quite convex.

The posterior median ventral (PMV) plate is lanceolate with a B/L index ca 60. One juvenile specimen, NMP 160726, shows two median ventral plates between the AVL plates (Fig. 6). The posterior element is narrow and lanceolate in form like the PMV plate of mature individuals. The anterior element is proportionately broader and is situated midway between the mesial margins of the AVL plates which contact each other anterior to the median bones. This precludes the possibility of the anterior plate in NMP 160726 being an AMV plate homologous to that of *Phyllolepis woodwardi* or euarthrodires. It is probable that this is an abnormality as sometimes occurs in the fractionation of plates in *Bothriolepis canadensis* (Stensiö, 1948: 262).

Austrophyllolepis youngi sp. nov.

Fig 2A-**2**; 9-13; 16; 18**A**, **B**; 19**A**; 20; 21; 22, 25**B**.

Etymology: After Dr Gavin Young, Bureau of Mineral Resources, Canberra.

Material: Holotype NMP 160718, complete individual preserved as a mould of both

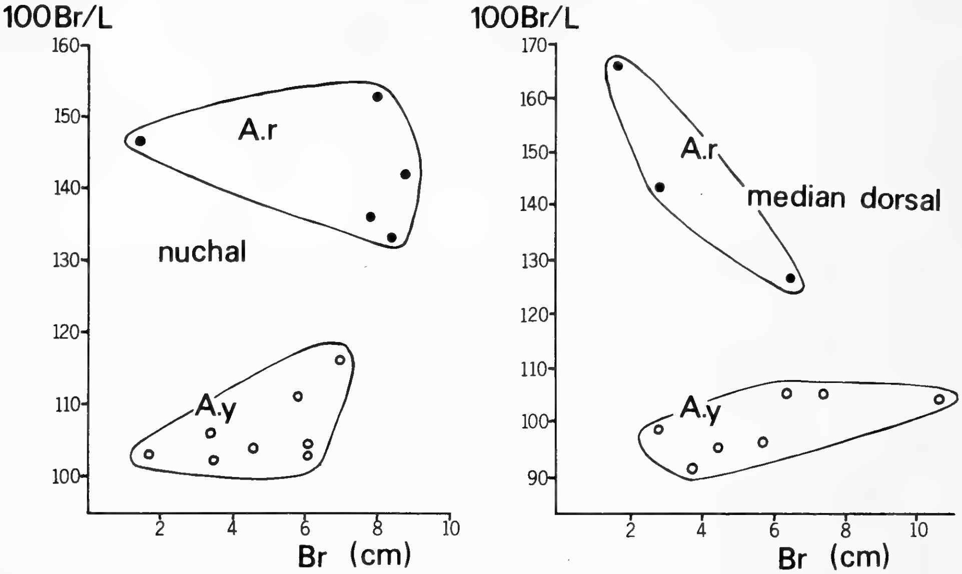


Fig. 8. Graphic representation of proportional differences between the nuchal and median dorsal plates of *Austrophyllolepis ritchiei* (A.r) and *A. youngi* (A.y) for all stages of growth. Vertical parameter is the breadth/length index, horizontal axis is plate breadth in centimetres.

dorsal and ventral surfaces (Figs 9, 10). Relatively complete individuals: NMP 160719, NMP 160720, NMP 160724, NMP 160725, NMP 160727, NMP 160730, NMP 160747, NMP 160749, NMP 160751, NMP 160752. NMP 160733, imperfect headshield. NMP 160739, portion of ventral surface. NMP 160740, imperfect ventral surface. NMP 160741, imperfect median dorsal plate. NMP 160746, imperfect ventral surface with tail and pelvic girdle. NMP 160756, imperfect headshield, portion of ventral surface of trunkshield.

Occurrence and age: From the main quarry and in the higher horizons above at Mt Howitt, in the lower mudstone of the Avon River Group exposed along the Bindaree section (Marsden, 1976).

Diagnosis: A slender *Austrophyllolepis* having a maximum mid-dorsal armour length up to 150 mm. The mature armour is longer than broad with a B/L index close to 80. Preorbital plate with an external B/L index from 90-140; paranuchal plate has an external B/L index from 45-52; nuchal plate has a B/L index from 100-112; median dorsal plate has a B/L index from 96-108. Anterior ventrolateral plate with an anteromesial angle around 70°, anterior division of plate around 23% of the plate length, B/L index close to 70. Posterior ventrolateral plate with a B/L index from 67-72.

Remarks: Austrophyllolepis youngi is distinguished from *A. ritchiei* only by the proportions of the dermal armour (Figs 8, 25), specifically the preorbital, paranuchal, nuchal, median dorsal, anterior and posterior ventrolateral plates. Although the ornament appears to be more finely developed in some specimens of *A. youngi* relative to *A. ritchiei* it is not a distinguishing feature for the species as a whole. The hypothesis that these two forms are sexual dimorphs of the one species is difficult to test. Sexual dimorphism in placoderms is only positively known in ptyctodontids where the males possess dermal clasping elements (Miles, 1967a; Ørvig, 1960; Miles and Young, 1977). Where large numbers of placoderms in various growth stages are known (as for example the

Escuminac Bay *Bothriolepis canadensis*) armour proportions are apparently not dimorphic, although this question requires a detailed biometric survey. The unusual pelvic girdle of *Austrophyllolepis* shows similarities to the pelvic girdle of primitive male chondrichthyans, such as *Cobelodus* (Zangerl, 1981). Specimens which show the long propterygial element belong to both *A. ritchiei* (NMP 160750) and *A. youngi* (NMP 160732, 160746; Figs 21, 22) which precludes the possibility of these two forms being sexual dimorphs of the same species, although it is feasible that the few specimens displaying the pelvic girdle represent males of each species. Unfortunately there are too few specimens with the pelvic girdle preserved to demonstrate whether the propterygial element is really a clasping organ or an extension of the pelvic fin. *A. ritchiei* appears to be present at Freestone Creek without *A. youngi*, supporting the view that these are separate species, although further work on the Freestone Creek material is necessary to confirm this opinion. In view of the absence of claspers in most placoderms (excluding ptyctodontids) it is safer to accept the latter explanation.

Description: Characteristic features of individual plates for the genus *Austrophyllolepis* along with specific features of *A. ritchiei* were given above. The following description merely summarizes proportional differences for plates which can be distinguished from *A. ritchiei.*

The preorbital plate (PRO) is characteristically narrower than for *A. ritchiei*, and in the holotype (Figs 9, 10) shows a more tubercular ornament. The supraorbital canal appears to run closer to the mesial margins of the PRO plates at the Nu margin than in *A. ritchiei.* In juveniles such as NMP 160733 (Fig. 11**A, C**) these canals converge at the posteromesial corners of the PRO plates.

The postnasal plate (PN) has a slightly larger external posterior margin than for the previous species, the ratio of this margin over the anterior margin being close to 44 for *A. ritchiei* and from 50-57 for *A. youngi.*

The postorbital plate (PTO) is indistinguishable between the species, although some examples of *A. youngi* display a finer ornament (e.g. NMP 160718, Fig. 9; NMP 160724, Fig. 11**D**; NMP 160747, Fig. 11**B**).

Aside from the proportions given in the diagnosis the only distinguishing feature of the paranuchal plate (PNu) of *A. youngi* is the slightly more acute angle of the anterior apex (compare Figs 4**A** and 9**B**).

The nuchal plate (Nu) of *A. youngi* is distinctly narrower and tapers more posteriorly, and on some specimens lacking ornamentation on the flanks between the central sensory line canal and the posterior pit line canal (NMP 160718, Figs 9**A**, 10; NMP 160720, Fig. 11**B**; NMP 160724, Fig. 12**B**; NMP 160727).

The median dorsal plate (MD) of *A. youngi* may also show regions on the flanks devoid of ornament (NMP 160718, Figs 9**A**, 10, to a lesser extent NMP 160725) but not consistently (NMP 160747, Fig. 12**A**). In some specimens there is a median dorsal ridge present, although this may only be an artifact of preservation (e.g. NMP 160718, Fig. 9**A**; 160725, Fig. 12**B**).

The anterior dorsolateral (ADL), interolateral (IL) and anterior lateral (AL) plates of *A. youngi* are virtually indistinguishable from those of *A. ritchiei.* The spinal plates (Sp) of *A. youngi* project beyond the AL plate for up to 37% of their total length (Fig. 11**D**), significantly more than for *A. ritchiei.*

The anterior ventrolateral plate (AVL) of *A. youngi* is readily distinguished from that of *A. ritchiei* by the proportions and angles stated in the diagnosis.

The posterior ventrolateral plate (PVL) is narrower than for *A. ritchiei* with a B/L index from 60-72.

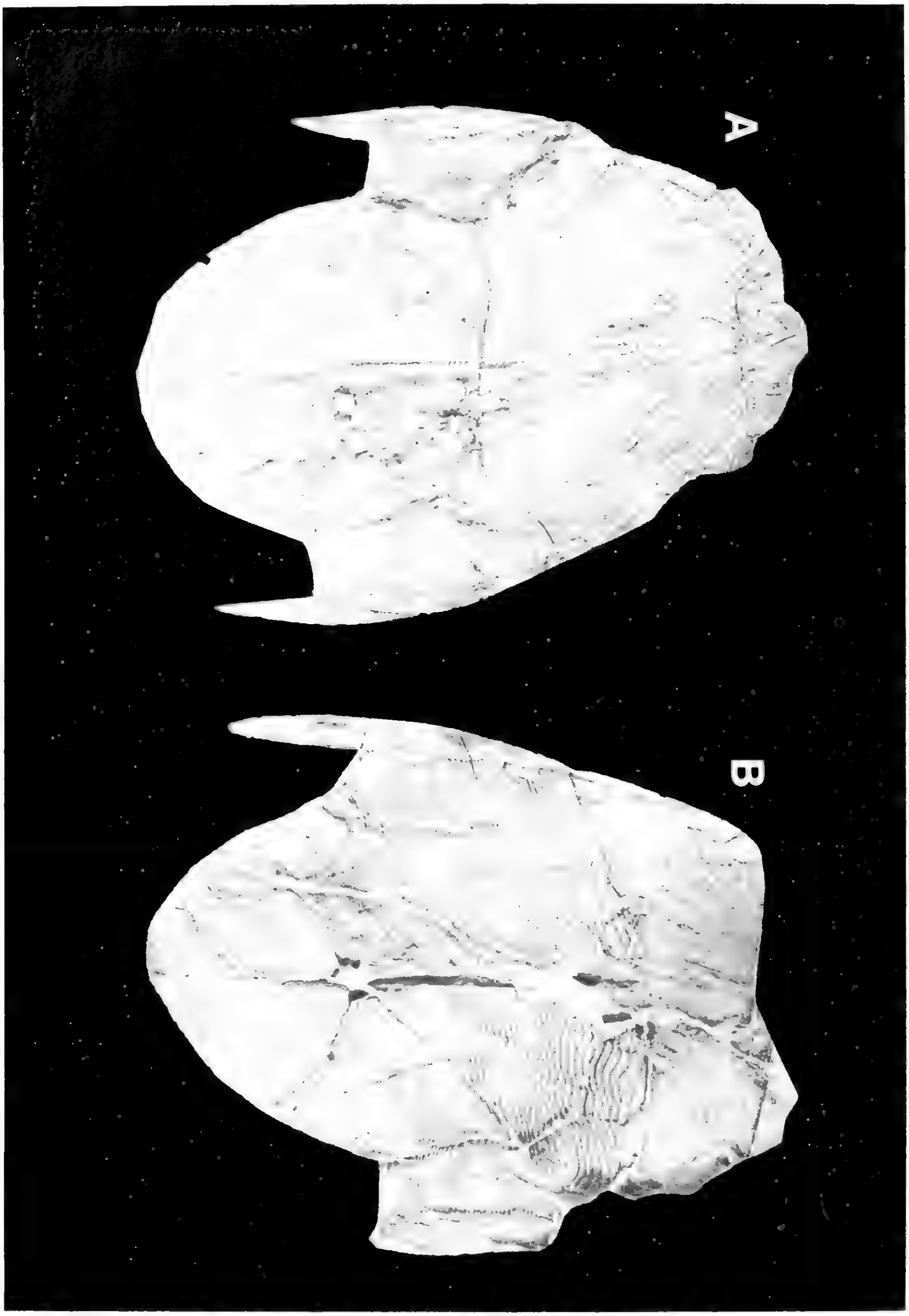


Fig. 9. Austrophyllolepis youngi gen. et sp. nov. Holotype, entire dermal armour in **A,** dorsal and **B,** ventral views. NMP 160718, latex cast whitened with ammonium chloride, natural size.

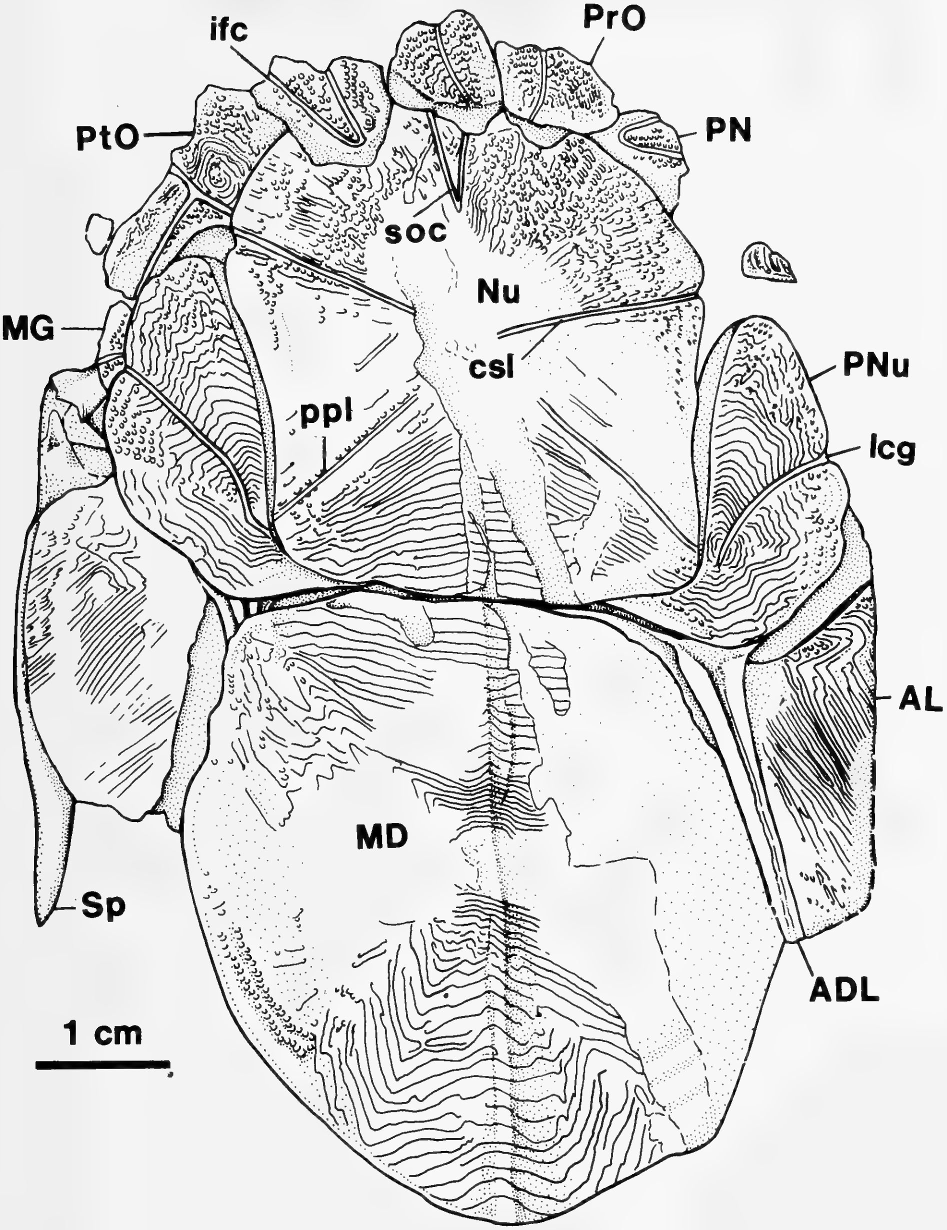


Fig. 10. Austrophyllolepis youngi gen. et sp. nov. Holotype armour in dorsal view, NMP 160718. Abbreviations as for Fig. 7.

NEW ANATOMICAL OBSERVATIONS

Headshield and Endocranium: The only observation worthy of note concerning the skull roof pattern of *Austrophyllolepis* is the infrequent presence of small plates between the PRO and PN plates (NMP 160721, NMP 160723; Figs 3**A**, 7**A**). These small plates probably result from fragmentation of larger adjacent plates.

The ventral surface of the headshield (Fig. 14) is characterized by the peripheral ridges and grooves which outline the dorsal surface of the endocranium, as in euarthrodires (Miles and Westoll, 1968) and antiarchs (Stensiö, 1948). The supraorbital vault (sov) is restricted to the anterior half of the PTO plate, thus differing from most placoderms where it extends onto the PRO. Posterior to the supraorbital vault on the PTO plate is a central thickening of bone (pr.ant) to which the small cheek plate (SO) firmly attaches. The posterior half of this plate bears a well-defined crista for the posterior postorbital process of the endocranium (pr.ppo). Lateral to this crista is a smooth region of bone which decreases in thickness near the margin. The extent of the postorbital process is clearly indicated by the ventral recess on the MG plate. The PNu plate possesses a short but well-defined paranuchal crista (cr.PNu) for the craniospinal process of the endocranium (pr.csp). The lateral line canal is sometimes discernible on the ventral surface by a low ridge (ri.lc). The anterior plates of the headshield are devoid of features on their ventral surfaces apart from the thickenings of bone below the laterosensory canals. The postethmoid region of the endocranium probably extended to the limit of the dermal exocranium, as suggested by the presence of many small pores at the anterior margin of the PRO and PN plates. As discussed above, the position of the rhinocapsular bone (rh, Fig. 15) was presumably directly anterior to the PRO plates, and anterolateral to the PN plates. This is the case for broad-shielded actinolepidoids such as *Aggeraspis* (Gross, 1962) and phlyctaenioids such as *Gaspeaspis* (Pageau, 1969).

The form of the endocranium can be reconstructed from the features of the ventral surface of the skull roof described above (Figs 14**B**; 15**B**). The anterior postorbital process (pr.ant) is weakly developed as in most euarthrodires (e.g. *Dicksonosteus,* Goujet, 1975; *Buchanosteus,* Fig. 15**C**; after Young, 1979). The posterior postorbital process (pr.ppo) is well produced, as for all euarthrodires, although it cannot be determined whether there is a single process in this region or a bifid structure with a paravagal fossa. The cucullaris fossa (cuc.f) is long relative to the size of the endocranium, extending almost half the total length.

The endocranium of phyllolepids was undoubtedly cartilaginous as suggested by Stensiö (1936, 1969) and Denison (1978). No bone is present under the headshield of the Mt Howitt specimens, despite the delicate preservation of the gnathalia and parasphenoid. The absence of dermal bones normally associated with the rhinocapsular, such as the rostral and pineal plates, indicates that the snout consisted of a soft rostrum, more likely to be shorter and broader than in Stensiö's reconstruction (1963: fig. 3**B**).

In most of the *Austrophyllolepis* specimens with the ventral aspect of the headshield preserved there are two dense calcareous bodies situated close to the centre of the headshield oriented slightly anterolaterally, but symmetrical about the midline (Figs 4**A**, **C**; 9**B**; 11**C**, **D**; 12**C**; 14**A**; 15; 17; 18**C**; 20**C**). They are calcareous as they dissolve in weak hydrochloric acid, and have a similar mineralized appearance to the bone of the plates. In cross section they are compressed, flat dense bodies. Imperfect specimens indicate that they are not hollow, and compression of the anterior ventrolateral plates around these structures testifies to their solidity. There is no surface ornamentation although some specimens have transverse ribbing somewhat radially directed (e.g. NMP 160731, Fig. 18**C**; NMP 160737, Fig. 17). In life these structures were internal,

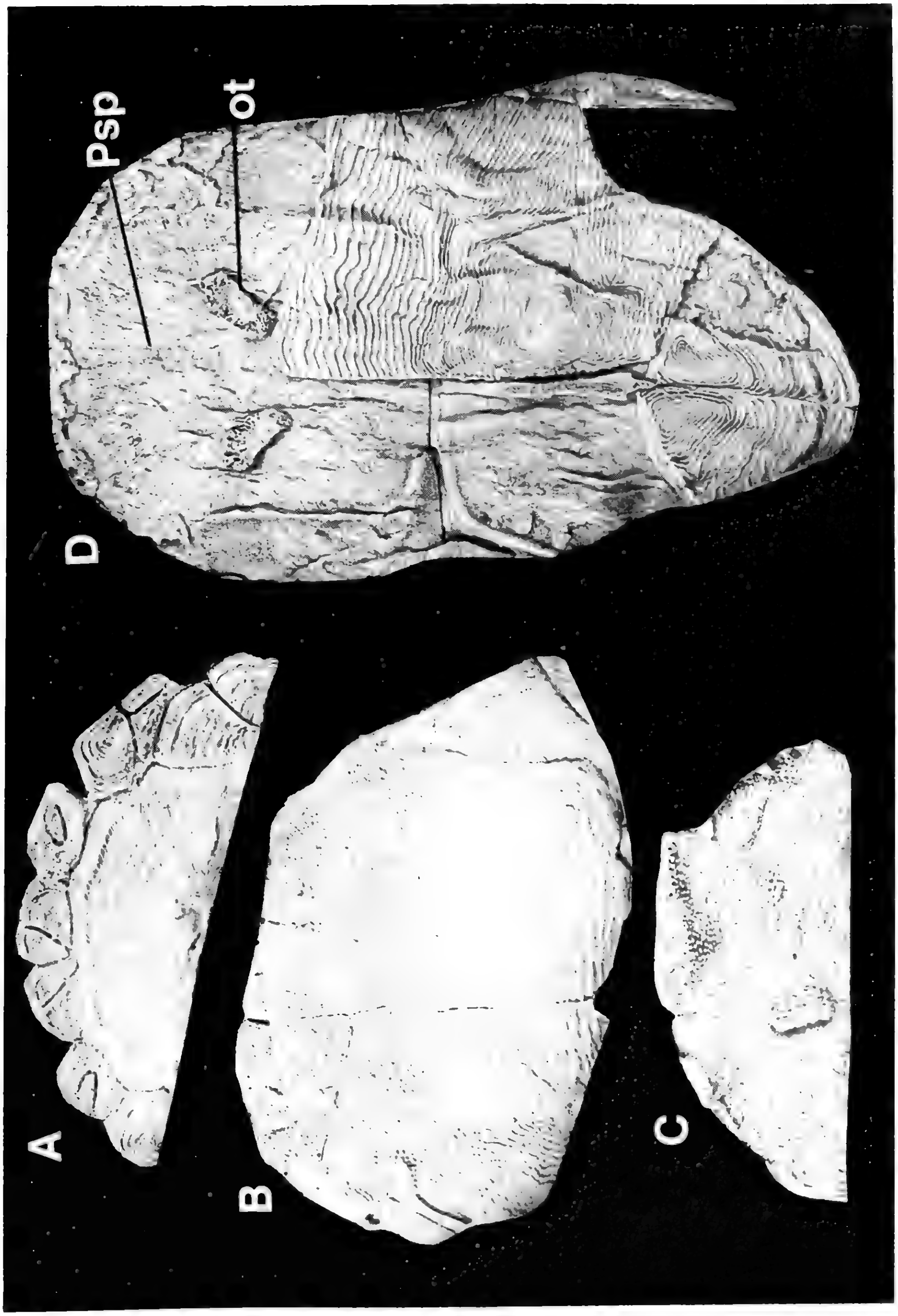


Fig. 11. Austrophyllolepis youngi gen. et sp. nov. **A, C,** juvenile partial headshield in dorsal and ventral views, NMP 160733, × 2. **B,** slightly disrupted headshield in dorsal view, NMP 160720, natural size. **D,** ventral view of armour with otoliths (ot) and parasphenoid (Psp) preserved, NMP 160725, × 2. Latex casts whitened with ammonium chloride.

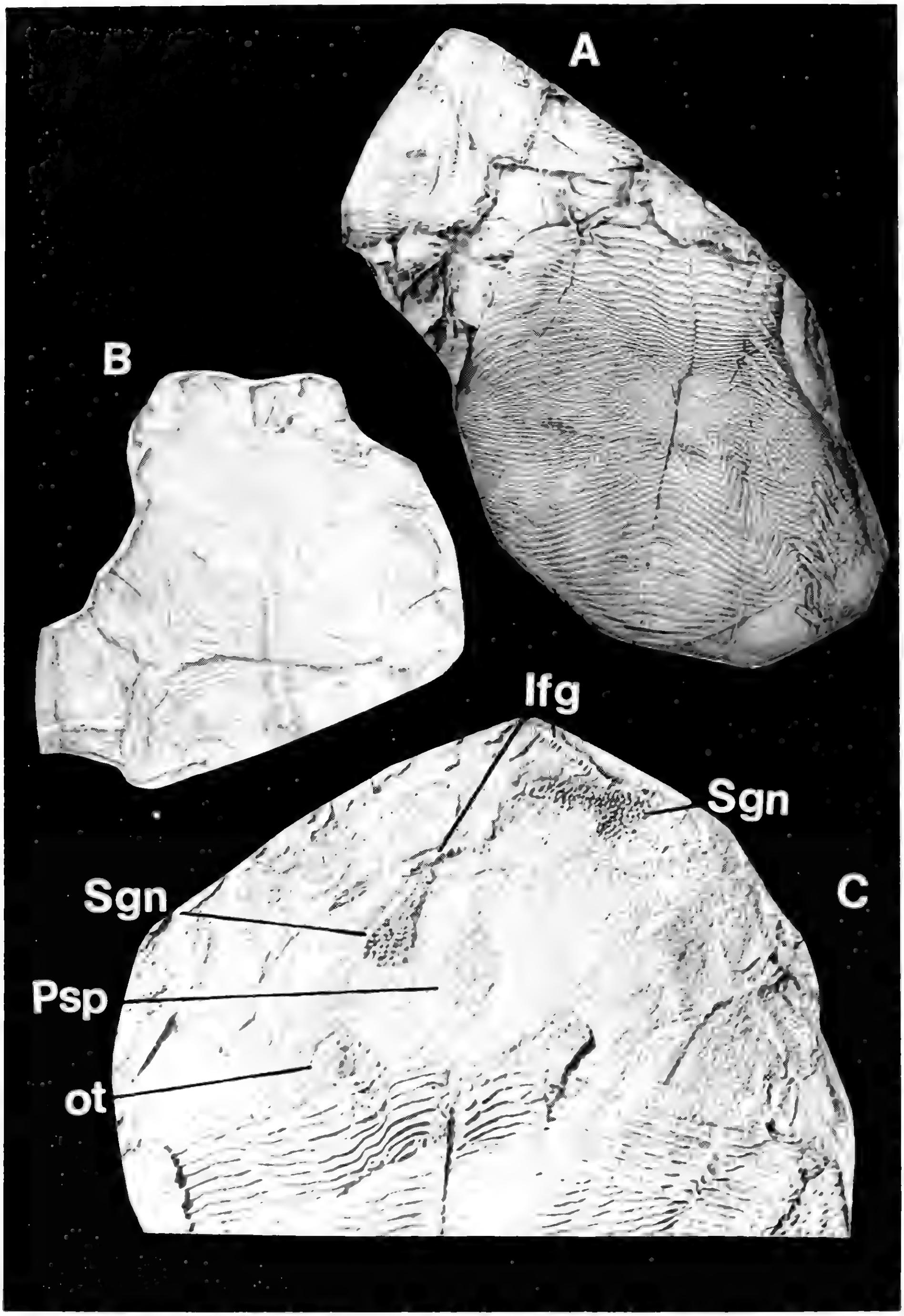


Fig. 12. Austrophyllolepis youngi gen. et sp. nov. **A,** imperfect armour in dorsal view, NMP 160747, natural size. **B,** headshield in dorsal view, NMP 160724, natural size. **C,** ventral aspect of headshield. NMP 160724. Ifg, inferagnathal; ot, otolith; Psp, parasphenoid; Sgn, supragnathal. Latex casts whitened with ammonium chloride

and their position corresponds well to the estimated location of the saccular cavities in *Buchanosteus* (Young, 1979), *Kujdanowiaspis* (Stensiö, 1963), and other euarthrodires with dorsal saccular thickenings (e.g. *Stuertzaspis,* Fig. 15). I regard these calcareous bodies to be otoliths secreted inside the sacculus of each membranous labyrinth. Otoliths have not been previously recorded in placoderms although they are known in acanthodians (Miles, 1973) and primitive osteichthyans (Long, 1982a). Elasmobranchs secrete small particles together to form statoconia, allowing entry of the grains into the saccular and other cavities by the open endolymphatic ducts (Lowenstein, 1971). In *Austrophyllolepis* there is no indication of an open endolymphatic duct on the paranuchal plates as in other placoderms. This evidence supports the idea that *Austrophyllolepis,* and perhaps all phyllolepids, secreted statoliths rather than statoconia. The otoliths are present in the smallest specimen (NMP 160726; Figs 3, 6) where they are proportionately much larger than for mature individuals.

Jaws and parasphenoid: The gnathalia and parasphenoid are well preserved in several specimens of *Austrophyllolepis* (NMP 160719, NMP160720, NMP160721, NMP 160724, NMP 160725, NMP 160726, NMP 160727, NMP 160731, NMP 160733, NMP 160734, NMP 160737, NMP 160750). There is a single pair of upper tooth plates which are opposed by narrow inferognathals. The parasphenoid is a broad denticulated bone situated between the midpoint of the supragnathals.

The supragnathals (Sgn, Figs 4**A, C**; 5; 6; 11**C**; 12**C**; 14**B**; 16; 17; 18**B, C**; 20) are broadest posteriorly with narrow apices which almost meet in the midline. There are numerous conical teeth arranged in radial growth rows, the largest teeth being at the anterior division. The teeth are sharply pointed, not blunt tubercles, numbering up to 160 in mature individuals. Along the margin of the toothed surface of each Sgn is a narrow edentulous rim. The dorsal surface of the Sgn is known from one specimen only (NMP 160734), where it is smoothly concave at the broad posterior end.

Only one specimen shows the complete series of upper jaw ossifications present (NMP 160737, Fig. 17); presumably this is only developed at maturity. Posterior to the Sgn is a broader semicircular ossification which is firmly attached to a third element bearing a median thickening. This last component can be identified as the quadrate (quad, Fig. 17) because of its posterior position on the palatoquadrate and the median ridge, common on the quadrate of euarthrodires (Miles and Dennis, 1979; Miles, 1971; Dennis and Miles, 1979, 1980). The large flat central ossification between the quadrate and Sgn is the median division of the palatoquadrate or metapterygoid, primitively ossified in placoderms (Schaeffer, 1975; Goujet, 1975). In euarthrodires the jaw suspension is autostylic with attachment of the posterior end of the palatoquadrate complex to the dermal cheek bones. As the cheek of *Austrophyllolepis* was completely reduced save for one small bone, it is likely that the palatoquadrate complex was attached to the ventral surface of the endocranium, with articulation of the meckelian cartilage at the quadrate not being supported by a hyomandibular element. If an epihyal was present it must have been cartilaginous, and extended from the centre of the PTO plate posteriorly to the soft cheek region. Corresponding to the extreme dorsoventral compression of the phyllolepid body is the broad, flat metapterygoid for insertion of the adductor mandibulae.

The inferognathals (Ifg, Figs 4**A, C**; 5; 6; 12**C**; 16; 17; 18**B**; 20) bear teeth throughout their extent. There is one row of pointed teeth along the biting edge with a narrow cluster of teeth at the posterior end. In cross section the Ifg is divided into two laminae meeting at right angles: a dentigerous dorsal blade and a smooth vertical lamina which covered the anterior edge of the meckelian cartilage. The non-biting section of this cartilage which extended from the posterior of the Ifg to the quadrate was not ossified, even the articular was cartilaginous. This is an unusual condition because

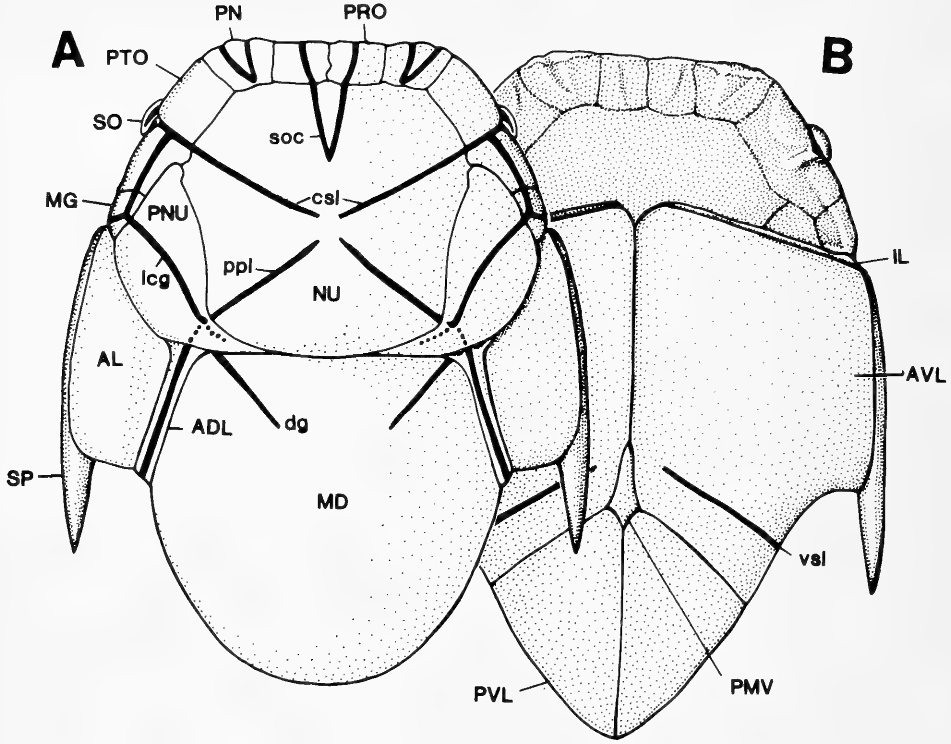


Fig. 13. Austrophyllolepis youngi gen. et sp. nov. Restored dermal armour in **A**, dorsal and **B**, ventral views. Abbreviations as for Fig. 7.

if the quadrate was ossified it would require equal strength in the articular region for maximum efficiency of the bite.

The parasphenoid (Psp, Figs 4**A**, **C**; 5; 6; 7**B**; 11**C**, **D**; 12**C**; 14**B**; 17; 18**C**; 20) is a broad bone with a subtriangular shape similar to that of *Buchanosteus* (Young, 1979). There is a broad edentulous margin around the central toothed area which encloses a small, paired buccohypophysial foramen (bhf), seen on the holotype of *A. ritchiei.* The anterior and lateral extensions of the margin are incised with radial striae in mature individuals, in juveniles there is no development of the smooth margin, only a toothed region. The lateral groove of the Psp is seen clearly as an indentation of the broad edentulous margin at the level of the buccohypophysial foramen. In this respect it is not like the Psp of *Buchanosteus* (Young, 1979) or higher euarthrodires such as coccosteomorphs (Miles and Dennis, 1979; Stensiö, 1969) which have well-developed lateral grooves invading the toothed centre of the bone, or occupying most of the ventral face of the bone. The Psp in phyllolepids was situated almost in the centre of the head, unlike most euarthrodires and the rhenanid *Kosoraspis* (Gross, 1931) which have the Psp anteriorly located. From this and the relative size of the gnathalia it can be deduced that the buccal cavity of phyllolepids was quite large.

Cheek: The cheek of *Austrophyllolepis* bears a single small bone (Figs 3**A**, **D**; 4**A**; 5; 7; 13; 14**A**; 16; 18**A**, **B**; 19) which firmly attached to the central bony process on the ventral surface of the PTO plate. It is preserved on few specimens (NMP 160719, NMP 160721, NMP 160722, NMP 160723, NMP 160737) but is always small and in-

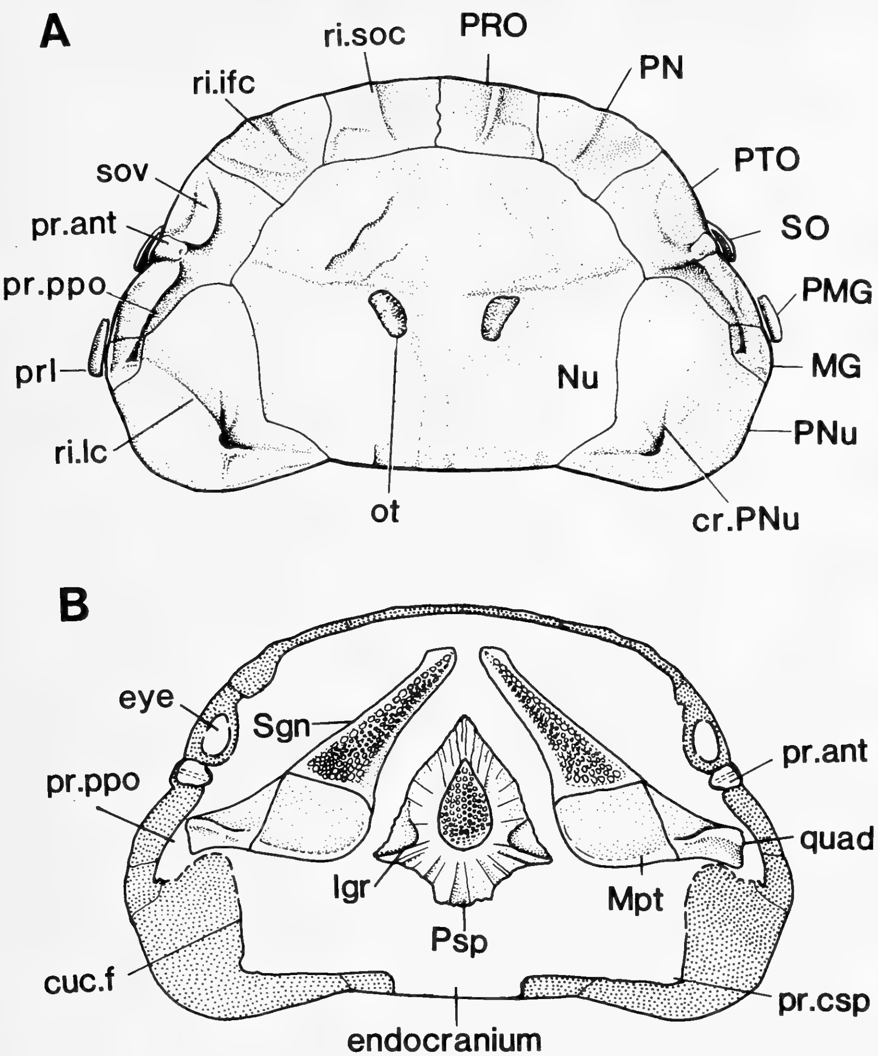


Fig. 14. **A,** restoration of the visceral surface of the headshield of *Austrophyllolepis ritchiei* gen. et sp. nov. **B,** reconstruction of the dorsal outline of the endocranium with gnathal bones and parasphenoid shown in position. cr.PNu, paranuchal crista; cuc.f; cucullaris fossa; lgr, lateral groove of parasphenoid; MG, marginal plate; Mpt, metapterygoid ossification of the palatoquadrate; Nu, nuchal plate; ot, otolith; PN, postnasal plate; PNu, paranuchal plate; pr.ant, anterior postorbital process of the endocranium; pr.csp, craniospinal process of the endocranium; prl, posterolateral corner of headshield; PRO, preorbital plate; pr.ppo, posterior postorbital process of the endocranium; Psp, parasphenoid, PTO, postorbital plate; ri.ifc, ridge below infraorbital canal; ri.lc, ridge below main lateral line canal; ri.soc, ridge below supraorbital sensory line canal; SO, suborbital plate; sov, supraorbital vault.

complete. It is difficult to homologize this bone with the suborbital (SO), postsuborbital (PSO) or submarginal (SM) plates of other placoderms because it lacks ornamentation, bears no distinct grooves for laterosensory lines and has a unique shape. The smooth surface on both sides of the bone is folded to form a double lamina with a large valley in between. It is oriented with the opening of the folded laminae on

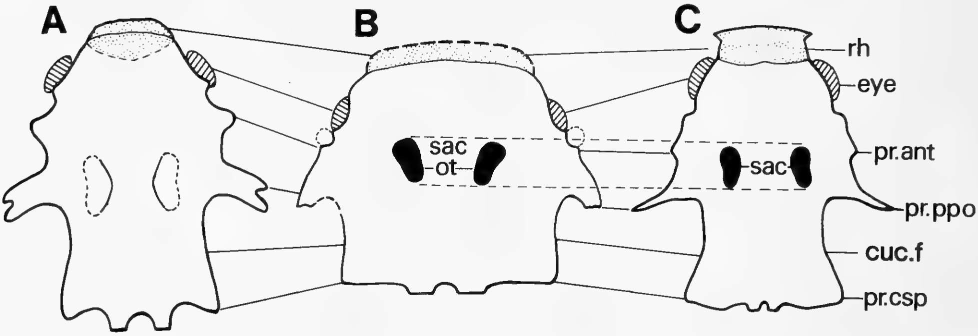


Fig. 15. Dorsal endocranial outlines of **A**, *Stuertzaspis,* (after Westoll & Miles, 1963) **B**, *Austrophyllolepis ritchiei* and **C**, *Buchanosteus* (after Young, 1979), showing the relative size of the saccular otoliths (sac ot) in *Austrophyllolepis* by comparison with the size and position of the saccular cavities (sac) of *Buchanosteus,* and their inferred position in *Stuertzaspis.* Homology of the endocranial processes is shown in relation to orbital position. Rhinocapsular regions (rh) stippled (conjectural for *Austrophyllolepis*). Abbreviations as for Fig. 14.

the dorsal side and the convex lateral side facing out from the notch in the PTO plate where the infraorbital sensory line departs the exocranium. This sensory line appears to run into the valley between the laminae of the cheek bone where the infraorbital sensory line of most placoderms divides to send a supraoral line ventrally. If this hypothesis is plausible then the cheek bone of *Austrophyllolepis* is probably a modified SO plate. The SO plate in euarthrodires and the palaeacanthaspidoid *Romundina* is situated opposite the PTO plate where the infraorbital sensory line leaves the skull roof. The PSO and SM plates are absent in phyllolepids.

An alternative explanation for the cheek bone in phyllolepids is that it could be a unique development which housed an electric organ. In Torpediformes such electric organs are located in the same position facing dorsally to stun prey swimming above the fish (Bennet, 1971). The internal area of the phyllolepid cheek bone housed the sensory line plexus where the infraorbital line probably divided into supraoral and infraorbital lines.

Postmarginal plate: In two specimens (NMP 160720, NMP 160723; Figs 19**B**, **C**; 20) there is a small bone adjacent to the MG plate. This bone is unornamented and lacks a laterosensory groove. In NMP 160720 it is clearly overlapped by the MG plate, as seen in ventral view (Fig. 20). It is possible that this bone is a small postmarginal plate (PMG) which was loosely attached to the cheek in phyllolepids. However as it is only seen on two specimens, and was not observed in the East Greenland material it cannot be confidently identified as a PMG plate. In NMP 160723 it is possible that the bone adjacent to the MG plate is actually a piece of the right IL plate which has been displaced.

Tail and axial skeleton: The tail of *Austrophyllolepis* is almost entirely preserved on NMP 160750, NMP 160751 and NMP 160732 (Fig. 22**A**), with sections of the tail preserved in NMP 160728, NMP 160746 (Figs 21; 22**B**), NMP 160752, NMP 160754 and NMP 160757. As in other placoderms perichondrally ossified neural and haemal arches surround the cartilaginous notochord (Miles and Westoll, 1968; Dennis and Miles, 1981). There is no submedian dorsal plate nor anal interseptal plate ossification. At least 40 vertebrae were present. The orientation of the tail elements is taken from the accompanying dermal armour. In NMP 160732 the armour is preserved in ventral view with the rows of Y-shaped arches having their notochordal saddles facing ven-

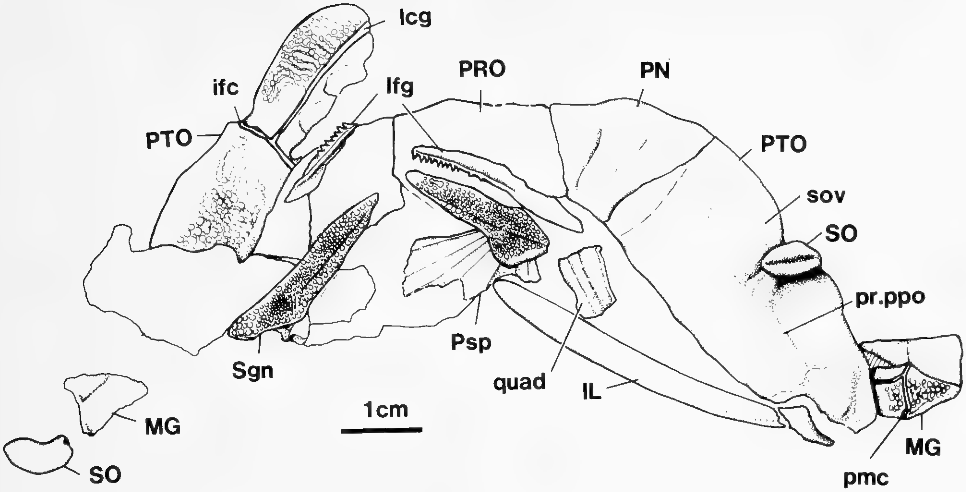


Fig. 16. Austrophyllolepis youngi gen. et sp. nov., ventral surface of slightly disrupted headshield. NMP 160719 (see also Fig. 18**B**). ifc, infraorbital sensory canal; Ifg, inferagnathal; IL, interolateral plate; lcg, main lateral line canal; MG, marginal plate; pmc, postmarginal sensory line canal; PN, postnasal plate; PRO, preorbital plate; pr.ppo, groove for posterior postorbital process of the endocranium; Psp, parasphenoid; PTO, postorbital plate; quad, quadrate; Sgn, supragnathal; SO, suborbital plate; sov, supraorbital vault.

trally, indicating that these were the haemal arches. The neural arches are paired, smaller elements which lie disrupted between the ordered rows of haemal arches.

The neural arches (neur) bear prominent anterior zygapophyses with lateral grooves on the neural spines for receiving the zygapophyses of the preceding vertebra. The saddle for the notochord is a strongly splayed cone of thin bone (n.gr). A slightly constricted neck joins the saddle to the neural arch. The neural arch elements do not vary much throughout their extent, unlike those of *Coccosteus* (Miles and Westoll, 1968) or *Ctenurella* (Ørvig, 1962).

The haemal arches (hae) comprise fused halves which meet to form a Y-shaped structure with a median groove (mg) in the confluence. The haemal spines are long, slightly compressed tubes with flared distal ends when they meet fin supports.

A cluster of additional perichondral tubes close to the dermal armour in NMP 160732 and NMP 160746 possibly represents the fin supports for a short dorsal fin behind the trunkshield. As a single dorsal fin is present on most placoderms (Denison, 1978) I have restored one on *Austrophyllolepis* (Fig. 23).

Pelvic girdle: The pelvic girdle is well preserved in NMP 160746 (Figs 19; 20**B**) and NMP 160750. It is situated immediately behind the trunkshield, and consists of two large perichondral ossifications: a broad basal pelvic plate (pel.b) and a slender propterygial element (pro). The basal plate is broadest at the proximal end where it appears to contact the PVL plate. The narrow posterior margin has a thickened articulation area for the propterygium. The lateral side of the basal plate has a distinct convex division separated in NMP 160746 from the broad proximal end by a concave anterior division. The convex division of the lateral margin bears short grooves (art) denoting serial divisions for articulation of cartilaginous pelvic fin ray elements. The anterior end of the propterygium is broader than the posterior end and has a large fossa for muscle attachment. The shaft of the propterygium narrows at the centre then expands slightly at the posterior end.

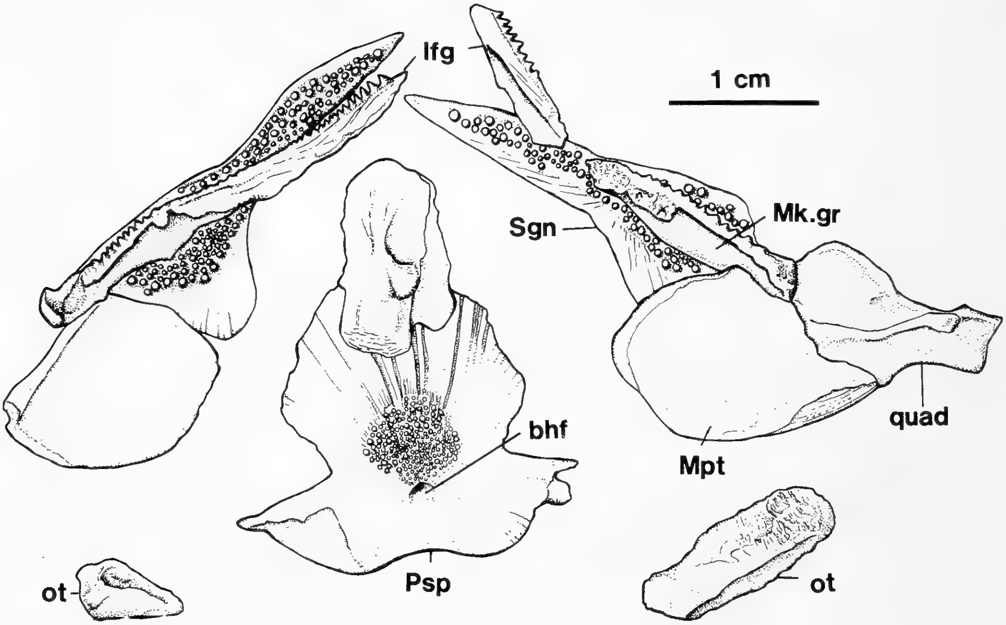


Fig. 17. Austrophyllolepis ritchiei gen. et sp. nov. Large individual showing the complete ossification series of the palatoquadrate, NMP 160737. bhf, buccohypophysial foramen; Ifg, inferagnathals; Mk.gr, groove for Meckel's cartilage; Mpt, metapterygoid; ot, otolith; Psp, parasphenoid; Sgn, supragnathal.

The pelvic girdle of *Austrophyllolepis* shows some resemblance to the male clasping organs of primitive chondrichthyans, particularly *Cobelodus* (Zangerl, 1981). As the long propterygial element of *Austrophyllolepis* is found in both species there is no case for sexual dimorphism producing the two varieties, yet it is feasible that sexual dimorphism may have occurred in both species but because there are too few specimens showing the pelvic girdle a female condition has not been observed.

COMPARATIVE ANATOMY OF PHYLLOLEPID FEATURES

Current hypotheses of placoderm interrelationships place the phyllolepids as the sister group to euarthrodires plus antiarchs (Miles and Young, 1977; Denison, 1978), as the sister group to antiarchs, euarthrodires and *Wuttagoonaspis* (Young, 1980) or as the sister group to euarthrodires (Goujet, 1984). As previous workers have taken only the form and arrangement of the armour into consideration, it is necessary to review the phylogenetic position of phyllolepids in the light of the new data provided by both *Austrophyllolepis* and *Placolepis.*

Headshield: One of the characteristic features of the phyllolepid headshield is the large Nu plate, or alternatively, if process is not invoked, undifferentiated Nu and Ce plates. A combined centronuchal plate is also known in *Wuttagoonaspis* (Ritchie, 1973), *Antarctaspis* (White, 1968; interpretation by Denison, 1978) and in an undescribed actinolepid euarthrodire from Severnaya Zemlya (Dr D. Goujet, pers. comm.). The potential for combining the Ce and Nu plates, or the loss of the Ce plates is restricted to phyllolepids, *Wuttagoonaspis* and some actinolepidoids.

A single pair of PNu plates is a synapomorphy uniting euarthrodires, antiarchs and phyllolepids according to Miles and Young (1977), and Young (1980), assuming that two pairs of PNu plates are primitive for placoderms. A single pair of large PNu

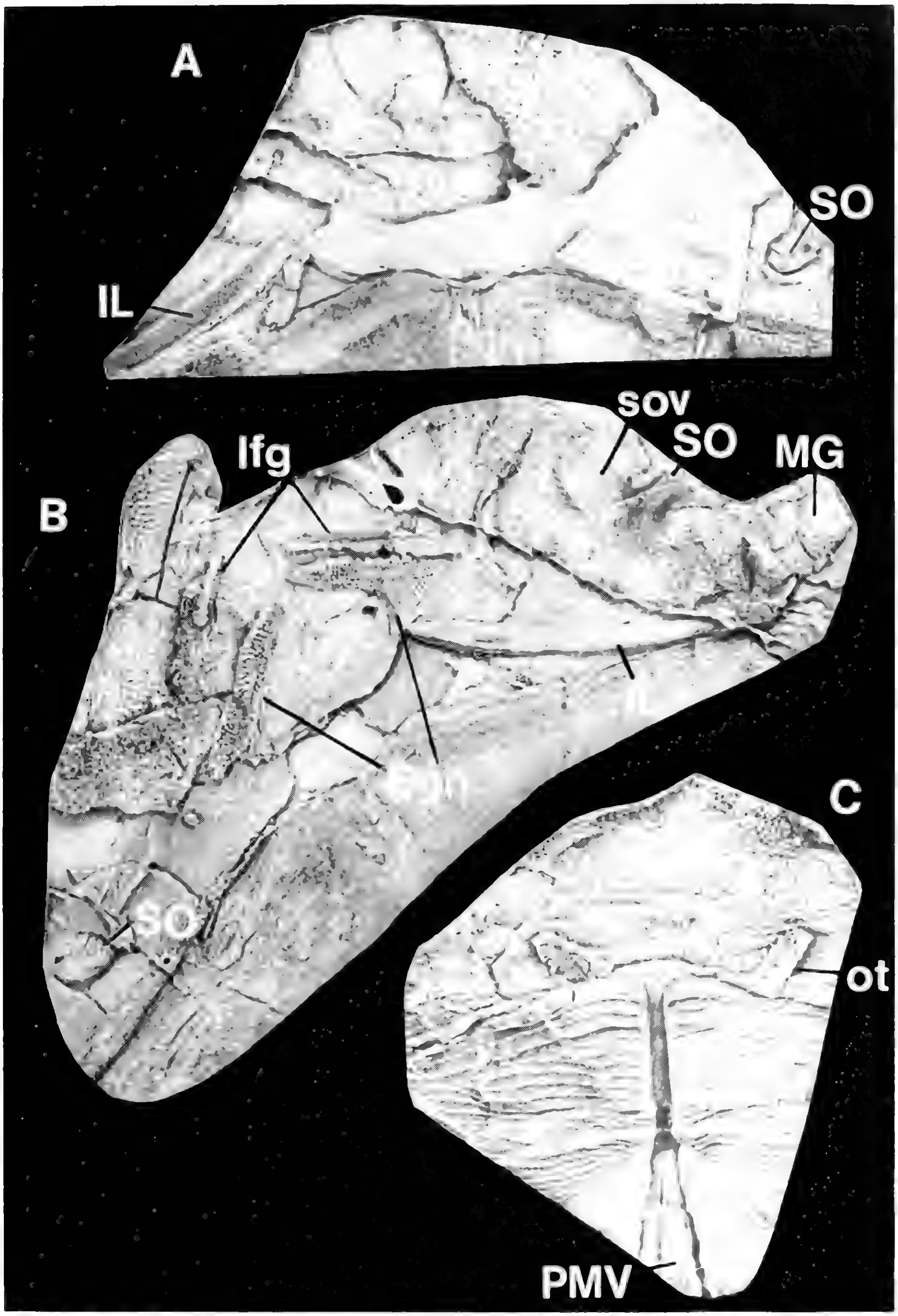


Fig. 18. **A, B.** *Austrophyllolepis youngi* gen. et sp. nov. Imperfect headshield in dorsal **(A)** and ventral **(B)** aspects, NMP 160719, natural size (see also Fig. 16). **C.** *Austrophyllolepis ritchiei* gen. et sp. nov. ventral aspect of juvenile, NMP 160731, × 2. Ifg, inferagnathal; IL, interolateral plate; Mg, marginal plate; ot, otolith; PMV, posterior median ventral plate; SO, suborbital plate; sov, supraorbital vault.

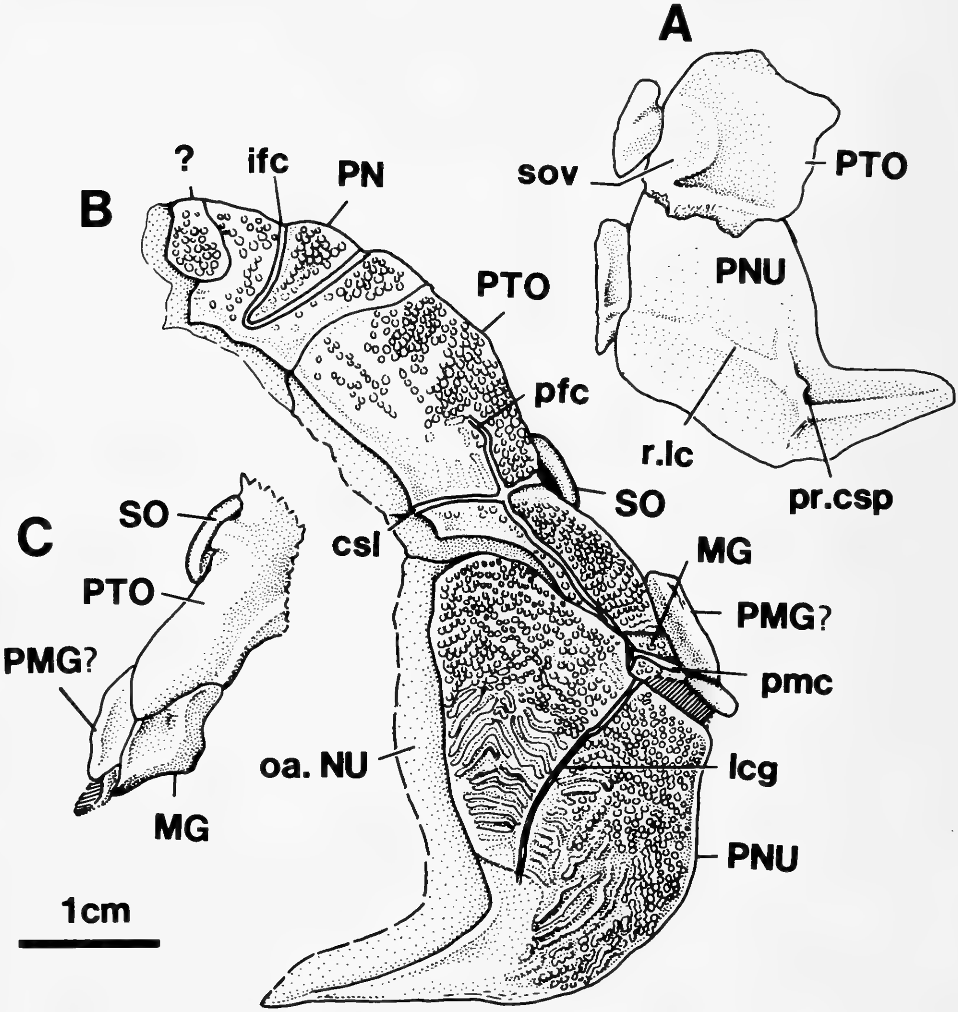


Fig. 19. **A.** ***Austrophyllolepis youngi*** gen. et sp. nov., visceral aspect of left side of headshield, NMP 160730. **B, C.** ***Austrophyllolepis ritchiei*** gen. et sp. nov., right side of headshield showing possible postmarginal plate, NMP 160723. csl, central sensory line canal; ifc, infraorbital sensory line canal; lcg, main lateral line canal; Mg, marginal plate; oa.Nu, area overlapped by nuchal plate; pmc, postmarginal sensory line canal; PMG, postmarginal plate?; pfc, profundus sensory line canal; PN, postnasal plate; PNu, paranuchal plate; pr.csp, craniospinal process ridge; PTO, postorbital plate; ri.lc, ridge underneath the lateral line canal; SO, suborbital plate; sov, supraorbital vault.

plates (covering most of the lateral occipital region of the skull roof) is a feature of phyllolepids and euarthrodires. Goujet (1984) uses the junction of the main lateral line canal with the posterior pit-line and occipital line of the PNu plate as a synapomorphy of phyllolepids and euarthrodires, presumably inferring the presence of an occipital pit line from the specimens of *Phyllolepis orvini* illustrated by Stensiö (1936: pl. 4, fig. 1; there appears to be a transverse extension of the main lateral line canal). If an occipital line was present in phyllolepids it would have transversed the neck superficially.

Paired PRO plates in mesial contact are found in ptyctodonts, some petalichthyids, the palaeacanthaspidoid *Kimaspis* (Mark-Kurik, 1973), the rhenanid *Brindabellaspis* (Young, 1980), most euarthrodires, and most phyllolepids (in *Phyllolepis orvini* they are separated). However, only in one actinolepidoid, *Actinolepis* (Mark-Kurik, 1973) and phyllolepids do the PRO plates not form part of the orbital margin, thus exhibiting a degree of variability not seen by other placoderms. *Actinolepis* and phyllolepids have the orbit confined to the PTO plate (Fig. 1).

Having a PTO plate considerably larger than the MG plate is a characteristic feature of phyllolepids and some primitive euarthrodires (most conspicuous in *Anarthraspis, Simblaspis, Proaethaspis, Baringaspis, Antarctaspis* (Denison, 1978), and in *Wuttagoonaspis* (Ritchie, 1973)). Because several advanced brachythoracid characters separate *Pholidosteus* from actinolepidoids (Young, 1981b; Dennis and Miles, 1983), its large PTO is considered to be a parallelism. The MG plates of ptyctodontids, palaeacanthaspidoids, petalichthyids and most euarthrodires are relatively large, sometimes as large as the Ce or PNu plates, and this is here taken as the plesiomorphous placoderm condition. Only on phyllolepids, *Antarctaspis* and *Wuttagoonaspis* is the MG plate exceptionally small.

PMG plates are found in euarthrodires, antiarchs and possibly phyllolepids. In primitive antiarchs the PMG is large (Zhang Guorui, 1978) becoming smaller in later forms. In primitive euarthrodires the PMG is relatively large in some taxa (actinolepidoids: *Kujdanowiaspis, Baringaspis, Proaethaspis;* phlyctaenioids: *Phlyctaenius, Groenlandaspis*, Denison, 1978), and proportionately smaller on others (*Simblaspis, Aethaspis;* Denison, 1978). In higher euarthrodires the PMG plate is universally diminished, particularly so in *Bungartius* and *Tafilalichthys.* In *Synauchenia* the PMG and SM plates are combined into one small element. Diminution of PMG size is associated with the change of position from the posterolateral corner of the skull roof to the upper part of the cheek complex. The cheek of higher euarthrodires is fixed firmly to the rest of the exocranium (Denison, 1978; Miles and Dennis, 1979). In phyllolepids the reduction or loss of the PMG plate is probably a parallelism with that of the higher euarthrodires which follow the trend of reduction of the whole dermal cheek complex. In phlyctaenioids and some actinolepidoids the PMG plate is almost completely covered by the SM plate (Goujet, 1972; 1975), and further reduction of the PMG plate would not be unusual if this trend continued in association with other modifications of the cheek.

The ventral surface of the headshield in antiarchs, euarthrodires and phyllolepids is characterized by depressions and ridges for the dorsal surface of the endocranium. In ptyctodontids and presumably petalichthyids the ventral surface of the skull roof is relatively featureless apart from the tubes for the laterosensory nerves (Miles and Young, 1977: fig. 16; Young, 1978: fig. 4; Stensiö, 1969). In *Romundina* and *Brindabellaspis* there is a combination of ridges on the peripheral dermal bones along with large pipe-like tubes for the laterosensory line nerves (Ørvig, 1975; Young, 1980). The development of dermal bone supporting the optic capsules is quite different in the various placoderm groups. In *Brindabellaspis, Romundina,* and *Macropetalichthys* there is no dermal bone rim for the optic capsules, only a recessed area on the lateral endocranial wall. In ptyctodontids there is a thickened rim for the optic capsules on the PRO, PTO and MG plates (Miles and Young, 1977). An extensive dermal thickening above the eyeball is therefore restricted to phyllolepids and euarthrodires, with the development of an extensive ventrally projecting lamina behind the eyeball being a synapomorphy of higher euarthrodires (Dennis and Miles, 1983).

Autapomorphous features of the phyllolepid headshield are: a large PN plate contacting the centronuchal area and separating the PRO and PTO plates; no orbital notches in the headshield; no dermal bones of the snout (rostral and pineal plates); no

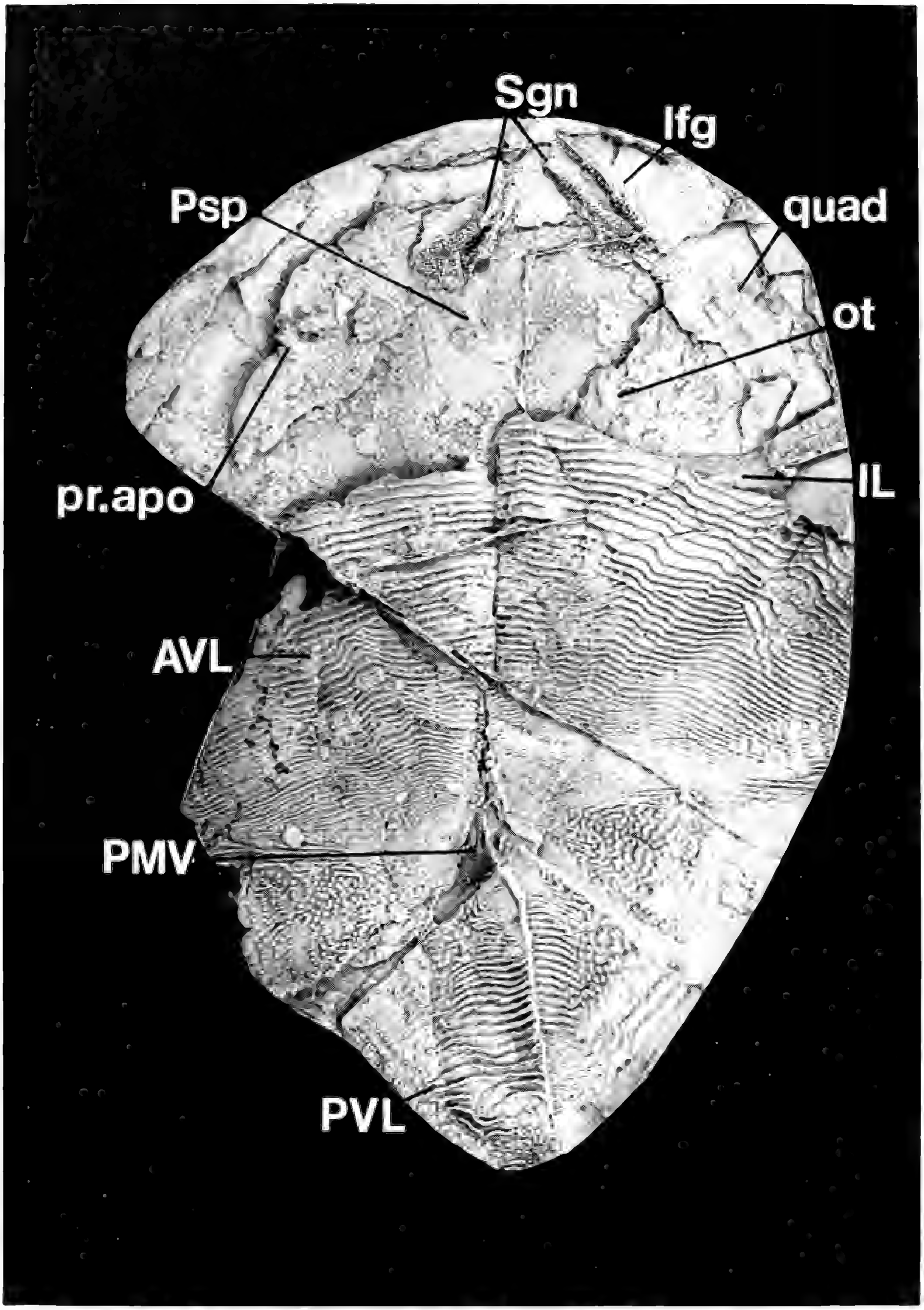


Fig. 20. Austrophyllolepis youngi gen. et sp. nov., ventral aspect of nearly entire individual, NMP 160720, natural size. AVL, anterior ventrolateral plate; Ifg, inferagnathal; IL, interolateral plate; ot, otolith; PMV, posterior median ventral plate; pr.apo, bony extension to the anterior postorbital process; Psp, parasphenoid; PVL, posterior ventrolateral plate; quad, quadrate; Sgn, supragnathal.

PSO and SM plates with extreme modification of the SO plate; and a completely flat exocranium which is proportionately broader than that of other placoderms.

Endocranium: Recent works since the monographs of Stensiö (1963, 1969) provide new data on the endocrania of placoderms (Goujet, 1975; Ørvig, 1975; Young, 1978, 1979, 1980) and permit more confident use of endocranial features in phylogenetic discussion. The endocranium of most placoderms was perichondrally ossified, but in phyllolepids and antiarchs it was presumably cartilaginous (also see comments in V. T. Young, 1983 regarding *Phlyctaenius*), and in ptyctodontids it was only partially ossified (Miles and Young, 1977). It follows that a well-ossified endocranium is the plesiomorphic condition for placoderms, secondary reduction of bone being a specialization of higher groups.

In phyllolepids and euarthrodires the endocranium has well-developed posterior postorbital processes, and a relatively large cucullaris fossa. The posterior postorbital processes are well produced in chondrichthyans, acanthodians and palaeoniscoids and it may be argued that these are a primitive gnathostome character (Schaeffer, 1981: 49). However in all recent schemes of placoderm interrelationships the euarthrodires are placed as a relatively derived group by comparison with petalichthyids, rhenanids (palaeacanthaspidoids and gemuendinaspidoids) and ptyctodontids. It follows that the absence of well-developed posterior postorbital processes in these primitive placoderm groups cannot be regarded as a synapomorphy of these groups on the grounds of character analyses put forward by several workers. I consider the well-developed posterior postorbital processes of euarthrodires and phyllolepids as a synapomorphy of these two relatively advanced placoderm groups, the distinction being that in these groups the posterior postorbital processes are more extended laterally than in any other placoderm group. Amongst the primitive placoderm groups these processes are perhaps best developed in *Romundina* (Ørvig, 1975; pls 1-3), and it is not unlikely that this represents the primitive placoderm condition for this character. Secondary extension (euarthrodires and phyllolepids) and reduction (other placoderms; except possibly antiarchs) of this endocranial process probably relate to differing placoderm feeding mechanisms and changes in the suspensorial framework (comments in Schaeffer, 1975, 1981; Miles 1967b, 1969; Young, 1980). The large cucullaris fossa of euarthrodires and phyllolepids is another synapomorphy of these groups related to the larger attachment area for the branchial constrictor and cucullaris muscles (Miles, 1967b). It is not known from the pattern on the ventral surface of the headshield of phyllolepids if the posterior postorbital process was bifid with a separate paravagal fossa.

Although the separation of the rhinocapsular from the postethmoid division of the endocranium is also seen in palaeacanthaspidoids (*Romundina,* Ørvig, 1975) and possibly in petalichthyids (*Macropetalichthys,* Stensiö, 1969: fig. 22), it is only in euarthrodires that the dermal exocranium shows two clear divisions which reflect the condition of the underlying endocranium. The separate terminal rhinocapsular of primitive euarthrodires, and presumably phyllolepids, is not seen on any other gnathostome group (De Beer, 1937), and could be regarded as a synapomorphy of these groups later modified in separate euarthrodire lineages. An example of this is the way dermal bones of the snout are fused to the rest of the exocranium, as is the condition in some phlyctaenaspids and most brachythoracids (Denison, 1978). I therefore regard this condition, viz., the dermal bones of the snout not fused to the rest of the exocranium leaving the rhinocapsular separate from the rest of the endocranium, as a synapomorphy of primitive euarthrodires and phyllolepids. This interpretation is more parsimonious than arguing monophyly for all euarthrodires with a separate rostral capsule (e.g. certain actinolepidoids and *Buchanosteus*).

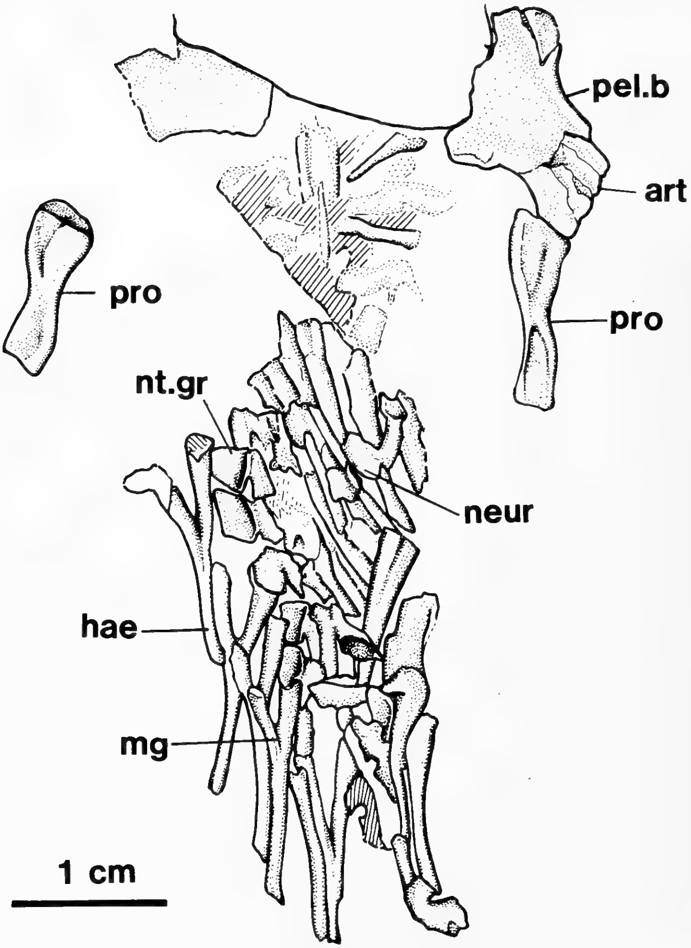


Fig. 21. Austrophyllolepis youngi gen. et sp. nov., pelvic girdle preserved in dorsal view, NMP 160746 (see also Fig. 22B). hae, haemal arch; mg, median groove on haemal arch; neur, neural arch; nt.gr, notochordal saddle on neural arch; pel.b, basal pelvic plate; pro, propterygial element of pelvic girdle.

Autapomorphous features of the phyllolepid endocranium are the internally secreted otoliths in the saccular cavities, and possibly the ossified extension to the anterior postorbital process on the ventral surface of the postorbital plate.

Jaws and Parasphenoid: The jaws and parasphenoid of placoderms are widely known for advanced euarthrodires (Stensiö, 1969: figs 140-142; Miles, 1971: figs 56-61; Miles and Dennis, 1979; Dennis and Miles, 1979, 1980, 1981, 1982, 1983) but otherwise known only in the phlyctaenioids *Dicksonosteus* (Goujet, 1975) and *Groenlandaspis* (Dr A. Ritchie, pers. comm.), the actinolepidoid *Kujdanowiaspis* (Stensiö, 1963: pl. 62) and possibly actinolepidoid gnathals from America (Denison, 1958). The jaws are known in antiarchs (Stensiö, 1948; Hemmings, 1978), gemuendinaspids (Gross, 1963) and ptyctodontids (Ørvig, 1962; Miles and Young, 1977) but are unknown in petalichthyids and palaeacanthaspidoids. Outside of euarthrodires and phyllolepids, the parasphenoid is only known in the palaeacanthaspidoid *Kosoraspis* (Gross, 1959)

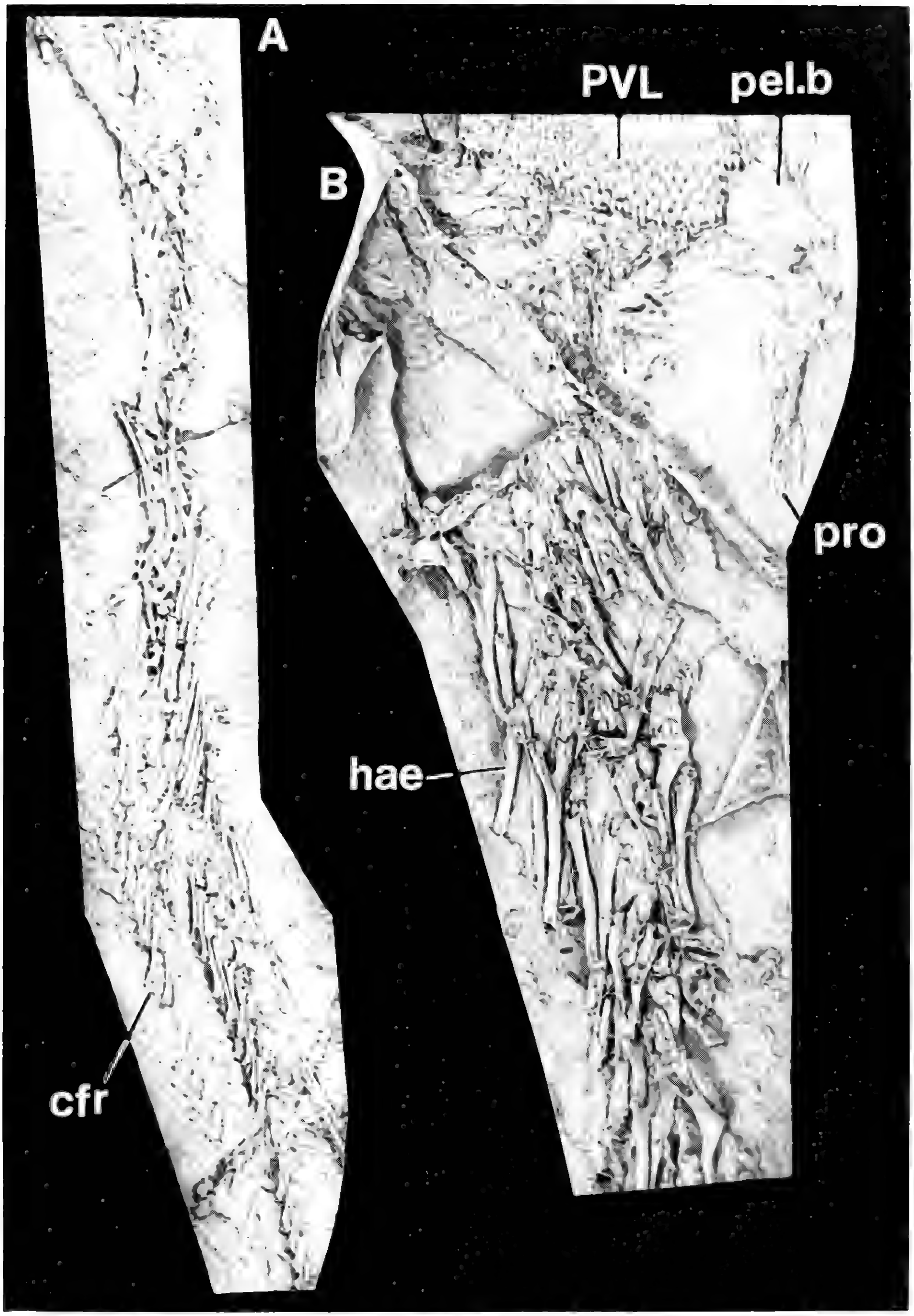


Fig. 22. Austrophyllolepis youngi gen. et sp. nov. **A,** almost entire tail, NMP 160732, × 3/4. **B,** pelvic girdle of NMP 160746, dorsal view (see also Fig. 21), × 2. Latex casts whitened with ammonium chloride. cfr, caudal fin radials; hae, haemal arch; pel.b, pelvic basal plate; pro, propterygial element of pelvic girdle; PVL, posterior ventrolateral plate.

and in the gemuendinaspid *Gemuendina* (Gross, 1963). The possession of two pairs of supragnathals is a synapomorphy uniting the euarthrodires as a monophyletic group (Miles and Young, 1977; Young, 1979; Dennis and Miles, 1983). However the euarthrodires are the largest group of placoderms and many taxa show specializations of the gnathal plates, such as the tubular ridging of *Holonema* (Miles, 1971), the durophagous gnathals of *Bullerichthys* and several other euathrodires (Dennis and Miles, 1979b), and various carnivorous adaptations of the toothplates by coccosteids and higher forms (Miles and Dennis, 1979; Dennis and Miles, 1983; Gross, 1967; Denison, 1978). The gnathals of *Groenlandaspis* are particularly interesting as there is a single median supragnathal bone, possibly formed by fusion of the anterior pair of supragnathals, giving an upper biting surface of three plates (observation of Mt Howitt *Groenlandaspis* specimens currently under study by Dr A. Ritchie). This demonstrates the potential for secondary fusion of the paired supragnathal plates in euarthrodires, and the possibility that in phyllolepids the two pairs have either fused to form one pair of supragnathals, or alternatively one pair was lost. This assumes that primitively there were two pairs of supragnathals in ancestral phyllolepids rather than one. For several reasons discussed at the end of this section I regard phyllolepids as derived from primitive euarthrodires, therefore as highly specialized placoderms. The absence of one pair of supragnathals is more acceptable as a secondary specialization than the alternative view which requires the refutation of several synapomorphies uniting phyllolepids and euarthrodires. The buccal cavities of all the known primitive euathrodires (*Kujdanowiaspis, Dicksonosteus, Groenlandaspis*) contain multicuspid tuberculate gnathal plates and similarly denticulate parasphenoids. As outgroup comparison of these features is rather weak it cannot be established if this is a plesiomorphous condition for placoderms or a synapomorphy of phyllolepids and primitive euarthrodires. The presence of lateral grooves on the parasphenoid is only known in euarthrodires and phyllolepids, although limited knowledge of the parasphenoids of other placoderms does not permit a broad enough comparison to identify this character as a synapomorphy. The distinctive non-biting division of the inferagnathal is used by Dennis and Miles (1983) and Young (1981b) to unite certain advanced brachythoracid euarthrodires. In phyllolepids this region was not ossified, and this must be regarded as representing the plesiomorphous euarthrodire condition.

Trunkshield: The most important features of the phyllolepid trunkshield are the sliding dermal neck joint and the absence of PL and PDL plates.

The dermal sliding neck joint of actinolepidoids and phyllolepids has been regarded as the primitive condition for euarthrodires, preceding the condyle and trochlear ginglymoid neck joint of the phlyctaenioid euarthrodires (Miles, 1967b; Denison, 1975). In other placoderms a dermal neck joint is present in ptyctodontids, petalichthyids, and antiarchs, with the neck joint of rhenanids being an endoskeletal articulation without dermal bone components (Young, 1980: 27). The resemblance between the dermal neck joint of ptyctodontids and petalichthyids is used by Goujet (1984) as a synapomorphy to unite these groups although Denison (1978: 39) notes that the development of this feature in petalichthyids is variable (e.g. no dermal neck joint in *Lunaspis*; vertical neck condyles in *Macropetalichthys*). Palaeacanthaspidoids and *Brindabellaspis* appear to have an endoskeletal neck articulation only, with glenoid processes present on the posterior endocranial face (Young, 1980: 27). Ørvig (1975: 49) alternatively suggests that in *Romundina* there may have been a sliding neck joint, although there is no ADL plate in the material to support this idea.

The well-developed dermal neck joints of phlyctaenioid euarthrodires is used as a synapomorphy uniting this large group of euarthrodires (Miles, 1973; Miles and Young, 1977; Young, 1979, 1981b; Dennis and Miles, 1983). Miles (1973) implies

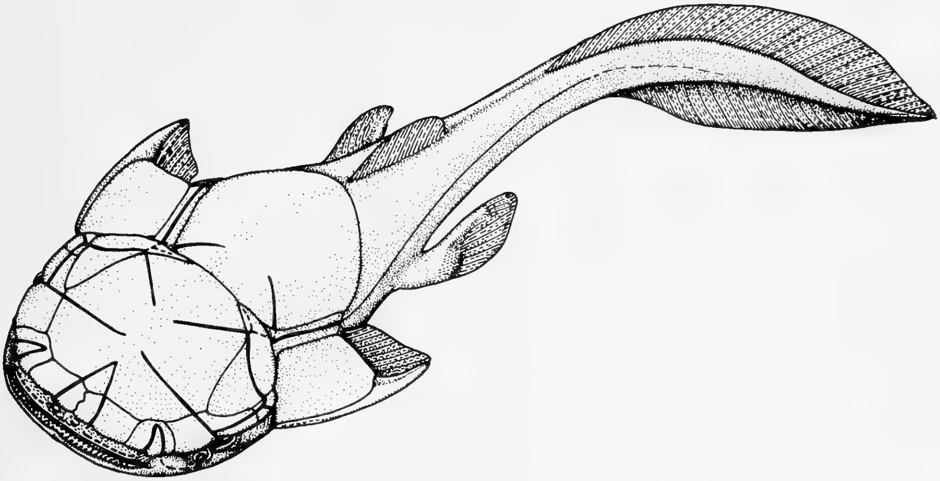


Fig. 23. Austrophyllolepis ritchiei gen. et sp. nov. Reconstruction of the living fish, based on a composite of all the Mt Howitt material, including details of the tail from *A. youngi.* Shape of caudal fin largely conjectural.

that the sliding neck joint of actinolepidoid euarthrodires is also a specialized character, perhaps defining a monophyletic group. The plesiomorphic condition relative to other placoderms would be the absence of a dermal neck joint. I concur with this hypothesis and, after comparison with other placoderm groups, reach the conclusion that the sliding dermal neck joint of actinolepidoids and phyllolepids is a synapomorphy of these two groups.

The absence of PL and PDL plates in the trunkshield of phyllolepids has been regarded as a plesiomorphous condition by Miles and Young (1977) and Young (1980). In antiarchs and euarthrodires the PL plate is primitively present in the trunkshield, but is later lost in some antiarchs by fusion with the PDL plate to form a mixilateral plate. In euarthrodires the PL plate primitively borders the pectoral fenestra posteriorly, and in pachyeosteomorphs the pectoral incision is open posteriorly, with the PL plate articulating with the PDL plate. A PDL plate is also found in palaeacanthaspidoids (*Kosoraspis,* Gross, 1959: *Romundina,* Ørvig, 1975) and petalichthyids (*Lunaspis,* Gross, 1961b) and is considered a primitive component of the placoderm trunkshield. The absence of the PDL plate in phyllolepids is regarded as specialized, especially when all other synapomorphies shared with euarthrodires are considered. An important distinction between the trunkshields of most other placoderms and phyllolepids is the extreme dorsoventral compression of the latter. The pectoral incision of phyllolepids does not face laterally or posterolaterally as in other placoderms, but posteriorly from the AL and AVL plates. It is a moderately large incision and cannot be regarded as primitive for euarthrodires (compare the small pectoral fenestrae of actinolepidoids such as *Bryantolepis,* Denison, 1962).

Amongst other extremely flattened euarthrodires are the homosteids and the heterosteids. In homosteids the lateral wall of the trunkshield is reduced by the loss of the PL plate, and by the unusual reduction and rearrangement of the ventral lamina (Heintz, 1968; but according to Dr E. Mark-Kurik, this plate is present on *Homostius* but somewhat reduced; pers. comm., 1983). In heterosteids the trunkshield has also undergone modifications due to compressed body form, as the pectoral incision opens posteriorly and the AL and ADL plates are fused (Ørvig, 1969: 284). It is evident that

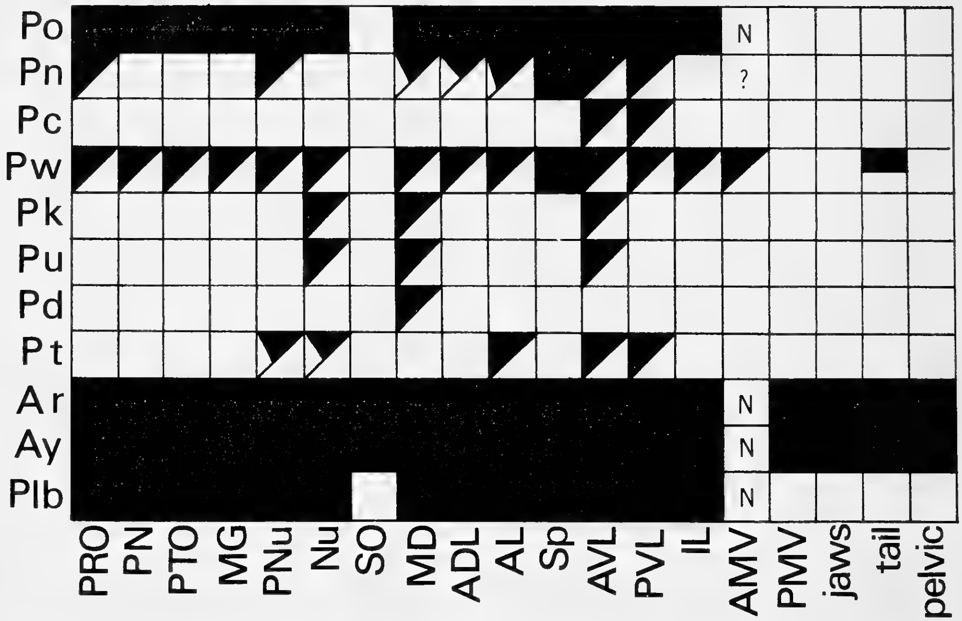


Fig. 24. Relative completeness of phyllolepid remains. Po, *Phyllolepis orvini*; Pn, *P. nielseni*; Pc, *P. concentrica*; Pw, *P. woodwardi*; Pk, *P. konincki*; Pu, *P. undulata*; Pd, *P. deliculata*; Pt, *P. tolli*; Ar, *Austrophyllolepis ritchiei*; Ay, *A. youngi*; Plb, *Placolepis budawangensis*. N indicates that this plate is probably not present in the complete armour. A fully shaded square indicates that the plate is known in both dorsal and ventral (or internal, external) views, where the top left half is shaded indicates only the dermal surface is known; the bottom left half indicates that the internal surface is known. A part of a plate surface (i.e. the complete or incomplete dorsal surface) is shown by a degree of shading of the above quadrants. Abbreviations as for Fig. 7.

the reduction and modification of the trunkshields of homosteids, heterosteids and phyllolepids relate to the constriction of space for fin and tail emergence following compression of body form. If the pectoral fin of phyllolepids extended only as far as the end of the Sp plates, as they do in *Groenlandaspis* (Dr A. Ritchie, pers. comm.) then the PL and PDL plates would have to reach the anterolaterally-facing margin of the small PVL plates. This arrangement would allow only an extremely small opening for the large tail, and thus in developing a specialized, flattened armour it is more efficient to lose certain dermal plates than constrict the unarmoured tail. It should also be noted here that the AL plates of phyllolepids cover the pectoral endogirdle and do not have a lateral component covering the body of the fish, or providing an overlap area for posterior lateral dermal trunk plates. Further specializations of the trunkshield in dorsoventrally compressed higher euarthrodires is seen in *Titanichthys* (Denison, 1978: 100). The mylostomatids are also flattened dorsoventrally although the posterior plates on the lateral wall are not well known.

The presence of either AMV or PMV plates in phyllolepids indicates that the primitive condition was probably a trunkshield with both elements present, as in euarthrodires and antiarchs. The absence of AV plates in phyllolepids was probably a parallelism with higher euarthrodires and not a shared synapomorphy in contradiction to the evidence from the dermal neck joint and other actinolepidoid synapomorphies discussed below.

The phyllolepid trunkshield resembles that of actinolepidoids in having a broad MD plate lacking a ventral keel, and a narrow ADL plate, although these features are of little phylogenetic value. A final point concerning the trunkshield is that Goujet (1984) argues that only in phyllolepids and euarthrodires is there a separate, well-developed IL plate, and this would be another synapomorphy uniting these groups if Goujet's interpretation of the shoulder girdle in placoderms is accepted.

Tail: The tail in phyllolepids, using *Austrophyllolepis* as the only known example, was relatively long compared to the dermal armour. In other placoderm groups the tail is generally short *(Gemuendina, Lunaspis, Pterichthyodes).* In actinolepidoids it is known completely in only one form (*Bollandaspis,* Schmidt, 1976), in which it is quite long. The tail of coccosteids is also relatively long (Miles and Westoll, 1968: fig. 48). It is concluded that a long tail relative to body size (irrespective of dermal armour size the trunk is taken from the head to the pelvic fins) is a specialized condition in placoderms. In ptyctodontids the tail region from the caudal peduncle is also extensive and this is regarded as a parallel development, particularly in view of the specialized swimming style and mode of life of ptyctodontids, which is believed to be similar to that of modern holocephalans (Miles, 1969).

The tail region in petalichthyids, rhenanids (Gross, 1961, 1963), primitive antiarchs (yunnanolepidoids, sinolepidoids; Zhang Guorui, 1978; Liu and Pan, 1958) and primitive euarthrodires (*Bollandaspis,* Schmidt, 1976; *Sigaspis,* Goujet, 1973) was covered with small scales of bony dermal denticles, this condition being primitive for placoderms. The well-preserved tail of *Austrophyllolepis* indicates that in phyllolepids the scale cover was absent. This is also seen as a specialized condition for placoderms (also seen in higher euarthrodires such as coccosteids, Miles and Westoll, 1968, and in higher antiarchs such as bothriolepids, Stensiö, 1948; Long, 1983a).

The unique pelvic girdle of phyllolepids is interpreted as an autapomorphy for the group. In primitive euarthrodires (*Sigaspis, Kujdanowiaspis,* Dr Goujet, pers. comm.) the pelvic endogirdle was closely associated with the scales immediately behind the trunkshield, whereas in higher euarthrodires the pelvic endogirdle is a completely internal perichondral ossification with long iliac processes (Miles and Westoll, 1968; Dennis and Miles, 1982). The close association of the phyllolepid basal pelvic plate with the trunkshield is similar to the primitive euarthrodire condition, and differs in this respect from the pelvic girdles of all other placoderm groups (Stensiö, 1969: figs 245-247).

RELATIONSHIPS OF PHYLLOLEPIDS

From the above discussion of phyllolepid character states I proposed that phyllolepids and euarthrodires are a monophyletic group which share the following synapomorphies: 1, endocranium with well-produced posterior postorbital processes; 2, endocranium with proportionately large cucullaris fossa; 3, endocranium primitively with separate ethmoid and postethmoid divisions which is reflected in the dermal snout bones as a separate rostral capsule; 4, headshield with a single large pair of PNu plates which contain the junction of the occipital and posterior pit lines and the main lateral line canal; 5, headshield with an extensive dermal thickening above the optic capsule. In addition Goujet (1984) unites phyllolepids and euarthrodires by 6, the possession of a true IL plate (assuming Goujet's interpretation of the IL plates of palaeacanthaspidoids and yunnanolepidoids is correct). Furthermore there are histological similarities between phyllolepid dermal bones and those of euarthrodires, recognized earlier by Stensiö (1934) and Gross (1934). Other characters shared by phyllolepids and euarthrodires, such as a large parasphenoid with lateral grooves, may prove useful in phylogenetic analysis when more is known about the anatomy of other placoderms. Phyllolepids and actinolepidoid euarthrodires (including *Wuttagoonaspis*)

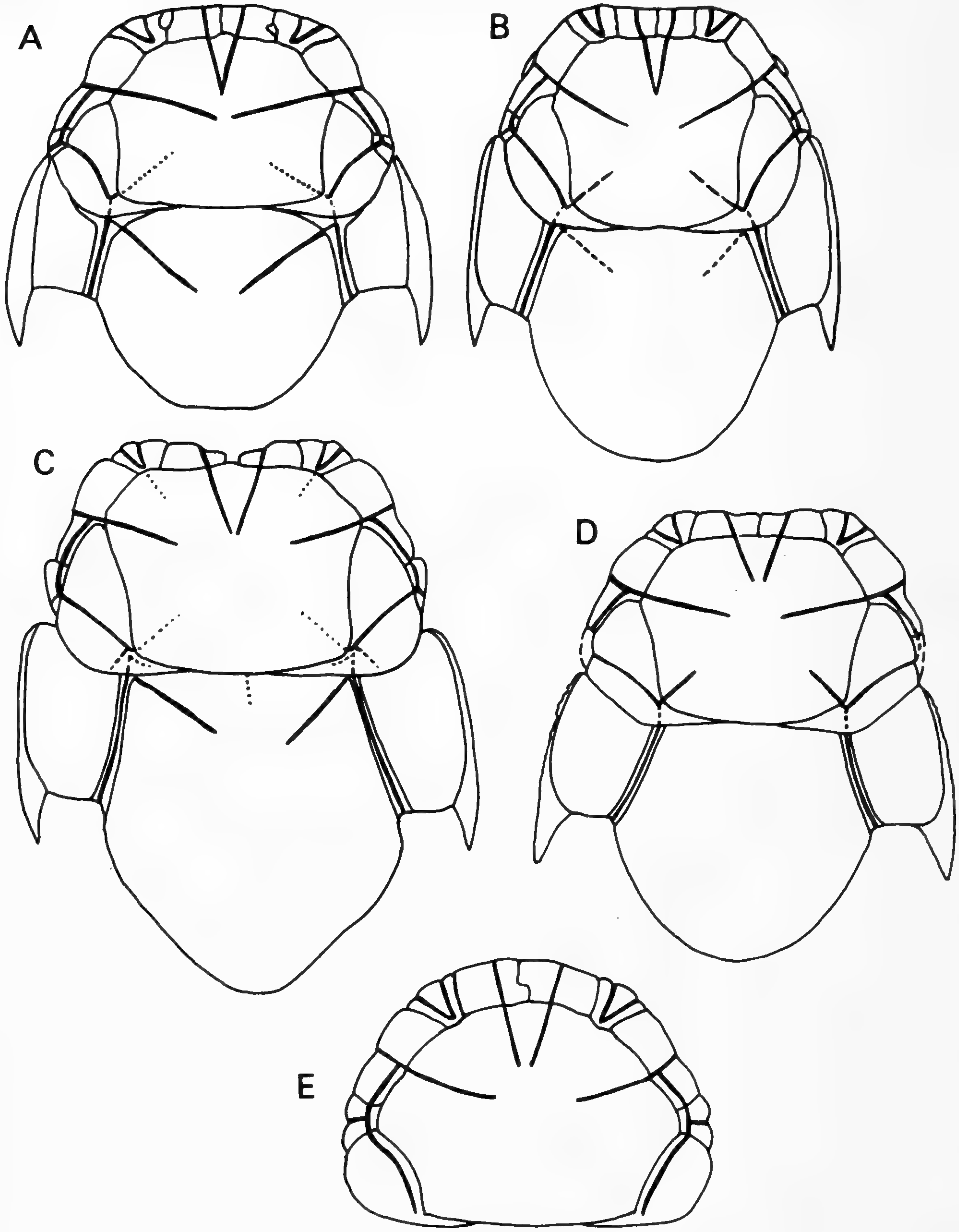


Fig. 25. Comparison of phyllolepid dorsal armours. **A,** *Austrophyllolepis ritchiei,* gen. et sp. nov. **B,** *A. youngi,* gen. et sp. nov. **C,** *Phyllolepis orvini* (after Stensiö, 1936). **D,** *P. woodwardi* (after Stensiö, 1939). **E.** *Placolepis budawangensis* (after Ritchie, 1984).

are united by 7, the possession of a sliding dermal neck joint; and 8, having PTO plates often larger, but never smaller, than the MG plates of the headshield.

The Euarthrodira as currently defined by Young (1979: 342) share (a) two pairs of supragnathals, (b) distinct posterolateral corners on the headshield (also shared with antiarchs, Young and Gorter, 1981; Dennis and Miles, 1983) (c) separate endocranial postorbital processes, (d) cucullaris fossa well developed, (e) paravagal fossa reduced or absent and (f) trunkshield incorporating a PL plate that encloses a pectoral fenestra. As stated in the previous section, the primitive phyllolepid trunkshield is assumed to have possessed PL plates. Phyllolepids appear to share the endocranial features of euarthrodires as far as reconstruction allows (although the presence of a paravagal fossa is indeterminate). The presence of one pair of supragnathals in phyllolepids is a character which may separate phyllolepids from euarthrodires if this is the primitive phyllolepid condition. Phyllolepids could in this case remain as a sister group to euarthrodires rather than a subgroup of the Actinolepidoidei, although this hypothesis would imply that a sliding dermal neck joint was independently acquired along with reduction of the MG plate in actinolepidoids. Alternatively it is feasible that one of the pairs of upper jaw toothplates was lost or fused in phyllolepids, as in *Groenlandaspis.* The diversity and complexity of the euarthrodiran gnathal apparatus (Miles, 1969; Ørvig, 1980; White, 1978), and the variations seen in the jaws of other fish groups (e.g. Holocephali, Actinopterygii) leave this question open, especially in view of our incomplete knowledge of the jaws of primitive euarthrodires. I leave the possession of two pairs of supragnathals as a synapomorphy of the euarthrodira (and possibly primitive phyllolepids), but maintain that, on the grounds of shared synapomorphies 1-8, phyllolepids are more probably a subgroup rather than a sister group of euarthrodires.

The hypotheses of Miles and Young (1977) and Young (1980), which place phyllolepids as the sister group to antiarchs and euarthrodires, use two characters to unite these groups: the presence of PL plates and PMV plates (assuming Gross's interpretation of *Lunaspis,* Gross 1961, is incorrect). Young and Gorter (1981) and Dennis and Miles (1983) add the presence of a well-developed obstantic margin (correlated with the broad posterolateral breadth of the headshield) as a synapomorphy of antiarchs and euarthrodires. In the previous discussion I have considered the problem of the PL plate, and I believe that the presence of a PMV plate in *Austrophyllolepis* clearly dismisses this feature as being restricted to antiarchs and euarthrodires. The broad posterolateral corners on the headshields of antiarchs and euarthrodires is only seen in the primitive members, or those retaining plesiomorphic characters, such as yunnanolepidoids, sinolepidoids, bothriolepidoids, actinolepidoids, phlyctaeniids and most brachythoracids. In specialized groups there is a secondary loss of this feature as headshield shape changes, for example, in asterolepidoids and some higher brachythoracids such as *Leptosteus, Oxyosteus, Belosteus, Brachydeirus* and *Synauchenia* (Denison, 1978). From this it can be deduced that if phyllolepids are specialized actinolepidoids it is possible that changes in the basic headshield shape, such as dorsoventral flattening, resulted in parallel secondary loss of the distinctive posterolateral corners. Once a sister group relationship for phyllolepids and euarthrodires is accepted there are several possible hypotheses of relationship for phyllolepids, actinolepids, *Wuttagoonaspis* and *Antarctaspis* (Fig. 26).

The actinolepidoids are regarded as the plesion sister group to other euarthrodires by Young (1981b) and Dennis and Miles (1983). Miles (1973) believed that actinolepidoids were a monophyletic group sharing a sliding neck joint. In addition to synapomorphies shared by actinolepidoids, phyllolepids and *Wuttagoonaspis* discussed above, the actinolepids share two additional synapomorphies: 9, a supraorbital process on the endocranium, and 10, AV plates.

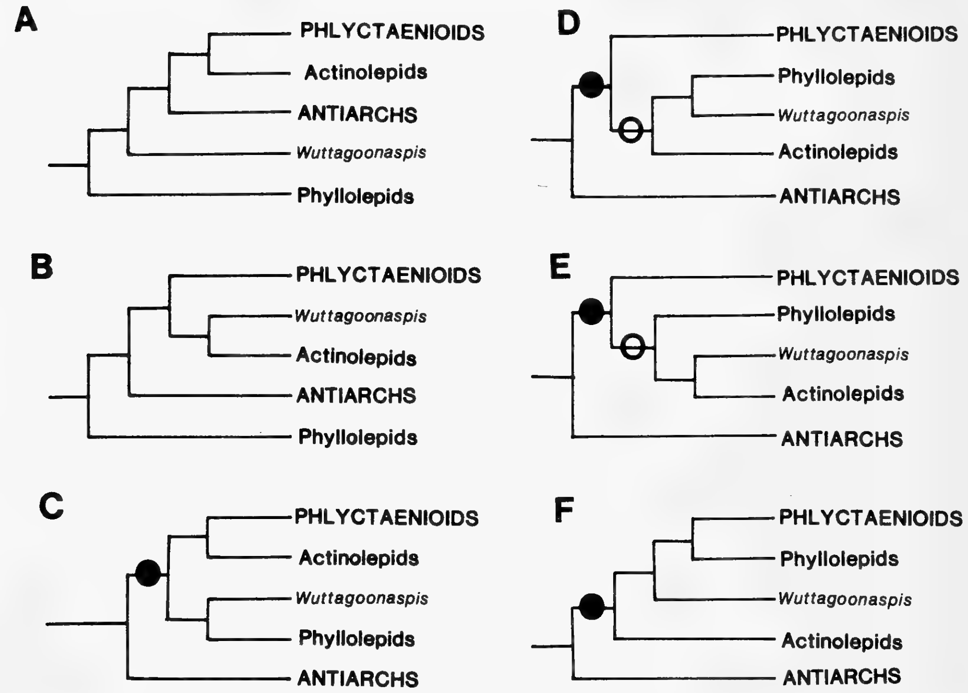


Fig. 26. Alternative hypotheses of relationships for phlyctaenioids, actinolepids, phyllolepids, *Wuttagoonaspis* and antiarchs. All synapomorphies listed in the caption to Fig. 27. **A,** hypothesis of Young (1980), excludes *Wuttagoonaspis* and phyllolepids from the euarthrodires and antiarchs because of the absence of broad posterolateral corners on the headshield (and obstantic margin, Young and Gorter, 1981), and absence of posterior lateral plates (not really known for *Wuttagoonaspis*). **B,** hypothesis of Miles and Young (1977) includes *Wuttagoonaspis* within the euarthrodires as a separate group of actinolepidoids. Hypotheses **C-F** assume monophyly of phyllolepids, *Wuttagoonaspis* and euarthrodires (shared synapomorphies 1-5; black circle). Hypothesis **C** involves either an independent acquisition of a sliding neck joint in actinolepids or its loss in phlyctaenioids, and a parallel acquisition of anterior ventral plates in *Wuttagoonaspis* and actinolepids. Hypotheses **D** and **E** assume monophyly of actinolepids, phyllolepids and *Wuttagoonaspis* using synapomorphies 6 and 7 (open circles). Hypothesis **D** proposes a sister group relationship between phyllolepids and *Wuttagoonaspis* using synapomorphies 12 and 13 (possibly 14). This also involves independent loss of anterior ventral plates in phyllolepids and phlyctaenioids. Hypothesis **E** unites *Wuttagoonaspis* and actinolepids by synapomorphy 9, but imples that the highly reduced marginal plates, small orbits (and possibly undifferentiated centronuchal plate) were acquired and lost in actinolepids. Hypothesis **F** assumes that the loss of anterior ventral plates in phyllolepids and phlyctaenioids was a synapomorphy, but involves the independent loss of synapomorphies 12, 13 (possibly 14) in phlyctaenioids.

Wuttagoonaspis is regarded as an actinolepidoid because it has a sliding dermal neck joint and AV plates (Dr A. Ritchie, pers. comm.). *Wuttagoonaspis* can be united with phyllolepids and *Antarctaspis* if the undifferentiated centronuchal area on the headshield is a valid synapomorphy. However, as this condition is also seen in an undescribed actinolepid from Severnaya Zemlya (Dr D. Goujet, pers. comm.) I regard this feature as too unstable a character for the study of relationships. *Antarctaspis, Wuttagoonaspis* and phyllolepids show similar specializations in the reduction of the orbits and small size of the MG plates. *Wuttagoonaspis* differs from phyllolepids and actinolepidoids in the unusual dermal skull roof pattern, although it still shares the basic pattern of paired PRO, PN, PTO, PMG and PNu plates (possibly with separate MG plates). The endocranium of *Wuttagoonaspis* is not divided into separate postethmoid and rhinocapsular ossifications (Ritchie, 1973) representing an apomorphic condition relative to phyllolepids and other actinolepidoids. On the existing evidence I relate *Wuttagoonaspis* to phyllolepids tentatively by the large Nu plate, reduced MG plate, and small orbits (possibly also by the meandrine ridge ornamentation), but regard *Wuttagoonaspis* as belonging to an aberrant group of specialized actinolepidoids which diverged from the main stock at an early stage. The absence of broad posterolateral corners on the headshield of *Wuttagoonaspis* (Young and Gorter, 1981) may be due to secondary changes in headshield shape such as occipital elongation.

Antarctaspis is too poorly known to be placed confidently in the cladogram. In the absence of other information I corroborate Denison's opinion (1978) that *Antarctaspis* is more closely related to phyllolepids than to other placoderms by sharing a large Ce-Nu plate and reduced MG plates.

Within the actinolepids there is much variation in the length and contact relationships of the Nu plate, size and degree of ossification of the dermal nasal capsule bones, and trunkshield shape. Actinolepids with a long Nu plate are regarded as plesiomorphic within the group by comparison with other placoderm groups. Petalichthyids possess a long Nu plate in contact with the PRO plates; primitive antiarchs possess a long Nu plate (yunnanolepidoids and sinolepidoids) and some palaeacanthaspidoids and related forms possess long Nu plates, such as *Brindabellaspis, Kimaspis, Romundina,* and *Kosoraspis* (Young, 1980; Mark-Kurik, 1973; Ørvig, 1975; Gross, 1959). The actinolepids possessing a long Nu plate in contact with the PRO plates (*Aethaspis, Proaethaspis* and *Baringaspis,* Denison, 1958; Miles, 1973) are considered as the plesion sister group to other actinolepids. Actinolepids with a long Nu plate not in contact with the PRO plates (*Stuertzaspis* and *Heightingtonaspis,* Westoll and Miles, 1963; White, 1969) are presumably less specialized than those with short Nu plates, and often other specializations such as broadened or lengthened armour (*Bryantolepis* and other actinolepids; Denison, 1978; Liu, 1979).

The resulting cladogram recognizes phyllolepids and *Wuttagoonaspis* as specialized lineages of the actinolepidoids. This hypothesis will no doubt be testable as new Devonian faunas are described from Australia and Antarctica where ancestral phyllolepids might be expected (Young, 1981a: 237). A final auxiliary criterion for assessing phylogenetic relationships, but one that has been strongly criticized or misused, is that of geological character precedence (Wiley, 1981: 148). Phyllolepids occur late in the geological record (Frasnian-Famennian) whereas the earliest antiarchs and euarthrodires appear in the Early Devonian (Siegenian, earlier for antiarchs, Pan Kiang, 1981), some thirty million years before. The unique specializations of phyllolepids within the Placodermi, such as otoliths and the absence of dermal nasal capsule bones, and their widespread distribution indicate that they are not primitive within the Placodermi, but are one of the most specialized and successful groups. The late appearance of phyllolepids suggests their derivation from actinolepids probably during the late Middle Devonian, and their successful dispersal from an east Gondwana source (Young, 1981a) probably during the Frasnian. The most specialized phyllolepids *(Phyllolepis orvini)* occur in the Famennian of East Greenland. This is comparable with the bothriolepid distribution pattern in which the most primitive species occur early in Australia and the most specialized forms (including *Bothriolepis groenlandica*) occur late in Europe and Greenland (Long, 1983a).

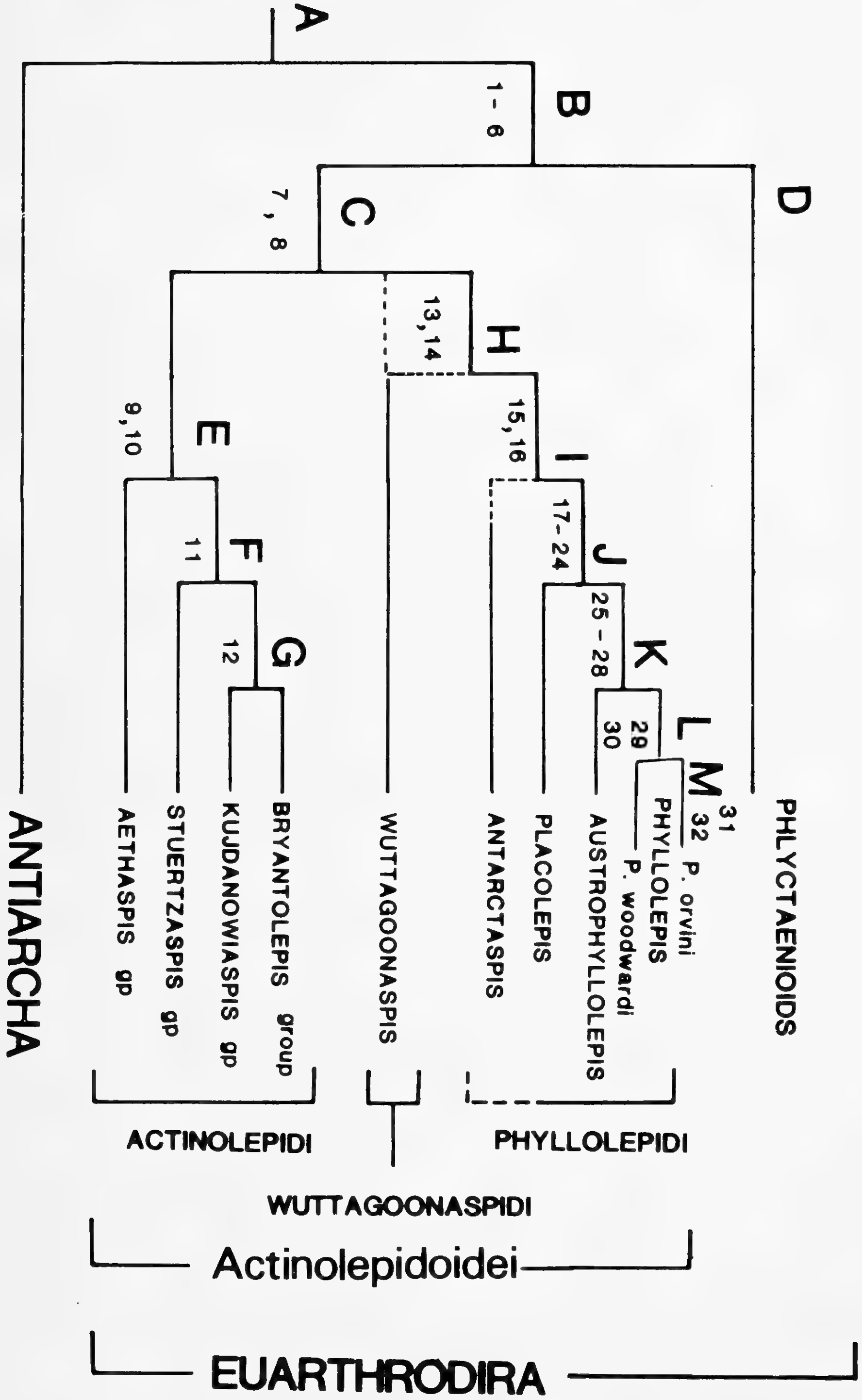
With the Phyllolepidae the relationships of *Placolepis, Austrophyllolepis* and *Phyllolepis* are determined by using actinolepidoids for outgroup comparison. Only *Phyllolepis orvini, P. woodwardi,* both species of *Austrophyllolepis,* and *Placolepis budawangensis* are relatively well known (Fig. 24), and so comments about the interrelationships of phyllolepids will be confined to these taxa. Fig. 25 illustrates the major differences in the dorsal aspects of the dermal armour of these phyllolepids.

It has been shown that a small MG plate is a specialized condition within the actinolepidoids, and therefore the large MG plate of *Placolepis* is regarded as plesiomorphic relative to *Austrophyllolepis* and *Phyllolepis.* The entry of the main lateral line canal into the PNu plate is anteriorly located in all actinolepidoids and *Placolepis,* whereas *Austrophyllolepis* and *Phyllolepis* are specialized in having the lateral line canal entering the PNu from about midway along the plate, and the MG plate separated from the centronuchal area by the PNu plate. In these respects I regard *Placolepis* as the plesiomorphic sister group to *Austrophyllolepis* and *Phyllolepis.* The most specialized of the phyllolepids is *Phyllolepis orvini* which has a pair of small PRO plates separated from each other medially in the mature armour. The large size of this species is another apomorphic feature relative to other phyllolepids. The trunkshields of *Placolepis* and *Phyllolepis orvini* are here considered as specialized in their absence of median ventral plates. *Austrophyllolepis* retains a PMV plate as a plesiomorphic character. It is more parsimonious to unite *Austrophyllolepis* and *Phyllolepis* by at least two shared synapomorphies of the headshield than to unite one species of *Phyllolepis* and *Placolepis* by the loss of the PMV plate. I envisage the ancestral phyllolepid as possessing two median ventral plates in the trunkshield with a headshield similar to that of *Placolepis,* but probably having smaller PN plates, or even differentiated Ce and Nu plates.

FUNCTIONAL MORPHOLOGY AND LIFESTYLE OF PHYLLOLEPIDS

The flattened body form of phyllolepids reflects a sedentary demersal lifestyle, paralleled by many other groups of fishes such as psammosteid heterostracans, gemuendinoid rhenanids, batoid chondrichthyans and pleuronectiform teleosteans.

Fig. 27. The most economical hypothesis of phyllolepid relationships. This involves accepting two assumptions (that primitive phyllolepids possessed posterior lateral plates and two pairs of superagnathals) on the evidence that phyllolepids and euarthrodires are more closely related than are antiarchs and euarthrodires because of synapomorphies 1-6. Synapomorphy scheme: A. Primitively possessing posterior lateral plates, headshield with broad posterolateral corners, posterior median ventral plate present. B. 1. Endocranium with well produced posterior postorbital processes. 2. Endocranium with large cucullaris fossa (1/3-1/2 total endocranial length). 3. Endocranium with separate rhinocapsular and postethmoid divisions, reflected in the arrangement of the anterior dermal headshield bones. 4. Single large pair of paranuchal plates with junction of the posterior pit-line, occipital pit-line and main lateral line canal; receiving the main lateral line canal from the marginal plate. 5. Extensive dermal bone thickening above optic capsules on headshield. 6. True interolateral plates present (*sensu* Goujet, 1984). C. 7. Sliding dermal neck joint. 8. Postorbital plates generally larger than marginal plates, (possible synapomorphies: a, long tail; b, denticulated tooth plates). D. Ginglymoid neck joint and other synapomorphies listed in Young (1981b) and Dennis-Bryan and Miles (1983). E. 9. Supraorbital process on endocranium (Dr D. Goujet, pers. comm.). 10. Anterior ventral plates present. F. 11. Nuchal plate not contacting preorbitals (separate nuchal and central plates assumed). G. 12. Nuchal plate shortened considerably (and various autapomorphies, e.g. broadened armour in *Bryantolepis*). H. 13. Greatly reduced marginal plates. 14. Diminution of orbital size, and possibly synapomorphy 15. I. 15. Combined centronuchal plate (or undifferentiated centronuchal area). 16. Postorbital plate narrow with long anterior and posterior divisions divided by the central sensory line canal. J. 17. Incorporation of postnasal plate into position between preorbital and postorbital plates. 18. Endocranium probably cartilaginous. 19. Absence of rostral and pineal plates. 20. Reduction or loss of postmarginal plate. 21. Body form dorsoventrally flattened (might corroborate synapomorphy 22). 22. Loss of posterior dorsolateral and posterior lateral plates. 23. Secretion of saccular otoliths. 24. Specialized pelvic girdle with long propterygia. K. 25. Further reduction of marginal plate size. 26. Marginal plate separated from nuchal plate by enlarged paranuchal plates. 27. Paranuchal plates with entry of main lateral line canal more posteriorly situated (70-50% of plate length). 28. External posterior margin of postnasal plate larger. L. 29. Elongated smaller marginal plate. 30. Postnasal plate with even larger posterior external margin. M. Autapomorphies of *Phyllolepis orvini* 31. Large size attained. 32. Separation of preorbital plates from mesial contact. X:loss of anterior median ventral plate; Y: loss of posterior median ventral plate.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AETHASPIS gp
STUERTZASPIS gp
KUJDANOWIASPIS gp
BRYANTOLEPIS group
WUTTAGOONASPIS
ANTARCTASPIS
PLACOLEPIS
AUSTROPHYLLOLEPIS
P. woodwardi
PHYLLOLEPIS
P. orvini
PHLYCTAENIOIDS
ACTINOLEPIDI
PHYLLOLEPIDI
WUTTAGOONASPIDI
Actinolepidoidei
EUARTHRODIRA

Fishes with depressiform bodies generally have small tails as there is no need for strong forward propulsion unless the head is streamlined for stability during swimming. A flat body is unsuitable for fast motion unless excessive lift is countered by large, manoeuvrable pectoral fins (Harris, 1938; Alexander, 1967). A long tail without macromeric squamation, as in phyllolepids, would result in a subanguilliform swimming style with a strong yawing effect. The unusual combination of a depressed body shape with a long tail is probably an adaptation for a fast take-off from a static benthic position. Unlike batoids and pleuronectiforms the take-off could not be initiated by pectoral fin undulation (Aleev, 1969), but relied on the powerful pushing action of the long tail. Further adaptation for a powerful thrust is seen in the axial skeleton of phyllolepids which is strengthened by articulating zygapophyses of the neural arches, as in coccosteid and higher euarthrodires (Stensiö, 1969: fig. 176).

The jaws and parasphenoid of phyllolepids indicate that the buccal cavity was large and adapted for gripping food rather than crushing, cutting, slicing or triturating. A gripping dentition implies the ability to catch active prey. The phyllolepid mouth was subterminal from the position of the toothplates, and the gape was probably restricted by the inefficient dermal neck joint and endocranial autostyly. A consideration of available food sources from the Mt Howitt deposit indicates that *Austrophyllolepis* probably fed on either soft mobile invertebrates or other fishes, most likely juvenile placoderms which swam close to the bottom of the lake.

The extensive dorsal laterosensory field of phyllolepids is associated with the formation of otoliths within the saccular cavities, and the absence of an open endolymphatic duct on the PNu plates. Otoliths act as statolith bodies responsive to any movements of water. In stationary fish this is advantageous for the detection of prey or predators especially in murky environments where vision is impeded (Lowenstein, 1971; Alexander, 1967). These features suggest strongly that phyllolepids were specialized benthic predators which relied more on an advanced acoustico-lateralis system than either vision or olfaction to detect prey. The reduced orbits of phyllolepids, and presumably reduced olfactory capsules, would be of little use in murky benthic habitats. I suggest that phyllolepids may have been slightly buried in the substrate waiting for unsuspecting prey to come swimming above them. The long tail of phyllolepids would provide the sudden thrust necessary to lurch up and catch the prey with the gripping dentition.

CLASSIFICATION AND FORMAL SYSTEMATICS

Order EUARTHRODIRA Gross 1932

Diagnosis: Placoderm fishes which primitively possess headshields with distinctive posterolateral corners and long obstantic margins; two pairs of supragnathals; endocranium perichondrally ossified or cartilaginous with well produced separate posterior postorbital processes, and a proportionately large cucullaris fossa; paravagal fossa reduced or absent. Trunkshield primitively with PL plates enclosing a small pectoral fenestra.

Remarks: The diagnosis of Young (1979: 344) is amended to include phyllolepid features described in this paper whilst accepting two assumptions of phyllolepid plesiomorphy: that PL plates and two pairs of supragnathals were probably present in primitive phyllolepids.

Suborder ACTINOLEPIDOIDEI Miles and Young 1977

Diagnosis: Euarthrodire placoderms which possess a sliding dermal neck joint and generally have a MG plate smaller than the PTO plate.

Infraorder: ACTINOLEPIDI Miles and Young 1977

Diagnosis: Actinolepidoid euarthrodires possessing AV plates and a supraorbital process on the endocranium.

Infraorder: WUTTAGOONASPIDI Miles and Young 1977

Diagnosis: Actinolepidoid euarthrodires possessing a long headshield with reduced orbits, small MG plates which may be incorporated or fused with the PTO plates and a long paraorbital plate below the orbit. AV plates present.
Remarks: This diagnosis is a short summary of the intrinsic characters of *Wuttagoonaspis* used in the above hypothesis of relationships. It will undoubtedly require amendment when this interesting genus is described in more detail.

Infraorder: PHYLLOLEPIDI nov.

Diagnosis: Actinolepidoid euarthrodires possessing a broad armour with an undifferentiated centronuchal area, and large PN plates between the PRO and PTO plates in contact with the Nu plate. Endocranium cartilaginous with ossified broad parasphenoid. Single pair of supragnathals present. Dermal cheek bones reduced to a single small SO element. Trunkshield of specialized forms without PL and PDL plates. Tail long, without scale cover, and long caudal fin. Pelvic girdle with long propterygial element.
Remarks: Diagnoses of the genus *Austrophyllolepis* and two species *A. ritchiei* and *A. youngi* are given and discussed in the section entitled systematic descriptions. Stensiö (1939) diagnosed the various species of the genus *Phyllolepis* and Ritchie (1984) has diagnosed *Placolepis budawangensis.* The order Phyllolepida Stensiö (1934) is made redundant, although the family Phyllolepidae Woodward (1891) can remain as a subdivision of the infraorder Phyllolepidi to include *Phyllolepis* and *Austrophyllolepis* until new material of phyllolepids comes to hand warranting revision of this scheme.

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The Phylogenetic Position of the Eugaleaspida in China

PAN JIANG (P'AN KIANG)
(Communicated by A. RITCHIE)

PAN JIANG. The phylogenetic position of the Eugaleaspida in China. *Proc. Linn. Soc. N.S.W.* 107 (3), (1983) 1984: 309-319.

Primitive vertebrates from the Middle Silurian and Lower Devonian rocks of China are grouped into a new major taxon, the Eugaleaspidomorphi, equivalent in status to the Cephalaspidomorphi and the Pteraspidomorphi. This is based upon a discussion of the cranial anatomy and the nature of the openings in the well ossified headshield.

Pan Jiang, Museum of Geology, Ministry of Geology and Mineral Resources, Xi-Si, West City, Beijing 100812, China. *A paper read at the Symposium on the* Evolution and Biogeography of Early Vertebrates, *Sydney and Canberra, February 1983; accepted for publication 18 April 1984, after critical review and revision.*

INTRODUCTION

This paper is essentially that read in February 1983 at the Symposium on the Evolution and Biogeography of Early Vertebrates under the sponsorship of The Australian Academy of Science, The Australian Museum and The Association of Australasian Palaeontologists, held in Sydney and Canberra.

Devonian agnathans were first listed from eastern Yunnan Province, south China (Fig. 1) by V. K. Ting and Y. L. Wang in 1937 (Ting and Wang, 1937; Young, 1939). It was not until 1965, however, that the Early Devonian agnathans from eastern Yunnan were first described by Liu Yuhai on the basis of material from near Qujing (Chutsing) (Liu, 1965). For the next eight years there was little new information about the Early Devonian Agnatha in China, until Liu (1973: 133-135) described another genus *Huananaspis,* placed in a new family Huananaspidae. Since then many new agnathan genera have been described (Liu, 1975; P'an, Wang and Liu, 1975; P'an and Wang, 1978; Cao, 1979; Pan and Wang, 1980, 1981; Wang *et al.,* 1980; Wang and Wang, 1982a, b), which may be placed in seven groups, as follows:

Middle Silurian
- Group 1 — Hanyangaspids
    - *Hanyangaspis guodingshanensis* P'an and Liu, in P'an *et al.*, 1975
    - *Latirostrasps chaohuensis* Wang, Xia and Chen, in Wang *et al.*, 1980

Early Devonian (including some in Late Silurian)
- Group 2 — Eugaleaspids
    - *Eugaleaspis changi* (Liu) 1976, emended Liu, 1980
    - *Eugaleaspis xujiachongensis* (Liu) 1975, emended Liu, 1980
    - *Yunnanogaleaspis major* Pan and Wang, 1980
    - *Sinogaleaspis shankouensis* Pan and Wang, 1980
    - *S. xikengensis* Pan and Wang, 1980
- Group 3 — Nanpanaspids
    - *Nanpanaspis microculus* Liu, 1965
- Group 4 — Polybranchiaspids
    - *Polybranchiaspids liaojiaoshanensis* Liu, 1965
    - *P. minor* Liu, 1975

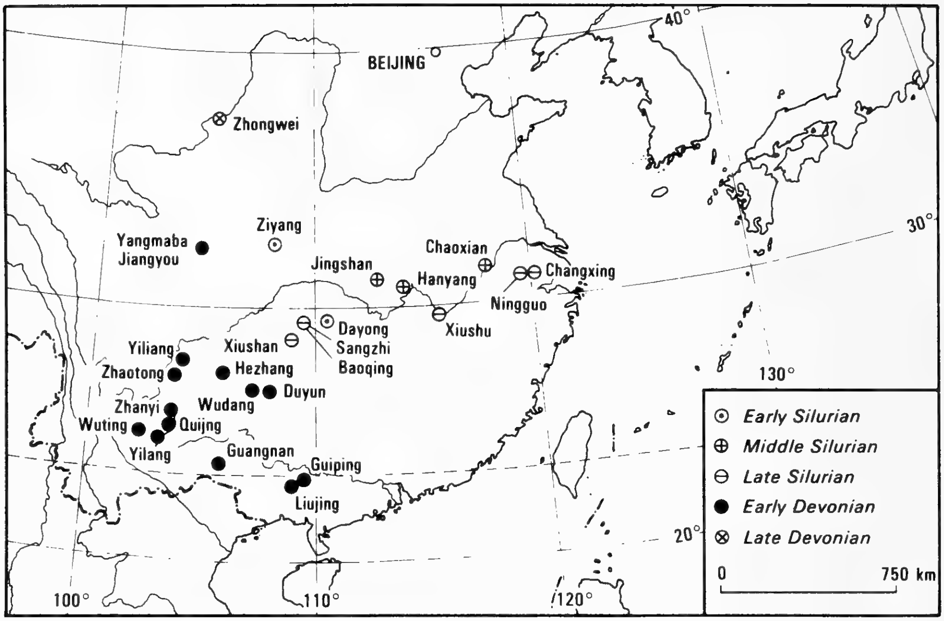

Fig. 1. Localities of Silurian and Devonian Agnatha in China.

P. yulongssus Liu, 1975
P. miandiancunensis P'an and Wang, 1978
P. zhanyiensis P'an and Wang, 1978
Siyingia altuspinosa Wang and Wang, 1982a
Laxaspis qujingensis Liu, 1975
L. rostrata Liu, 1975
Dongfangaspis major Liu, 1975
D. qujingensis Pan and Wang, 1981
Diandongaspis xishancunensis Liu, 1975
Damaspis vartus Wang and Wang, 1982b
Cyclodiscaspis ctenus Liu, 1975
Kwangnanaspis subtriangularis Cao, 1979

Group 5 — Duyunolepids
Duyunolepis paoyangensis (P'an and Wang) 1978, emended Pan and Wang, 1982
Paraduyunaspis hezhangensis P'an and Wang, 1978
Neoduyunaspis minuta P'an and Wang, 1978

Group 6 — Huananaspids
Huananaspis wudinensis Liu, 1973
Asiaspis expansa P'an, in P'an *et al.*, 1975
Sanqiaspis rostrata Liu, 1975
S. zhaotongensis Liu, 1975
S. sichuanensis P'an and Wang, 1978
Sanchaspis magalarostrata Pan and Wang, 1981

Group 7 — Lungmenshanaspids
Lungmenshanaspis kiangyouensis P'an and Wang, in P'an *et al.*, 1975

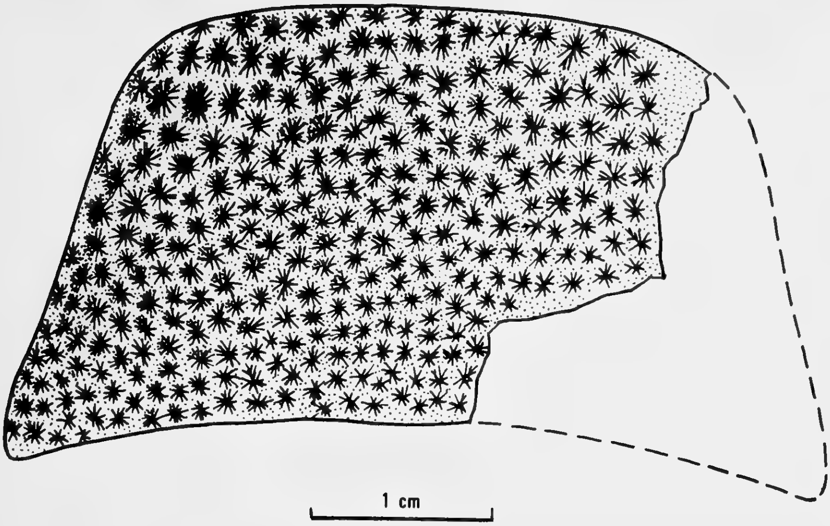

Fig. 2. Latirostraspis chaohuensis Wang, Xia and Chen. An example of the trapezoidal anterior ventral plate (VA001, Museum of Geology, Beijing). Middle Silurian, Fentou Formation, Chaohu, Chaoxian County, Anhui Province.

> *Sinoszechuanaspis yanmenpaensis* (P'an and Wang) in P'an *et al.,* 1975, emended P'an and Wang, 1978
> *Qingmenaspis microculus* Pan and Wang, 1981

Latirostraspis chaohuensis (Wang *et al.,* 1980), a genus within the Hanyangaspidae (P'an, Wang and Liu, 1975) differs slightly from the other members of the group in the shape of the anterior ventral plate (Fig. 2), and in the position of the anterior dorsal median opening.

These various forms, which may generally be referred to as 'eugaleaspidomorphs', include agnathans of varying size. Typically, the anterior portion of the body is covered dorsally and laterally by a single plate, forming the cephalic shield. Along the rostral and lateral margins the cephalic shield is folded ventrally, forming an even, hemicyclic, ventral rim in *Polybranchiaspis liaojiaoshanensis* (Liu, 1975: fig. 5B) and *Asiaspis expansa* (Fig. 3), or an even, ventral rim on either side of which is joined the interzonal part of the cephalic shield in *Hanyangaspis guodingshanensis* (Fig. 5). A section through the posterior part of the cephalic shield in *Asiaspis expansa* is shown in Fig. 3**B.** This genus is similar in several features to the polybranchiaspids, but differs from them in that (a) the rostral process and cornua are well developed, (b) there is a different cross-section of the posterior part of the shield (Fig. 3**B**, **C**), and (c) the shield has a higher lateral wall.

The Eugaleaspidomorphi, proposed here as a new endemic group of Agnatha, are so far only known from Early Silurian (Llandovery) to Late Devonian (Famennian) strata in China (Fig. 1), but very possibly they also occur elsewhere in southeast Asia, such as in Vietnam. Relevant new discoveries in China, not yet described, include polybranchiaspids and hanyangaspids which were recently (1981-82) recovered from an Early Silurian formation in western Hunan Province of south China, and in southern Shaanxi Province, west China. In the same year, many incomplete cephalic

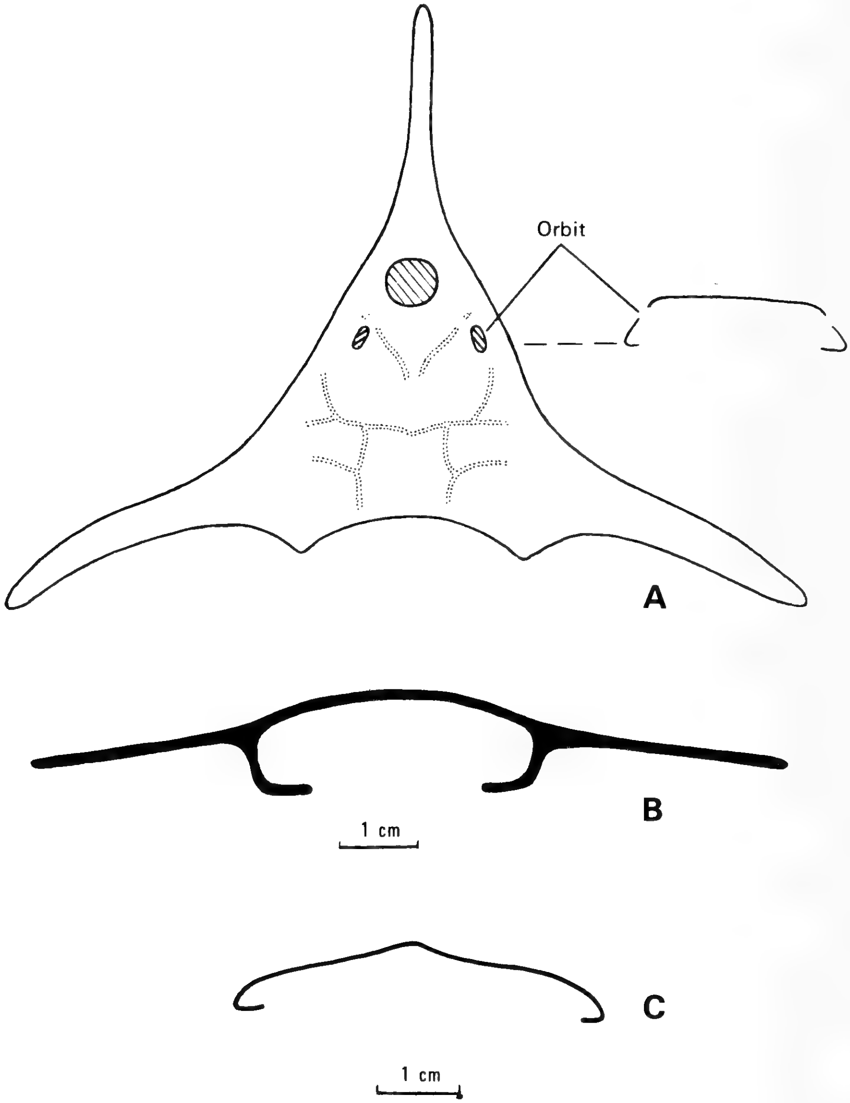

Fig. 3. **A, B.** *Asiaspis expansa* P'an. **A,** Cephalic shield in dorsal view, showing section through the orbital region (after V1314a, Museum of Geology, Beijing). **B,** section through the posterior part of the shield. **C,** *Polybranchiaspis liaojiaoshanensis* Liu. Section through the posterior part of the cephalic shield.

shields of a large polybranchiaspid were discovered in Late Devonian red sandstones in Ningxia, west China. These polybranchiaspids are associated with the antiarch *Remigolepis*, and are the youngest representatives of the group so far known from China.

DISCUSSION

As the eugaleaspidomorphs are unlike any previously described agnathans, their relationships to the other known major groups have become a subject of controversy (Liu, 1975; Janvier, 1975; Halstead, Liu and P'an, 1979). The various groups possess

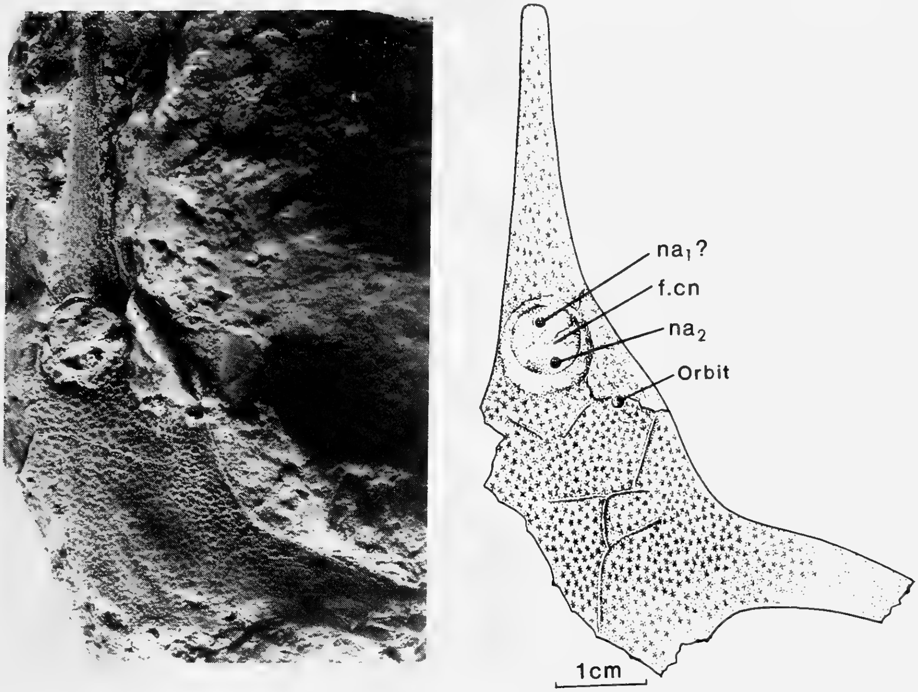

Fig. 4. Asiaspis expansa P'an. Headshield in dorsal aspect (V1336, Museum of Geology, Beijing) *f.cn,* circumnasal fossa; *na*$_1$, opening of hypophysial duct; *na*$_2$, nasal opening.

a bony carapace covering the anterior part of the body dorsally and laterally, as in osteostracans. Their three main dorsal openings on the cephalic shield, and separate gill openings, may be regarded as specializations shared with osteostracans and anaspids. The most controversial structure is the dorsal median opening. This has been observed in many new fossils discovered in south China since 1965 (e.g. *Sinogaleaspis, Yunnanogaleaspis, Sanchaspis, Kwangnanaspis, Hanyangaspis,* etc.). The dorsal median opening was first interpreted as a naso-hypophysial opening in *Eugaleaspis* (very long, slit-like in form) by comparison to that of the Cephalaspidomorphi, and as a mouth in *Polybranchiaspis,* comparable to that in some Heterostraci (Liu, 1965, 1973, 1975; P'an *et al.,* 1975: P'an and Wang, 1978; Cao, 1979).

Halstead *et al.* (1979) described small plates in *Polybranchiaspis* and *Galeaspis* which apparently covered the dorsal median opening in life. However, it is surprising that among more than two hundred excellently-preserved specimens of eugaleaspidomorphs recently collected in Yunnan, Guizhou (Kueichow), Sichuan (Szechuan), Guangxi (Kwangsi), Hunan, Hubei, Jiangxi (Kiangsi), Zhejian (Chekian), and Anhui (Fig. 1), no similar cover plate has been observed in position over the opening. It is my opinion that the dorsal median opening served as an inhalent nasohypophysial opening, and there is also evidence that very possibly this opened directly into the buccal cavity, as in hagfish (Myxinoidea). If this evidence and interpretation are correct, the retention of a naso-pharyngeal duct in eugaleaspidomorphs would be evidence against grouping them with the Cephalaspidomorphi.

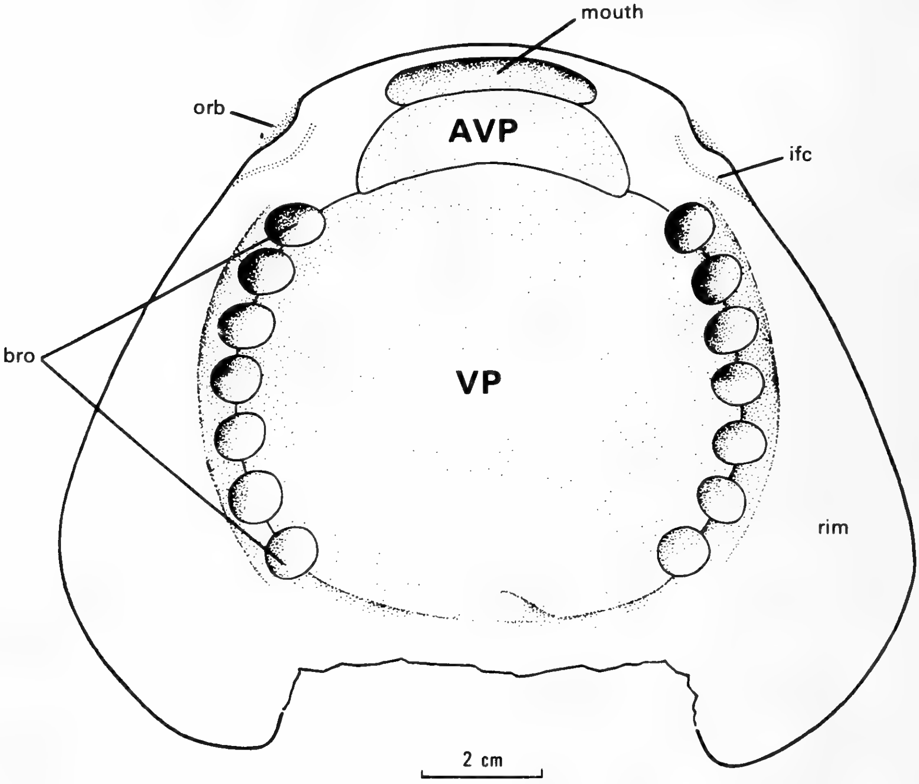

Fig. 5. Hanyangaspis guodingshanensis P'an and Liu. Articulated specimen in ventral view, showing the circular ventral shield replacing the zone of polygonal tesserae. Other features are the seven branchial openings, the shape of the anteroventral plate, and the broad ventral rim (VH001, Museum of Geology, Beijing). *AVP,* anteroventral plate; *bro,* external branchial opening; *ifc,* infraorbital sensory canal; *orb,* orbit; *VP,* ventral shield.

Recently two very small tubes have been discovered within the dorsal median opening of *Asiaspis expansa* (P'an *et al.,* 1975: pl. 6, fig. 2). The anterior one is interpreted as the opening of the hypophysial duct or pharyngeal duct (na_1?, Fig. 4), and the posterior one as a nasal opening proper (na_2). The dorsal median opening is termed a circumnasal fossa *(f.cn).* In addition, in this specimen there is no visible pineal opening between the orbits.

Under this interpretation the inner margin of the rostral ventral rim marks the anterior margin of the mouth, as in cephalaspids and some heterostracans. This region is preserved in many new specimens (e.g. *Hanyangaspis guodingshanensis* P'an and Liu, *Dongfangaspis* spp., *Polybranchiaspis* sp., and some new genera from south China). The anterior margin of the antero-ventral plate or ventral shield must have marked the posterior margin of the mouth in eugaleaspidomorphs (Fig. 5).

The internal anatomy of the eugaleaspid carapace is now well known. The round structure arising from beneath the anterior and posterior semi-circular canals and situated between them and the brain in *Duyunolepis* may be interpreted as the sacculus (see Halstead, 1979: fig. 3).

Each branchial chamber (gill pouch) is associated with a separate branchial

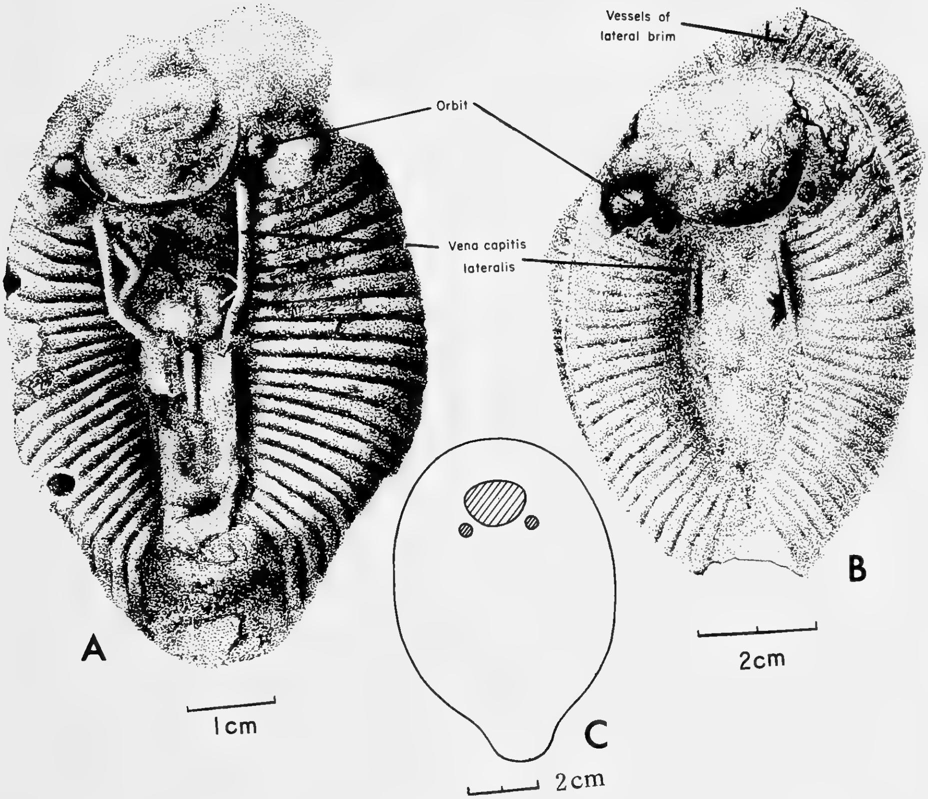

Fig. 6. Duyunolepis ('Duyunaspis') paoyangensis (P'an and Wang). Casts of the internal cavities and canals of the cephalic shield in dorsal view. **A,** VG001; **B,** VG002 (Museum of Geology, Beijing). Early Devonian, lowermost part of the Shujiapin Formation, Paoyang, Duyu, Guizhou (Kueichow) Province. **C.** sketch of cephalic shield in dorsal view, showing position of the orbits adjacent to the posterolateral margins of the dorsal median opening.

opening along the ventrolateral margin of the cephalic shield in *Asiaspis, Polybranchiaspis, Hanyangaspis,* and *Duyunolepis.* Markings on the undersurface of the dorsal shield have been interpreted by Liu Yuhai, Wang Shitao, and the author as representing the former position of the upper parts of branchial chambers, but alternatively they were regarded as 'somites or segmental muscle blocks' by Halstead (1979: 836). In the author's opinion these structures can be best interpreted as the upper parts of the branchial chambers.

The positions of the nasal sacs and lobes are more difficult to decide, but in all known jawless vertebrates, the olfactory organ is never very far from the telencephalic division of the brain cavity. It would thus be more appropriate to consider the olfactory organ of *Duyunolepis paoyangensis* and *Paraduyunaspis hezhangensis* as situated in the posterior part of the recess surrounding the naso-hypophysial cavity, as already proposed by P'an and Wang (1978). An alternative interpretation by Halstead (1979: fig. 3) placed the nasal sac in the recess interpreted here as the orbit. Halstead's interpretation has been rejected by Janvier (1981), who supports our original interpretation (P'an and Wang, 1978) of the position of the nasal sac. However Janvier

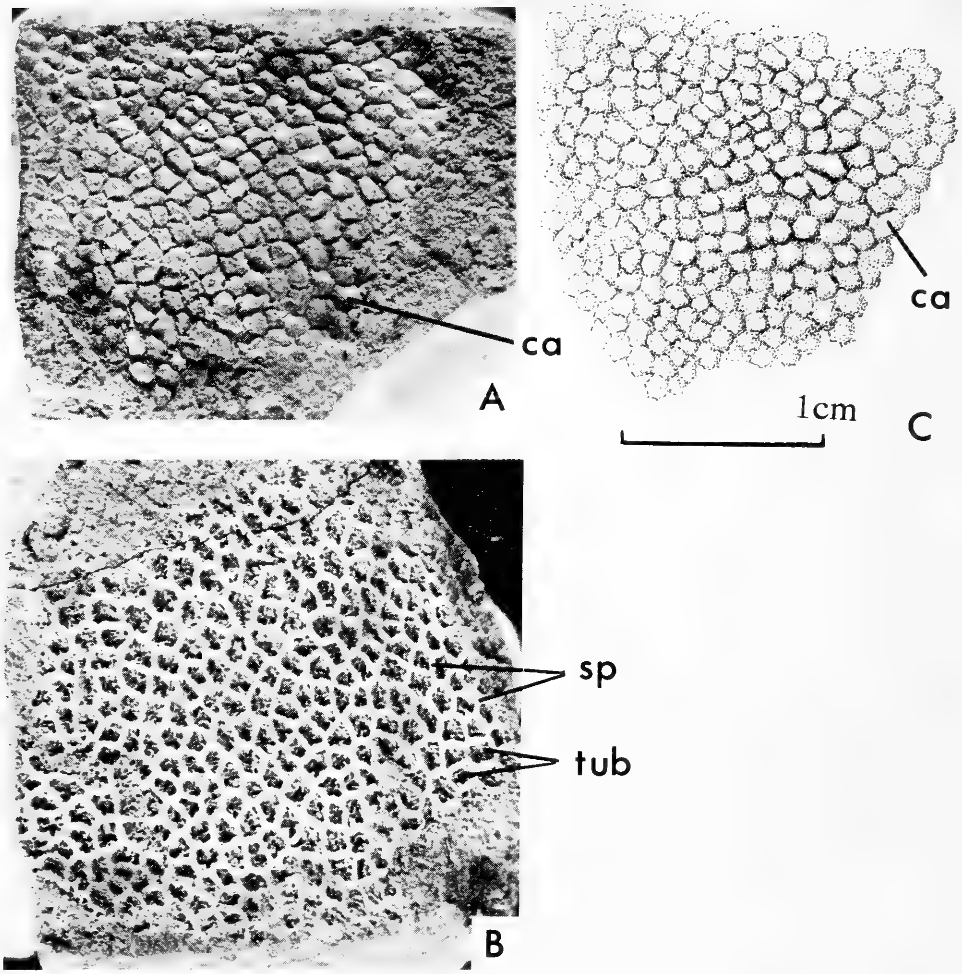

Fig. 7. Specimen showing the structure of the eugaleaspid exoskeleton (possibly *Sinogaleaspis* sp.). VJ001 (Museum of Geology, Beijing) from the Late Silurian-Early Devonian Xiking Formation, Xiking, Xiushui, Jiangxi Province. **A,** natural cast of the internal surface of a fragment; **B,** natural cast of the external surface of the same specimen, showing impressions of tubercles of the dermal ornament *(tub),* and the septa of honeycombs of the cancellous layer *(sp);* **C,** redrawn from photograph A, showing impressions of honeycomb structure of the cancellous layer *(ca).*

has followed Halstead (1979) in interpreting the 'lateral elevations' of P'an and Wang (1978: fig. 1, *pmic*) as the orbits. On the evidence of additional specimens (Fig. 6), it is maintained that the orbits of *Duyunolepis* are positioned adjacent to the posterolateral margins of the dorsal median opening, and thus in a somewhat different position to other genera (*Eugaleaspis, Polybranchiaspis, Hanyangaspis, Huananaspis,* etc.). Halstead (1979) also reinterpreted the canal first identified (P'an and Wang, 1978) as for a branch of the vagus nerve. According to Halstead this canal contained the dorsal aorta, but there are arguments against this (Janvier, 1981: 147). This paired canal, which runs posterolaterally from the myelencephalic division of the brain cavity along the inner side of the branchial chambers, is best interpreted as for a branch of the vagus nerve (X).

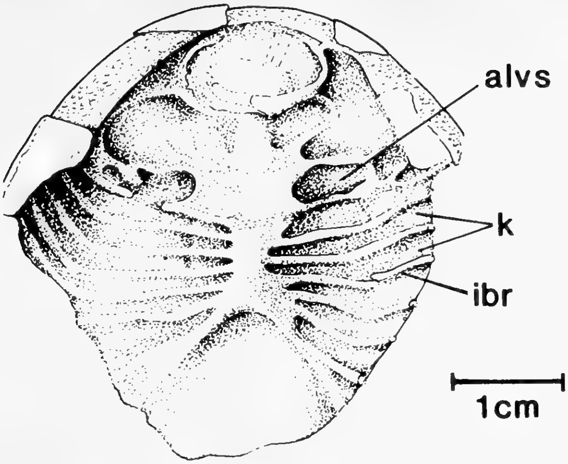

Fig. 8. Polybranchiaspis liaojiaoshanensis Liu. Internal view of head shield (V3027, Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing). *alvs,* anterior sinus for vena capitis lateralis; *k,* position of the dorsal part of the branchial fossae; *ibr,* interbranchial ridge. (modified after Halstead, 1979: fig. 1).

By comparison, the position of the anterior sinus for the vena capitis lateralis in *Polybranchiaspis liaojiaoshanensis* (Fig. 8) is in the region labelled 'internal nasal fossa' and 'internal nostralis' by Liu (1975: fig. 5C). The 'internal nostralis' is more difficult to identify, but the position of the sinus is likely to be adjacent to the anterior part of the branchial area, and rather as in *Duyunolepis paoyangensis* and *Paraduyunaspis hezhangensis* (P'an and Wang, 1978: 300-311, figs 1-5, pls 27, 37).

Some very fine ridges occur around the dorsal median cavity (opening) in the holotype of *Paraduyunaspis hezhangensis* (see P'an and Wang, 1978: 307-309, figs 4, 5, pl. 27, fig. 4), which supports the interpretation of the dorsal median cavity as an olfactory organ, with these ridges (Fig. 9) representing traces of the olfactory epithelium. This would be rather as in Heterostraci (e.g. Janvier, 1981: fig. 12D), but there is no evidence in this specimen as to whether this cavity opened directly into the buccal cavity or not.

As already pointed out, the eugaleaspidomorphs, Osteostraci, and Anaspida all have separate gill openings and three main dorsal openings on the head. Considering also the well ossified cephalic shield, there is an apparent similarity between eugaleaspidomorphs and the Osteostraci, with the exception of the presence of dorsal and lateral sensory fields and a pineal opening in the latter.

Features which appear to link the eugaleaspidomorphs with the heterostracans include a simple brain, pineal body covered by the external armour, and a very large ventral shield. In addition, the middle layer of the exoskeleton is very similar to the cancellous layer (honeycomb structure) in that of the Heterostraci (Fig. 7).

The phylogeny of eugaleaspidomorphs is still relatively obscure, mainly because of the uncertainty as to their sister group (Janvier, 1981: 148, fig. 14D-F). In the author's opinion, the various eugaleaspids and polybranchiaspids possessed a combination of osteostracan and heterostracan features (Stensiö, 1964, 1968). They are neither typical Cephalaspidomorphi nor true Pteraspidomorphi. To conclude, the author believes that the hanyangaspid, eugaleaspid, polybranchiaspid, nanpanaspid, duyunolepid, huananaspid, and other new Chinese groups can be united into a single major high-rank taxon, the Eugaleaspidomorphi, equivalent in status to the Cephalaspidomorphi and to the Pteraspidomorphi.

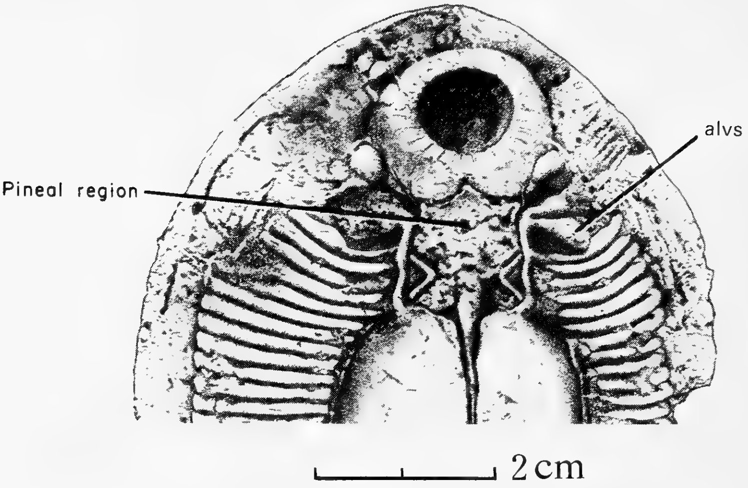

Fig. 9. Paraduyunaspis hezhangensis P'an and Wang. Anterior part of a cast of the internal cavities and canals of the cephalic shield in dorsal view, showing fine ridges around the opening of the dorsal median cavity (holotype, V1543, Museum of Geology, Beijing). *alvs,* anterior sinus for vena capitis lateralis.

ACKNOWLEDGEMENTS

I wish to thank Professor K. S. W. Campbell, Professor D. L. Dineley, Dr P. Forey, Dr D. F. Goujet, Dr A. Ritchie, Dr H. P. Schultze and Dr G. C. Young for fruitful discussions in Sydney. I am grateful to Dr L. B. Halstead and Dr P. Janvier for valuable advice and discussions in Beijing (Peking). Acknowledgement goes to Professor D. L. Dineley, Dr P. Forey, and Dr G. C. Young for valuable help with the manuscript.

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A new Placoderm, *Placolepis* gen. nov. (Phyllolepidae), from the Late Devonian of New South Wales, Australia

A. RITCHIE

RITCHIE, A. A new placoderm, *Placolepis* gen. nov. (Phyllolepidae) from the Late Devonian of New South Wales, Australia. *Proc. Linn. Soc. N.S.W.* 107 (3), (1983) 1984: 321-353.

A rich concentration of Late Devonian (Frasnian) placoderm fish remains from a horizon low in the Devonian sequence on the western margin of the Budawang Range, southeastern New South Wales, Australia, contains abundant well-preserved plates of an antiarch, *Bothriolepis* sp., associated with a distinctive new genus and species of phyllolepid.

Placolepis budawangensis gen. et sp. nov. is closely related to, but readily distinguishable from, *Phyllolepis* ss. from the Late Devonian of Europe (including European U.S.S.R.), Greenland, Australia and Antarctica. The poorly known *Antarctaspis* White, from the Late Devonian of Antarctica is not considered here to be a phyllolepid, leaving *Phyllolepis* and *Placolepis* gen. nov. as the only two known genera of the family Phyllolepidae whose origins and affinities with other placoderms remain obscure.

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INTRODUCTION

Phyllolepis, a Late Devonian placoderm, is a distinctive, specialized armoured fish whose remains are widely distributed in continental deposits in Greenland, Europe, Australia and Antarctica. Until recently *Phyllolepis* has been the sole genus in the family Phyllolepidae Woodward (1891) with seven described species and several more occurrences awaiting description. The only known articulated specimens have been those from northern hemisphere sites and the origins and relationships of *Phyllolepis* have been the subject of considerable discussion.

New discoveries of phyllolepid remains, including well-preserved articulated specimens, from sites in southeastern Australia throw new light on the morphology and relationships of this placoderm. From the Mount Howitt area east of Mansfield, Victoria (Marsden, 1976: 122) have come many fine specimens of a new species of *Phyllolepis* currently under preparation and study by Mr J. Long, Monash University. The other major new phyllolepid find, the subject of this paper, came to light in late 1980 from a site on the western margin of the Budawang Range, northeast of Braidwood in southern New South Wales.

From personal examination of the Mt Howitt and Budawang Range phyllolepid material the writer has confirmed that they represent two quite distinct taxa and the New South Wales material is sufficiently different from all known examples of *Phyllolepis* spp. that it must be placed in a new genus for which the name *Placolepis* is proposed. *Placolepis* gen. nov. is thus only the second genus recognized in the Phyllolepidae.

Until recently all known *Phyllolepis* occurrences came from the youngest Devonian continental deposits (Famennian) and there were even suggestions that it may have survived into Early Carboniferous times. From the Australian occurrences of phyllolepids it is now clear that the genus is present not only in the Famennian but also in the preceding Frasnian stage, reviving an earlier suspicion that the Phyllolepidae, which make rather a sudden late appearance in the northern geological record, perhaps originated in the southern hemisphere (Young, 1974, 1981).

All authors with the exception of Denison (1978: 41) have regarded *Phyllolepis* as the sole genus in the Order Phyllolepida. The writer does not accept Denison's claim that the very poorly known *Antarctaspis* White (1968) from the Late Devonian Aztec Siltstone of southern Victoria Land, Antarctica, should be included in the Phyllolepida; *Phyllolepis* ss. is now known to be present in the Aztec Siltstone vertebrate fauna.

PREVIOUS DISCOVERIES OF *PHYLLOLEPIS*

Since its first discovery in Europe in the early 19th century the nature, origins and relationships of *Phyllolepis* have been in dispute. The first remains described came from the Late Devonian Rosebrae Beds (Upper Old Red Sandstone) of northeastern Scotland. *Phyllolepis concentrica* Agassiz (1844) was a moderately large species represented only by a few isolated plates. Isolated phyllolepid plates also came to light in the 1850s during the excavation of the famous Upper Old Red Sandstone (or Late Devonian) site at Dura Den, Fife, Scotland. As Woodward (1891: 313) pointed out these problematical plates were variously referred to 'Holoptychian Crossopterygii' and also to the 'head-bones of Palaeozoic Dipnoi'. Woodward himself preferred 'the suggestion of Newberry that the plates are truly referable to some so-called "Placoderm", though we would compare them with *Coccosteus* and its allies rather than with *Pterichthys*'.

It is rather ironic, however, that when an almost complete specimen of *Phyllolepis* came to light during renewed excavation of the Dura Den site in 1912 and 1913 Woodward felt compelled to reinterpret it as a fossil agnathan (Woodward, 1915: 122-3, fig. 4). He concluded that 'there is, therefore, not much doubt that *Phyllolepis* is a genus of Ostracoderms most nearly allied to the Drepanaspidae or Psammosteidae' (see also Woodward, 1920: 31, fig. 3).

The earliest records of phyllolepids from continental Europe were of small isolated plates from the Famennian in two areas of Belgium. Lohest (1888: 157-167, pls 10, 11) described two genera and three species (*Phyllolepis undulata* Lohest, *P. corneti* Lohest and *Pentagonolepis konincki* Lohest).

In a re-examination of these forms Leriche (1930: 7-14, pls 1, 2) concluded that there was only evidence for one species *P. undulata* Lohest and that the other two, *P. corneti* and *Pentagonolepis konincki* were junior synonyms. Leriche accepted Woodward's interpretation of *Phyllolepis* as a heterostracan ostracoderm allied to the Drepanaspidae.

The discovery of abundant well-preserved Late Devonian fish remains in East Greenland in the late 1920s and early 1930s provided the solution. *Phyllolepis orvini* Heintz (1930: 31-46, pls 1-4) has subsequently become the best known species of this genus through the later discovery of abundant isolated plates and a few partly articulated individuals, and from the accounts of Stensiö (1934, 1936, 1939). Stensiö and Gross (1934) simultaneously came to the conclusion that *Phyllolepis* was not an agnathan and ostracoderm but a gnathostome and a placoderm.

Phyllolepis orvini Heintz (Figs 2**A**, **B**, 14**A**) was a large phyllolepid in which the head and trunk shields reached a length of over 40 cm. A second species, *P. soederberghi* Stensiö (1934) is now regarded as synonymous with *P. orvini*. Stensiö later (1939) described another species *P. nielseni* from the Lower Remigolepis Series of East Greenland.

Stensiö reviewed the Belgian material, at first (Stensiö, 1934: 34) accepting only *P. undulata* Lohest but later (Stensiö, 1939: 10, text figs 4B, 6B) resurrecting *P. konincki* (Lohest) as a valid species. Initially, he (Stensiö, 1934, 1936) accepted Traquair and

Woodward's original identification of the *Phyllolepis* material from the Scottish Dura Den fauna as *P. concentrica* Agassiz but later (Stensiö, 1939) placed it in a separate species, *Phyllolepis woodwardi* Stensiö.

Phyllolepis has also been recorded from the U.S.S.R. *P. tolli* Vasiliauskas (1963: 427-30, figs 3-6, pls 1-4; cf. also Obruchev, 1967: 255, pl. 4, fig. 4) is known from isolated plates from the Famennian of Latvia in the Baltic area and the genus is also reported from Northern Timan in northwestern U.S.S.R.

The only other records of *Phyllolepis* come from the Late Devonian of Australia and Antarctica but, until the recent discoveries, none has been sufficiently complete to warrant specific description.

Fragmentary plates attributed to *Phyllolepis*, largely on the basis of their distinctive ornament, come from the Late Devonian of Taggerty, central Victoria (Hills, 1931: 212-3, fig. 2; 1936: 164, pl. XII, figs 1, 2); from Hervey's Range, northeast of Parkes, central New South Wales (Hills, 1932: 852, pl. LVI, figs 2, 3); from Mansfield, central Victoria (Hills, 1936: 164, text fig. 4, pl. XII); and from the Dulcie Range, Northern Territory, 320 km northeast of Alice Springs, N.T. (Hills, 1959: 175, pl. VIII, figs D, E).

Another supposed *Phyllolepis* occurrence, from the Mulga Downs Group of western New South Wales (Rade, 1964) has since been shown to be mistaken. Placoderm plates with an ornament superficially similar to *Phyllolepis* were later shown to belong to an unusual Early-Middle Devonian genus, *Wuttagoonaspis,* whose relationships to *Phyllolepis* and to the Arthrodira *ss.* are still uncertain (Ritchie, 1969, 1973; cf. also Miles and Young, 1977; Young, 1980).

Elsewhere in eastern Australia isolated phyllolepid plates have been recovered from: the Cloghnan Shale, Jemalong Range, west of Forbes, N.S.W. (Ritchie, 1975; Campbell and Bell, 1977); Catombal Group, northwest of Canowindra, N.S.W.; 'Khan Yunis' near Krawaree, southeast of Captains Flat, N.S.W. (Johnson, 1964); near Pambula, southeast coast, N.S.W. (Young *in* Fergusson *et al.,* 1979); Freestone Creek, northeast of Briagolong, eastern Victoria (discovered by the writer, early 1981).

In Victoria however the most important phyllolepid occurrence is unquestionably that from the Frasnian Bindaree sequence, near the head of the Howqua River, east of Mansfield. The Mount Howitt fauna, as it is generally called, includes several genera of dipnoans, acanthodians and palaeoniscids in association with *Bothriolepis, Groenlandaspis* and phyllolepids. Many of the phyllolepid specimens are articulated and virtually complete.

It is now clear that, in eastern and central Australia, *Phyllolepis* spp. occur over a much greater stratigraphic range than in the northern hemisphere where the genus appeared suddenly in the Famennian and thus forms a useful index fossil for that stage. In Australia *Phyllolepis* occurs usually in association with species (mostly awaiting description) of *Bothriolepis, Remigolepis, Groenlandaspis* and others in various combinations which make it of more limited use for stratigraphic purposes, at least until the associated faunas and sequences have been studied in detail.

DISCOVERY OF *PLACOLEPIS* GEN. NOV.

In October 1980 a student party from the New South Wales Institute of Technology, Sydney, led by Dr R. Rogerson, discovered a rich Late Devonian fish site on the western limb of the Budawang Range Synclinorium in southeastern N.S.W. (Fig. 1). Several blocks containing abundant, well-preserved fish plates were forwarded for identification to the writer by Dr G. Gibbons, head of the department of Geology, N.S.W.I.T.

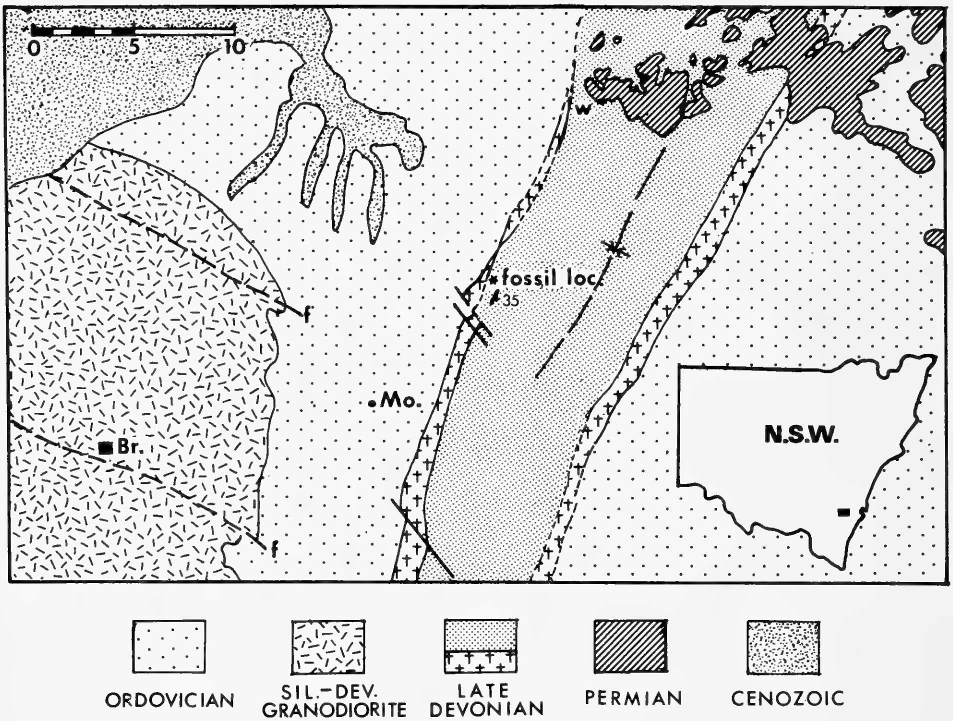


Fig. 1. Geology of the area east of Braidwood, New South Wales, showing the location of the *Placolepis/Bothriolepis* site on the west side of the NNE-SSW Budawang Range synclinorium. The fish bed occurs near the junction of the Comerong Volcanics (crosses), the basal Devonian formation in this area, and the overlying Merrimbula Group (fine stipple).
Br. = Braidwood (surrounded by Braidwood Batholith); Mo = Mongarlowe; * = fossil fish site; w = Wog Wog marine invertebrate fauna (Frasnian). Scale in km.

The fossil site lies on the south bank of a northern tributary of Nettletons Creek, 9 km northeast of Mongarlowe, east of Braidwood, New South Wales (G.R. 014336; Corang sheet 8927-111-N).

The bulk of the material consisted of dissociated plates of two typical Late Devonian placoderm fishes, the antiarch *Bothriolepis* and what, at first sight, appeared to be *Phyllolepis*. In November 1980 a preliminary excavation, carried out by the writer, Mr R. K. Jones, Mr M. Leu and Dr Rogerson, producing most of the material described here. In January 1982 the writer, Mr Jones, Mr B. A. Ritchie and Mr T. Cogger re-excavated the site and clarified the position of the fish horizon in the section and its relationship to the marine invertebrate faunas of the overlying Merrimbula Group

The fish plates occurred at various levels throughout a red and green mottled siltstone unit about 75 cm thick. Although *Bothriolepis* and phyllolepid plates predominated several specimens of crossopterygian plates and scales and an acanthodian fin-spine were also recovered. Some of the *Bothriolepis* trunk plates and pectoral fin skeletons were still articulated and the bulk of the fish material, although dissociated, had clearly not moved very far after death. One bedding plane almost completely covered with *Bothriolepis* plates also bore an assemblage of phyllolepid plates almost certainly derived from the head and trunk shield of a single individual, the first such occurrence of a phyllolepid from the Devonian of New South Wales. This specimen, AM F.61748 (Fig. 3**A**, **B**) has been selected as the holotype of a new genus and species of phyllolepid, *Placolepis budawangensis*, described here.

The Nettletons Creek phyllolepid material consists mainly of isolated head and trunk plates most of which were apparently complete at the time of burial and show little evidence of transport or abrasion. Many of the larger plates had been extensively fractured after burial, probably during the compaction of the sediment but, for the most part, even the smallest fragments have retained their original association. In the majority of specimens the original bone material, although still present, had either weathered or become so fragile as to be irrecoverable. The bulk of the material was therefore prepared as external moulds, the remaining bone being removed by dilute hydrochloric acid before casting in latex.

STRATIGRAPHIC SETTING

The Budawang Range Synclinorium, on the west flank of which the *Placolepis/Bothriolepis* assemblage was discovered (Fig. 1) forms the northern part of an extensive, elongate and narrow rift zone which extends some 300 km from south of Eden on the far southeast coast of New South Wales, northwards to Yalwal, west of Nowra, on the southern margins of the Sydney Basin.

McIlveen (1975: fig. 1, table 2) in an overall account of the Eden-Comerong-Yalwal Rift Zone, reviewed earlier work and demonstrated the clear similarities and correlations between the Eden-Merimbula Devonian sequence and that of the more extensive Budawang Range Synclinorium. Both begin with a considerable thickness of acid, and some basic, volcanics of probable Givetian-Frasnian age, succeeded by a much thicker sedimentary sequence, the Merrimbula Group, of Frasnian-Famennian age. The Eden-Merimbula area has since been shown by Fergusson *et al.* (1979) to be much more complex than had previously been thought. The earlier volcanic sequence, formerly the 'Eden Rhyolite' and the 'Locheil Formation', now renamed the Boyd Volcanic Complex, apparently formed in a terrestrial zone of extension before the whole area was blanketed by the Merrimbula Group

Farther north, in the Budawang Range Synclinorium, the Devonian sequence is confined within a narrow belt 160 km long and 6-13 km wide. The basal volcanic suite, the Comerong Volcanics, consists of rhyolite, felsite, basalt, rhyolite breccia and interbedded sediments overlain, apparently conformably, by the sediments of the Merrimbula Group.

Earlier estimates of the thickness of the Merrimbula Group sediments in the Budawang Range (McElroy and Rose, 1962) have been shown to be conservative by Powell *(pers. comm.)*. In early 1982 Powell and two students from Macquarie University measured detailed E-W sections through the Budawang Range along a line some 10 km north of the fish site. They were able to confirm that in this region the structure is a simple syncline with dips up to 70° on the eastern limb and 90° on the western limb. The total thickness of the Merrimbula Group here is estimated to be over 4 km, considerably greater than any recorded in the Eden-Merimbula area where Steiner (1973) estimated it to be some 870 m thick.

The best evidence for the age of the lower part of the Merrimbula Group in the Budawang Range comes from a rich marine fossil assemblage recovered from Wog Wog, 8 km north of Nettletons Creek and the fish locality. Wood (*in* McElroy and Rose, 1962: 59, loc. U.P.4) identified *Orthis* sp., *Chonetes* sp., *Cyrtospirifer* sp., productids, *Bellerophon* sp., *Tentaculites* sp., *Pterinea* sp. and crinoid fragments, a characteristic Late Devonian assemblage but one that needs revision and detailed study. The presence of tentaculitids in abundance is particularly significant as this group is not known to have survived into Famennian times. The Wog Wog faunal assemblage is thus Frasnian in age. It is estimated to lie several 100 m above the youngest unit of the Comerong Volcanics in the same area.

In the tributary north of Nettletons Creek the only known exposure of the *Placolepis/Bothriolepis* fish bed lies less than 2 m above the youngest exposed rhyolite of the Comerong Volcanics. Powell (1983) and Jones *(pers. comm.)* measured the section independently and estimate that the fish bed lies in the lower part of the Comerong Volcanics, at least 350 m above the base and about 700 m below the junction with the overlying Merrimbula Group.

Mr R. K. Jones measured the Devonian section upstream from the fish-bed to establish its relationship with the later marine incursions in the Merrimbula Group. He located at least three distinct marine horizons containing abundant, but poorly preserved, shelly faunas none of which, at present, can be accurately correlated with the Wog Wog occurrence farther north.

The first marine band, 920 m above the fish-bed, produced abundant productid brachiopods, crinoid ossicles and small ramose bryozoans but none well enough preserved for specific identification.

The higher marine horizons, 1390 m and 1520 m above the fish-bed, contain abundant brachiopods (*Cyrtospirifer* cf. *subdisjunctus, Sinotectirostrum* sp. a new species of rhynchonellid and occasional productids) together with a bivalve similar to *'Leptodesma'*. This assemblage is reminiscent of the Lambie facies marine faunas found at Mt Lambie and Gap Creek in central N.S.W. which are thought to be Famennian in age (R. K. Jones *pers. comm.*).

The Wog Wog Frasnian marine assemblage is certainly higher stratigraphically than the lower part of the Comerong Volcanics (containing the fish-bed) but older than the marine horizons located in the Nettletons Creek section. The latter section must therefore include the Frasnian/Famennian boundary although this cannot be precisely located on available evidence.

At the northern end of the Budawang Range Synclinorium the Devonian sequence is covered by the Permian of the Sydney Basin and is only exposed in rugged and relatively inaccessible tributaries of the Shoalhaven River. In two of these, Ettrema and Jones Creeks, a 30 m thick limestone unit has been shown to contain a late Frasnian conodont fauna associated with atrypid brachiopods, rare phillipsastreid corals and *Cyrtospirifer* (Pickett, 1973). The Ettrema Limestone Member, the only known Frasnian limestone in New South Wales, is believed to be equivalent to an horizon in the Merrimbula Group.

Other information relevant to the age of the *Placolepis/Bothriolepis* assemblage comes from the Eden-Pambula area of southeastern N.S.W. Young (*in* Fergusson *et al.,* 1979: 97-8, 102-3) reviewed the known, but still largely undescribed, Devonian fish finds from the Boyd Volcanic Complex and the Merrimbula Group. The earliest fish remains, from the Bunga Beds (Facies 2) in the lower part of the Boyd Volcanics, are thought to be late Givetian or early Frasnian (Young, 1982). Fragmentary remains of *Bothriolepis* sp. and *Phyllolepis* sp. first appear in the later Facies 3 (arkosic-volcanolithic clastic facies) in the Boyd Volcanics of the Pambula district and are interpreted as Frasnian from the presence of late Frasnian marine invertebrates in the overlying Merrimbula Group of the same region.

It is suggested here that the *Placolepis/Bothriolepis* assemblage from the Comerong Volcanics in Nettletons Creek must be either early or middle Frasnian in age.

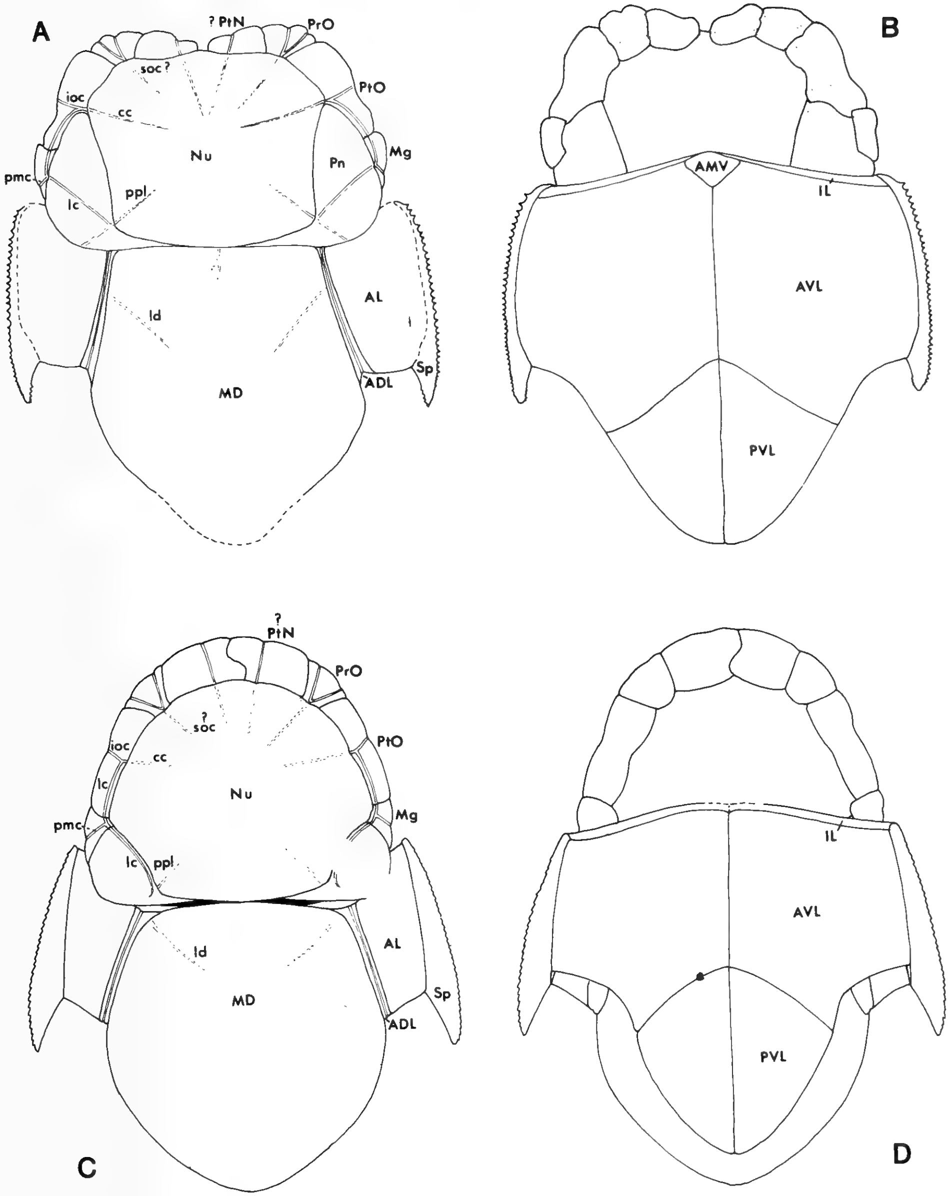


Fig. 2. Dorsal and ventral restorations on the head and trunk shields of *Phyllolepis orvini* Heintz and *Placolepis budawangensis* gen. et sp. nov. for comparison.

The *Phyllolepis* figures (**A**,**B**) are modified after Denison (1978: fig. 29) and Stensiö (1969: figs 132, 199). An attempt has been made, for the first time, to indicate the extent of the overlap areas in the ventral view of the headshield (**B**). In *Placolepis* (**C**,**D**) allowance has been made for the probable convexity of the dorsal and ventral shields (cf. also Figs 8, 14).

Abbreviations:— ADL — anterior dorsolateral plate; AL — anterior lateral; AMV — anterior median ventral; AVL — anterior ventrolateral; IL — interolateral; Mg — marginal; MD — median dorsal; Nu — nuchal; Pn — paranuchal; Pro — preorbital; ?PtN — ?postnasal; PtO — postorbital; PVL — posterior ventrolateral; Sp. — spinal; cc — central canal; ioc — infraorbital canal; lc — lateral canal; pmc — postmarginal canal; ppl — posterior pit-line; soc — supraorbital canal.

PREVIOUS INTERPRETATIONS OF *PHYLLOLEPIS*

Before describing *Placolepis* gen. nov., it is appropriate for comparative purposes to review briefly past and current interpretations of *Phyllolepis*, as the two genera are so alike in many respects.

The distinctive, ridged dermal ornament of *Phyllolepis* is so characteristic that hitherto even small fragments of plates have been confidently referred to this genus. The new material described here shows that ornament alone is not a reliable basis for such an identification.

In the best known species from the Famennian of East Greenland, *Phyllolepis orvini* Heintz (1930; Stensiö, 1934, 1936, 1939, 1969: figs 132, 199a, b; Denison, 1978: fig. 29) and Scotland, *Phyllolepis woodwardi* Stensiö (1936: text figs 3, 5; 1939: text figs 2, 3) the fish was clearly dorsoventrally flattened in life. The headshield was broad and flat, consisting of a greatly enlarged nuchal plate bordered by a series of small paired plates. The latter, originally labelled 'marginals 1-5' by Stensiö (1934, 1936, 1939), have been variously interpreted by other authors to include the homologues of the arthrodiran paranuchals, marginals, postorbitals, preorbitals and (less certainly) the postnasals (Denison, 1978: fig 29, 41-42; cf. also this paper Figs 2, 8**E**, 8**F**).

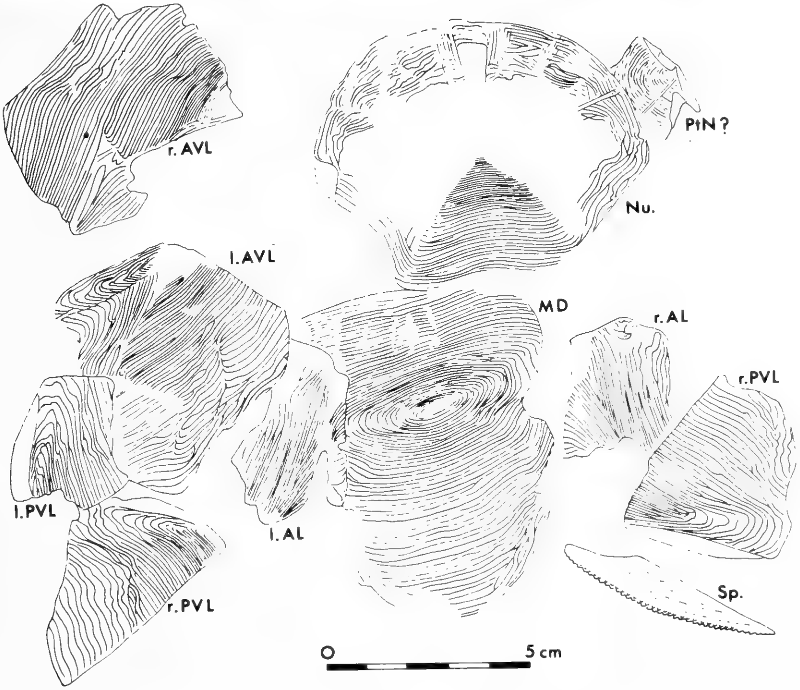
The rostral and pineal plates are not developed in the Phyllolepida and the anterior and lateral margins of the headshield were probably unarmoured. There is little evidence for the position and size of the eyes, and some disagreement about their probable position. It has even been suggested that *Phyllolepis* may have been blind (Westoll, 1979: 350). Stensiö (1969: figs 3B, 132; this paper Fig. 14**A**) depicted an extensive soft area in front of the headsdhield with the eyes anteriorly placed and directed, an interpretation accepted by Obruchev (1967: fig. 69), Romer (1966: fig. 34), Moy-Thomas and Miles (1971: fig. 8, 15) and others. However Denison (1978: 41-42, fig. 29) suggested that the eyes were more antero-laterally placed in a much narrower unarmoured marginal strip. This interpretation is accepted here in the closely related *Placolepis* gen. nov. (Fig. 14**B**).

The phyllolepid cranio-thoracic joint consists of simple flanges on the anterior margin of the trunk shield which underlie, and articulate with, the paranuchal plates of the headshield. The trunk shield is short, broad and comparatively flat. The component plates are well known (Fig. 7**A, B**). Posterior dorsolateral (PDL) and posterior lateral (PL) plates are not known in *Phyllolepis*. Opinions differ as to whether this absence is a primitive or derived condition in that genus. Although a very small triangular anterior median ventral (AMV) plate has been depicted in both *Phyllolepis orvini* and *P. woodwardi* the evidence for its presence in the former is regarded as equivocal, as discussed below. The only evidence for the presence of a posterior median ventral (PMV) plate in *Phyllolepis* was a minute sliver of bone in *P. woodwardi* (Stensiö, 1936: text fig. 5) but evidence for such a plate has recently come to light in the new Victorian material (J. Long *pers. comm.*).

The pectoral fin skeleton of *Phyllolepis* is unknown but it is obvious that the pectoral fenestra was open posteriorly and must have housed such a fin. The shape of the

Fig. 3. Placolepis budawangensis gen. et sp. nov. (holotype) and *Bothriolepis* sp.; this specimen (AM F.61748) and all other figured specimens from Late Devonian (Frasnian), tributary of Nettletons Creek, west flank of Budawang Range, New South Wales. **A** — above) latex cast whitened with ammonium chloride sublimate; bedding plane with abundant *Bothriolepis* plates and the slightly dissociated remains of a single *Placolepis* individual, selected as the holotype. Scale in millimetres.

B) interpretation of *Placolepis* remains seen in **A**); abbreviations as in Fig. 2. Note that right posterior ventrolateral plate (r.PVL) lying adjacent to the spinal (Sp), and slightly obscuring a fine example of a *Bothriolepis* headshield, belongs to a second *Placolepis* individual.


r. AVL
PtN ?
Nu.
l. AVL
MD
r. AL
r. PVL
l. PVL
l. AL
r. PVL
Sp.
0
5 cm

trunk and tail posterior to the trunk shield is known only from remains of an ossified vertebral column in *Phyllolepis woodwardi* Stensiö (1936: text fig. 3) but more information should become available when the well-preserved, articulated material from the Mt Howitt fauna in Victoria is fully prepared and evaluated.

DESCRIPTION OF THE *PLACOLEPIS* GEN. NOV. MATERIAL

The holotype of *Placolepis budawangensis* gen. et sp. nov. (F.61748) consists of a localized concentration of dorsal and ventral plates (Fig. 3**A**, **B**), which are clearly derived from a single adult individual with the exception of an adjacent right PVL (cf. also Fig. 13**F**).

These form the basis for a complete restoration by providing the relative proportions for the major head and trunk plates. The individual plates are also represented by numerous isolated examples, covering a wide range.

CRANIAL SHIELD

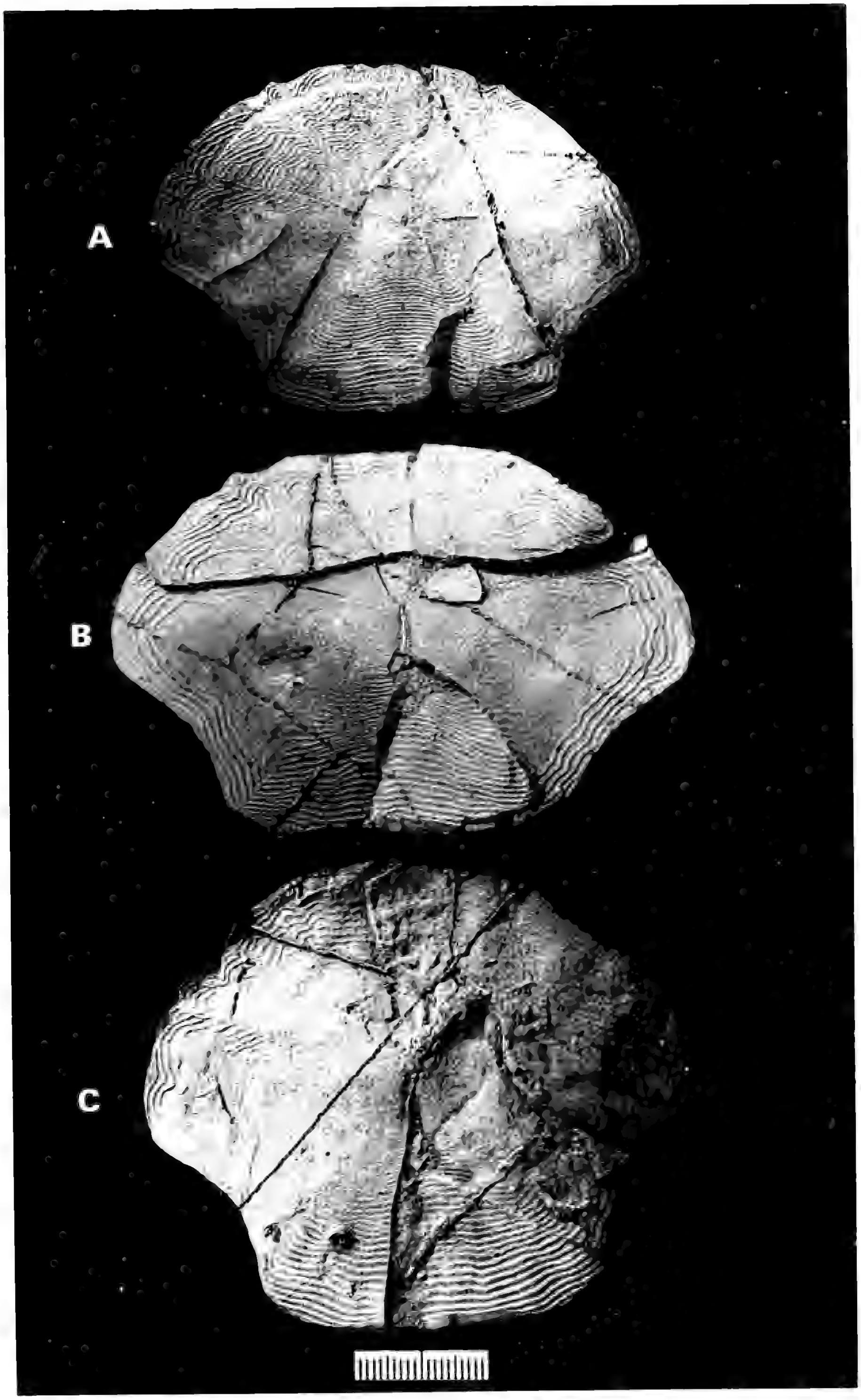
Before considering the cranial elements of *Placolepis* in detail an error in Stensiö's restoration of the headshield of *Phyllolepis* should be noted. The ventral plate boundaries of the headshield are always depicted as identical to those of the dorsal surface (Stensiö, 1969: fig. 199B, 503; Denison, 1978: fig. 29). In fact the nuchal plate overlaps all the smaller circum-nuchal plates and these overlap one another. The ventral plate pattern of the *Phyllolepis* (and *Placolepis*) headshield is thus quite different from that of the dorsal surface as indicated here (Figs 2, 8**A**, **D**).

Nuchal plate (Nu) — in addition to the type nuchal (Fig. 3) many other examples of the Nu of *Placolepis budawangensis* are available, covering a wide size range.

Both dorsal and ventral surfaces are displayed (Figs 4, 5, 6). The nuchal plate dominates the headshield of *Placolepis,* as in *Phyllolepis*, but its shape is markedly different. The widest part of the Nu in *Placolepis* lies opposite, or slightly posterior to, the centre of the plate; in *Phyllolepis* the greatest width is always considerably anterior to the midline. In addition, the general outline of the *Placolepis* Nu is less angular, with a broad rounded, sub-circular anterior and anterolateral margin. The posterolateral margins are gently concave and the posterior margin slightly convex. The posterior margin is around 0.6 of the maximum width. There is considerable variation in the length: width ratio of the nuchal plate ranging from 0.61-0.87; an intermediate figure (0.73) has been used in the reconstruction of the headshield (Fig. 8**A**) but some allowance for original curvature has been made in Figs 2**C** and 14**B**.

The *Placolepis* Nu carries the proximal portions of four pairs of sensory canals which converge on the centre of ossification as shallow, often indistinct grooves cutting across the subconcentric dermal ornament (Figs 2**C**, 4, 6**A**, 8**A**). These canals compare closely with those present in *Phyllolepis orvini* (Fig. 2**A**) and in *P. woodwardi.* From the rear they may be homologized with the posterior pit line *(ppl),* the central canal *(cc),* the supraorbital canal *(soc)* and an anteriorly directed pair whose homology remains uncertain. This interpretation of the various canals is basically in accord with that proposed by Denison (1978: fig. 29) but conflicts with that of Stensiö (1969: fig. 132).

Fig. 4. Placolepis budawangensis gen. et sp. nov., three nuchal plates (Nu) in dorsal view. **A**) AM F.61901a; **B**) F.61902a; **C**) F.61919; (same specimens as in Fig. 5). Latex casts whitened with ammonium chloride sublimate. Scale in millimetres.


A
B
C

The dermal ornament of the Nu of *Placolepis budawangensis* consists mainly of subconcentric, slightly undulating ridges whose regular arrangement breaks down completely in two subtriangular areas lying between the centre of ossification and the posterolateral margins. Here they zig-zag almost randomly or are largely undeveloped (Figs 4, 6**A**, 8**A**) leaving extensive smooth areas free of ridges. The region between the posterior margin of the Nu and the centre of ossification is occupied by a clearly demarcated triangular area of transverse parallel ridges bordered anterolaterally by the faintly developed left and right posterior pit-lines *(ppl).*

Smaller cranial plates — Stensiö (1934, 1936, 1939) recognized and described in detail five pairs of 'marginal' cranial plates bordering the Nu. He numbered them M1-M5 but only one pair of these plates (M5) is undoubtedly homologous to the true 'marginal' plates of Arthrodira. Stensiö's original nomenclature has long been discarded but was later (1969: fig. 132; 1971: 165) replaced with other names which have not been (or appear likely to be) widely accepted.

Denison's interpretation (Denison, 1978: fig. 29) is the one accepted and followed here but, for convenience, it may be useful to list the various names applied to these plates:

Stensiö (1934, 1936, 1939)	Stensiö	Denison	Abbrev.
Marginal 1	Preorbital	Postnasal?	PtN?
Marginal 2	Dermosphenotic	Preorbital	PrO
Marginal 3	Intertemporal	Postorbital	PtO
Marginal 4	Paranuchal	Paranuchal	Pn
Marginal 5	Intertemporal-supratemporal-extrascapular	Marginal	Mg

In *Phyllolepis orvini* and the other species each of these smaller plates, with the sole exception of the marginal, is overlapped by the nuchal whilst both the PtO and Mg plates are overlapped by the plates lying anterior and posterior to them (Figs 2**B**, 8**F**).

In *Placolepis budawangensis* the same five plates can be readily identified but their relative proportions and inter-relationships reveal important differences (Figs 2**C, D**, 6, 7, 8**A, D, E**). They will be considered in order beginning with the most posterior, the paranuchal.

Paranuchal (Pn) — many fine examples of the *Placolepis* Pn are available (Fig. 6 **A-C, E-G**). The *Placolepis* Pn is much shorter than that of *Phyllolepis* and lacks the broad ornamented area anterior to the lateral canal. In *Placolepis* the *lc* follows closely the nuchal/paranuchal margin and passes anteriorly off the Pn onto the small marginal plate and not midway along the lateral margin as in *Phyllolepis*. Posteriorly the *lc* curves sharply towards, but terminates short of, the cranio-thoracic articulation. There is no trace of a posterolaterally directed branch canal like that depicted in *Phyllolepis* (Fig. 2**A**) but it should be noted that this feature appears on only one of Stensiö's (1936: pl. 4, fig. 2) figured specimens. Along its entire inner margin the *Placolepis* Pn has a well-developed overlap area which underlay the posterolateral, and part of the posterior margin of the Nu. Immediately underlying the inner angle of the Pn there is a prominent rounded process (Figs 6**E-G**, 8**D**). From its shape and position this process

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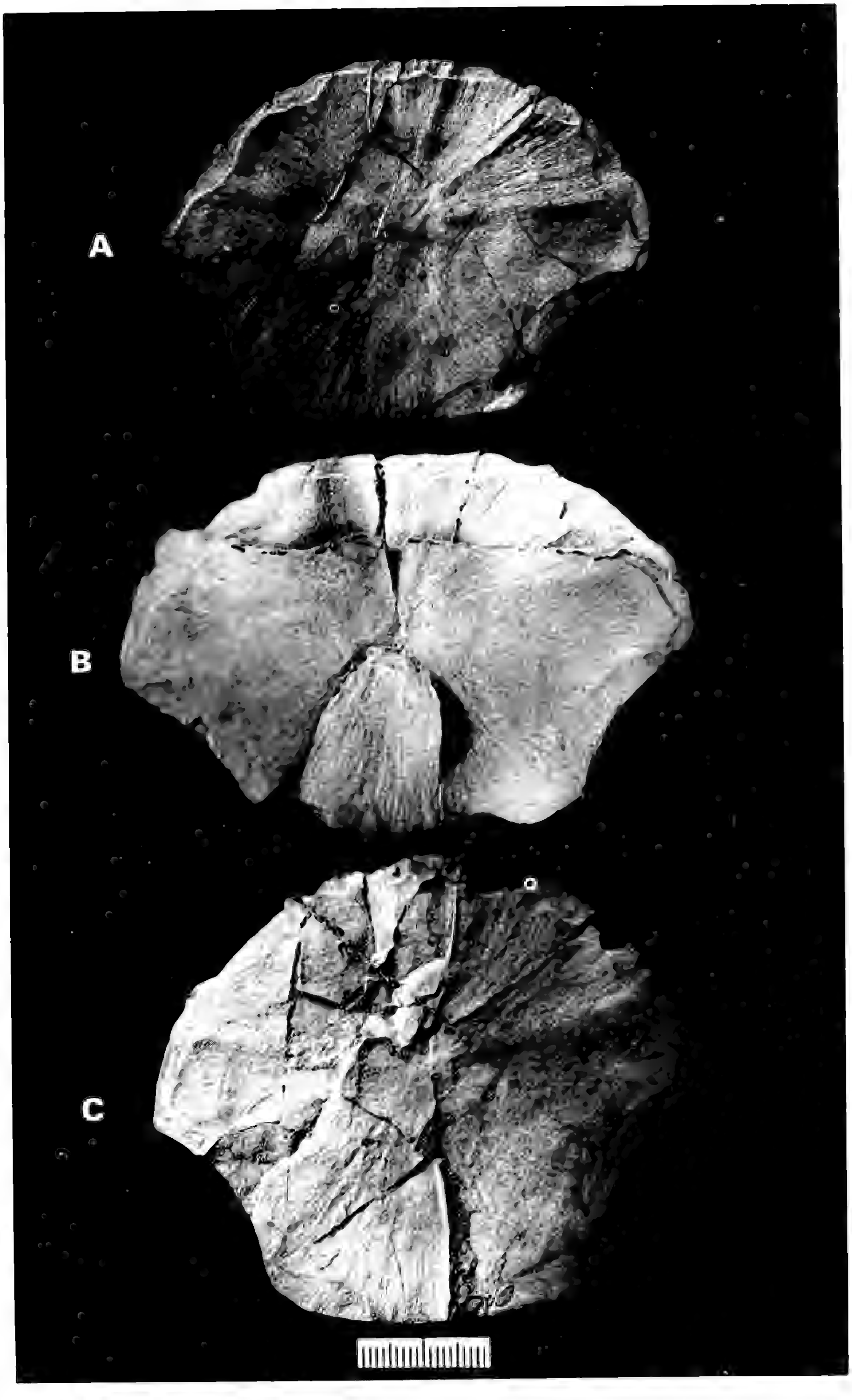
Fig. 5. Placolepis budawangensis gen. et sp. nov., three nuchal plates (Nu) in ventral view; (same specimens as in Fig. 4). **A**) AM F.61901b; **B**) F.61902b; **C**) F.61921. Latex casts whitened with ammonium chloride sublimate. Scale in millimetres.


A
B
C

was probably in contact with the concave anterior margin of the anterior dorsolateral (ADL) plate to form a relatively simple cranio-thoracic articulation with limited range of movement. In several *Placolepis* specimens this process has been crushed as if it were originally hollow, suggesting perhaps that it may have housed the ductus endolymphaticus, or the craniospinal process of the endocranium.

Marginal (Mg) — the course of the lateral canal of the Pn indicated that the smaller adjacent marginal plate was anteriorly placed and, unlike that of *Phyllolepis*, must have been in direct contact with the lateral margin of the Nu. This is confirmed by the presence of overlap areas on the Nu (Figs 5, 6**D**, 8**D** oa Mg). Three plates of the appropriate size and shape (Figs 7**K-M**, 8**A**, **D**, **E**) are regarded as left and right marginals. They are subcircular to ovate, 15-16 mm long and 12-13 mm wide with a triangular ornamented area. Each bears two sensory canal grooves, a very short, curved portion of the *lc* and, meeting it at right angles, a longer, radially-directed branch, the postmarginal (or preopercular) canal (Fig. 2**C** *pmc*). The Mg has well-developed anterior, posterior and proximal overlap areas for the PtO, Pn and Nu respectively.

Postorbital (PtO, Fig. 7 **G-J**). This plate is relatively long, narrow and subrectangular (Figs 2**C**, **D**, 8**A**, **D**, **E**). The lateral canal follows the nuchal margin until it meets, at an obtuse angle, the central canal (*cc*) leaving the Nu. The infraorbital canal (*ioc*), in *Placolepis* as in *Phyllolepis*, passes anterolaterally off the PtO onto the unarmoured lateral margin of the head.

On its visceral surface immediately underlying the *ioc,* the PtO displays a prominent rounded process which may be for the articulation of the hyomandibula. It is perforated transversely by a fine canal which emerges laterally, and immediately ventral, to a slight indentation in the outer margin of the PtO (Figs 7**H**, 8**D**). In *Placolepis* the PtO was in contact with, and overlapped by, the Nu over its full length, unlike the PtO of *Phyllolepis* which was partly separated from the Nu by an anterior extension of the Pn (Fig. 8**F**).

Preorbital (PrO) — immediately anterior to the PtO and overlapped by it was a smaller, subtriangular plate, here interpreted as the preorbital (Figs 2**C**, **D**, 7**B-F**, 8**A**, **D**, **E**). Like its homologue in *Phyllolepis* (Figs 2**A**, 8**F**) it differs from that of most other placoderms in bearing two well-developed sensory canal grooves which converge proximally and meet near the PrO/Nu border in line with the distal end of the supraorbital canal *(soc).* In *Placolepis* these converging canals are more symmetrically placed than are the same canals in *Phyllolepis* but with a few exceptions (Fig. 7**F**) one can readily distinguish between left and right PrOs.

Postnasal (PtN) — the anterior overlap areas on the *Placolepis* nuchal plate (Figs 5, 6**D**, 8**D**) show that the anterior margin of the headshield was formed by a pair of reasonably large, transversely oriented plates which met in the midline, much as in *Phyllolepis*. Although in *P. orvini* Heintz these plates have been depicted as more widely spaced and separate (Stensiö, 1936: text fig. 9) his figured specimens showing the dermal surface (1936: pl. 25) and the inner surface and overlap areas of the Nu (1936: pl. 5) indicate that the median gap was much smaller than shown in the reconstruction (this paper

Fig. 6. Placolepis budawangensis gen. et sp. nov., nuchal (Nu) and paranuchal (Pn) plates. Latex casts whitened with ammonium chloride sublimate. Scale in millimetres for **A**, **B**, **C**, **D**, **E**, **F**; **G** is × 2.
A, **D**) dorsal and ventral views of nuchal with associated paranuchal, AM F.63873 (dorsal); F.63874 (ventral); **B**, **F**) dermal and visceral surfaces of left paranuchal, F.61755a,b; **C**, **E**) dermal and visceral surfaces of right paranuchal, F.61756a,b; **G**) left paranuchal, visceral view, F.61925 (× 2).

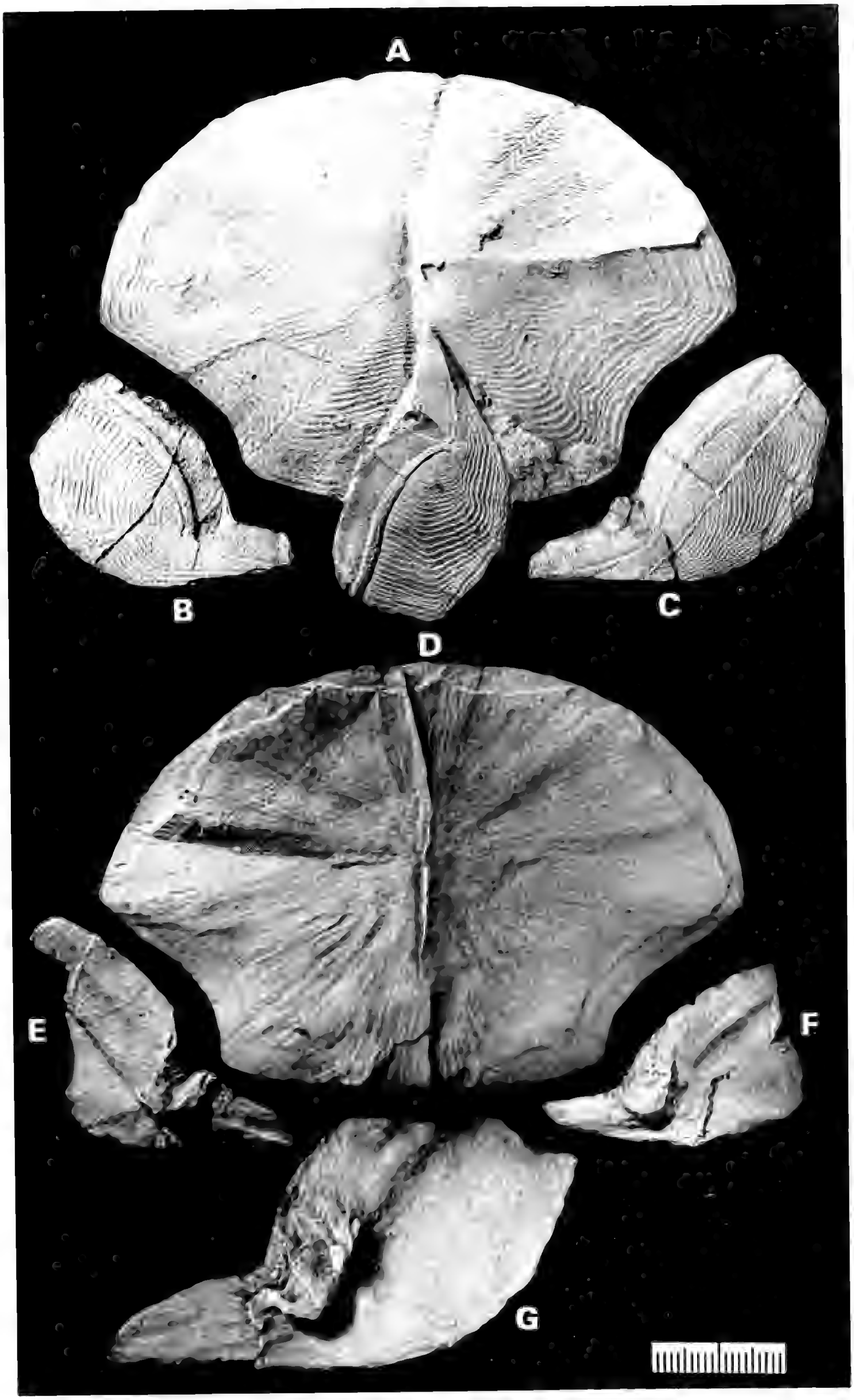

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Fig. 2**A, B**) and the plates may have met and overlapped in the midline as in *P. woodwardi* (Stensiö, 1936: text fig. 3; 1939: text fig. 3).

There is little doubt that this was the condition in *Placolepis.* The plate interpreted here as the postnasal (F.61760, Fig. 7**A**) is much deeper than the PtN in *Phyllolepis orvini* (Figs 2**A, B,** 8**F**) and in the new Australian genus the left and right PtNs appear to have met along a sinuous median suture, each partly overlapping the other.

The PtN is traversed by a short straight canal which is clearly a continuation of one of the anterior pair of canals on the nuchal, the interpretation of which presents a problem. Denison (1978: 42, fig. 26A, roc) has suggested that it may be homologous to the short 'rostral' canal of *Lunaspis.*

TOOTHPLATES OF *PLACOLEPIS* GEN. NOV.

The Nettletons Creek material includes two small tuberculated plates which appear to be placoderm toothplates (Fig. 10 **N-Q**). The only other placoderm in the same fauna as *Placolepis* is the antiarch *Bothriolepis,* the gnathal elements of which are well known and quite different. Impressions of similar toothplates have been observed *in situ,* underlying the headshield, in several specimens of *Phyllolepis* sp. nov. from the Frasnian Mt Howitt fish fauna of central Victoria (Marsden, 1976: 79, 122). The isolated elements found with *Placolepis* appear to represent both superognathal and inferognathal elements.

The superognathal (Sg) is a small, flat, subtriangular plate 8 mm long and 5.5 mm wide, covered with 9 or 10 radiating rows of small conical denticles which increase in size distally (F. 61920, Fig. 10**P, Q**). The rows of denticles converge on one corner, possibly anteriorly, but because the original orientation of the plates remains uncertain it has been figured in two positions.

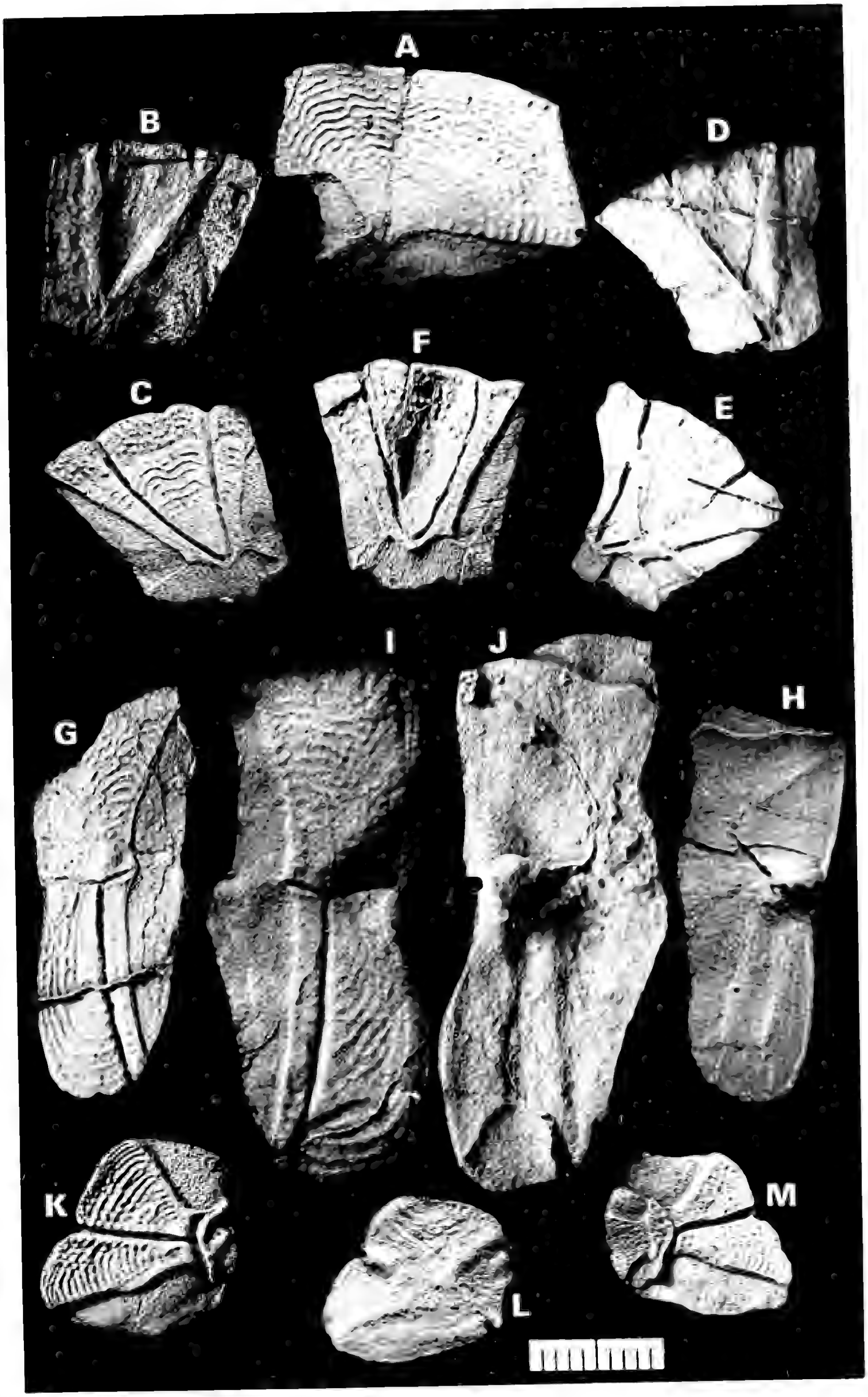
The second denticle covered plate, interpreted here as the inferognathal (Ig), is quite different in shape (F.61761, Fig. 10**N, O**). It is lenticular, 14 mm long and 4 mm wide in the middle and pointed at both ends. As with the Sg the small conical denticles are arranged in radial rows. Some 16 or 17 slightly curved rows of tubercles converge midway along the straighter of the lateral margins. Again the original orientation of the plates remains conjectural. The closest equivalent in other placoderms would appear to be the superognathal plate of the phlyctaeniid arthrodire, *Dicksonosteus arcticus* Goujet (1975: figs 3, 4).

TRUNK SHIELD

The thoracic shield of *Placolepis* (Fig. 8**B, C**) is developed basically like that of the various species of *Phyllolepis* with several minor but significant differences.

Median dorsal (MD) — relatively complete and uncrushed specimens of the MD of *Placolepis budawangensis* indicate that this plate was more convex in cross section than the MD of *Phyllolepis orvini* as depicted by Stensiö (1936: fig. 12). The *Placolepis* MD (Figs 8**B**, 9**A-E**) is subpentagonal in outline but more rounded and less angular than that of

Fig. 7. Placolepis budawangensis gen. et sp. nov., smaller cranial plates. **A**) right ?postnasal (PtN), dermal surface, AM F.61760; **B-E**) left and right preorbitals (PrO) in visceral and dermal views; both specimens on same block (F.61915, counterpart F.61916) and probably from same individual; **F**) right ?preorbital, F.61921; **G, H**) left postorbital (PtO), dermal and visceral view, F.61757a,b; **I, J**) right postorbital, dermal and visceral view, F.61759a, b; **K**) left marginal (Mg), dermal surface, F.61758; **L, M**) right marginal, visceral and dermal views, F.63873, F.63874. Latex casts whitened with ammonium chloride sublimate. Scale in millimetres.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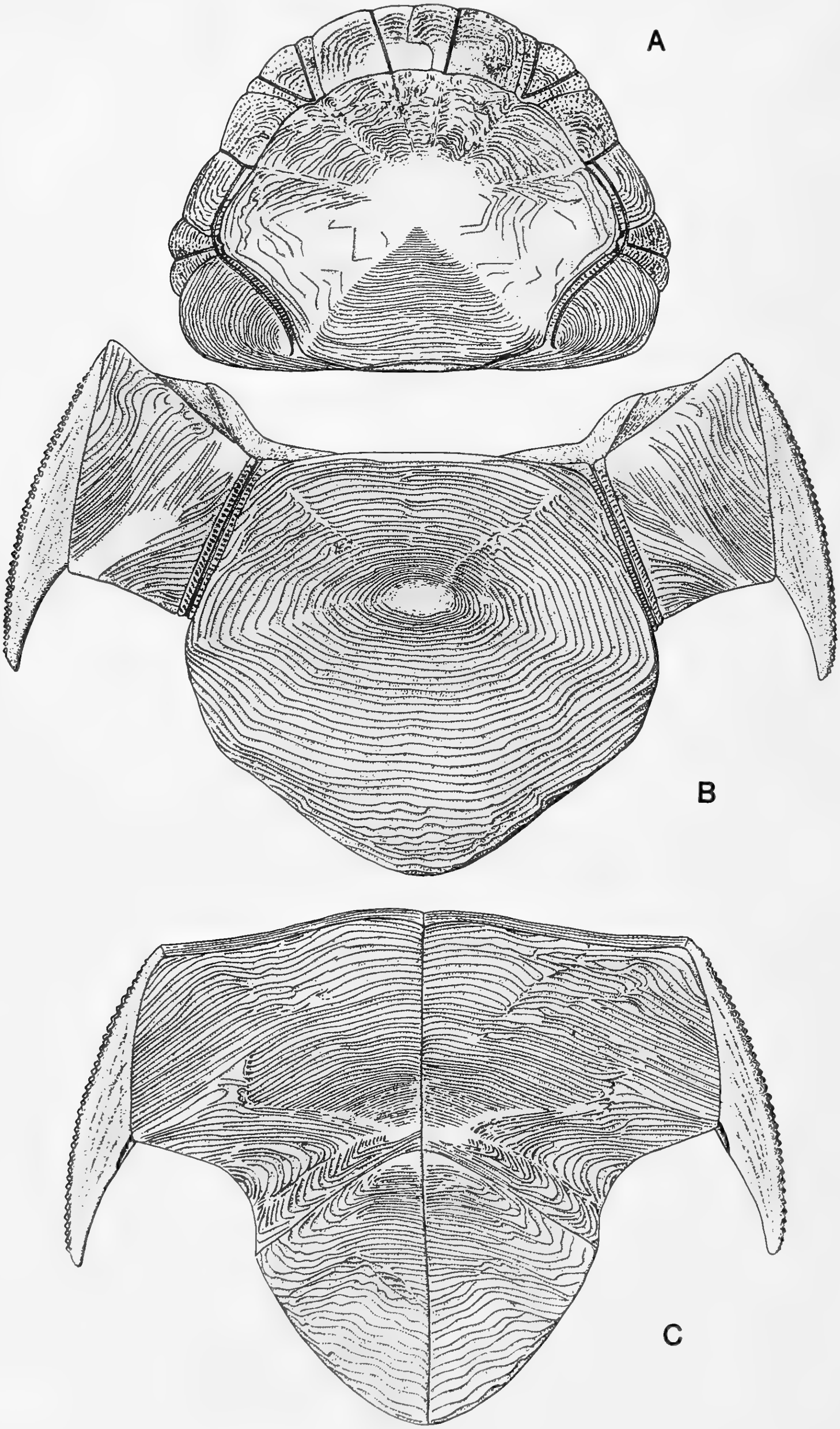
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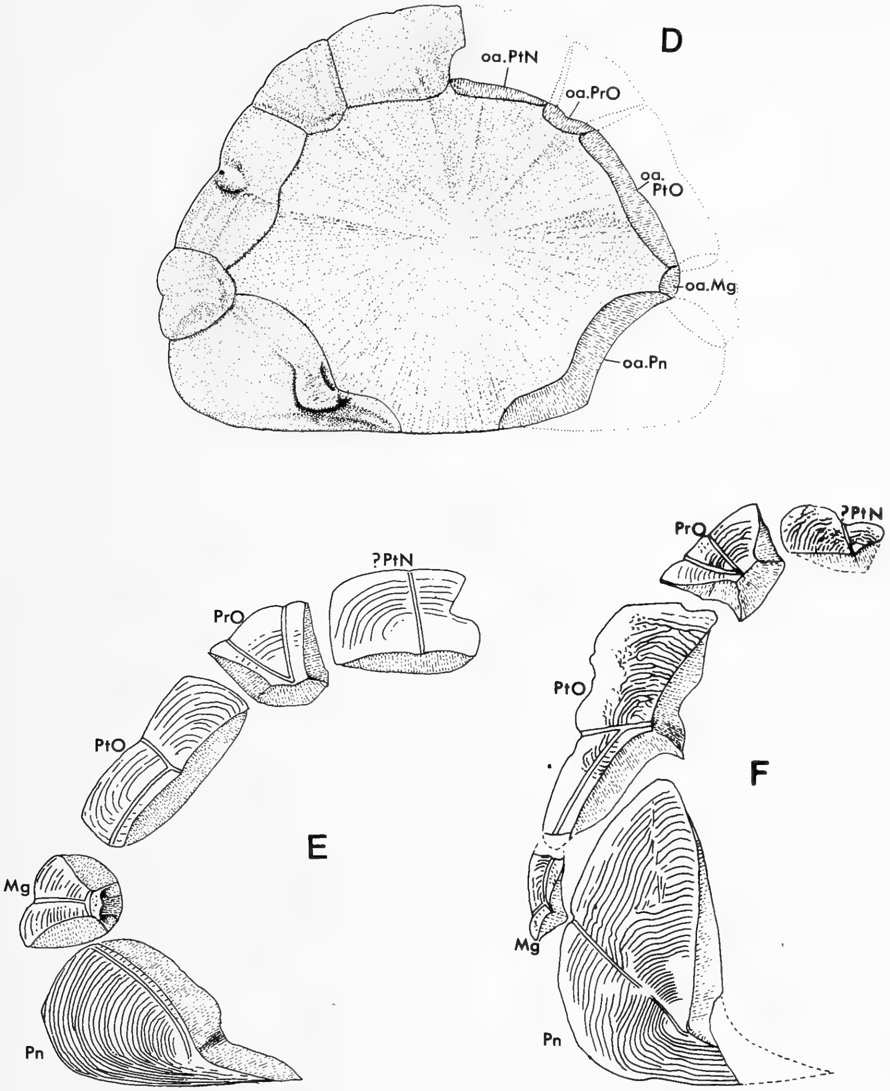


Fig. 8. Placolepis budawangensis gen. et sp. nov., restorations of head and trunk shields, dorsal and ventral. Approximately natural size.

A) headshield in dorsal view; nuchal shield based on information from several figured examples, of intermediate length: width proportions. Depicted as if flattened in horizontal plane; no allowance made for original curvature (cf. Figs 2**C, D**, 13).

B) dorsal trunk shield and **C**) ventral trunk shield, both in dermal view; depicted as if flattened in horizontal plane. Relative proportions based initially on relevant plates of the holotype (AM F.61748, Fig. 3**A, B**) with additional details from other, more complete, examples.

D) headshield in ventral view with left cranial plates removed to reveal extent of overlap areas on nuchal plate (cf. Fig. 5 **A-C**, Fig. 6 **A,D**). Abbreviations as for Fig. 2 with following additions: oa.PtN?, oa.PrO, oa.PtO, oa.Pn — overlap areas for relevant plates.

E, F) smaller cranial plates of *Placolepis* gen. nov. (**E**) and *Phyllolepis orvini* (**F**) separated to show relative positions and extent of overlap areas. The *P. orvini* plates are redrawn from Stensiö as follows:— Pn (1934: fig. 19 = M4); Mg (1936: fig. 15 = M5); PtO (1934: fig. 18 = M3); PrO (1934: fig. 17 = M2): PtN? (1936: fig. 13 = M1).

Phyllolepis orvini, P. woodwardi or either of the Belgian species, *P. konincki* or *P. undulata* (Leriche, 1930: pl. 1, figs 2a, 3a, pl. 2, fig. 1a; Stensiö, 1939: text fig. 5).

The length/width of the *Placolepis* MD varies between 0.8 and 1.0 perhaps partly as a result of post-mortem flattening and crushing.

The centre of ossification, and of the subconcentric ornament, is more anteriorly situated than in the various species of *Phyllolepis* where it is virtually central. In *Placolepis* about 35% of the plate length lies anterior to the ossification centre and 65% posterior to it. The strongly-developed, ridged ornament is less angular and zig-zag than that of *Phyllolepis* spp. As in *P. orvini* (Stensiö, 1969: fig. 132; this paper Fig. 2**A**) a branch of the lateral canal passes postero-dorsally onto the MD from the lateral canal on the ADL, but in *Placolepis* this canal emerges near the anterolateral corner of the MD and not farther back as in *Phyllolepis* (Figs 8**B**, 9**A**, **B**, **D**). This canal is not always clearly developed.

No trace has been found in *Placolepis* of a short 'canal' midway along the anterior margin of the MD as depicted in *Phyllolepis orvini* (Stensiö, 1969: fig. 32, *dx*) but it should be noted that in *Phyllolepis* this feature is only known from one specimen (Stensio, 1936: pl. 10) and should probably be regarded as an individual aberration in the ornament.

The visceral surface of the *Placolepis* MD is smooth, completely lacking any development of a keel but with a short and very low median ridge lying just behind the anterior margin. The antero-lateral margins of the MD display an extensive L-shaped overlap area for the anterior dorsolateral (ADL).

Anterior dorsolateral (ADL) — in *Placolepis* (Fig. 10 **A-C**), as in *Phyllolepis*, the exposed portion of the ADL is extremely narrow. The anterior margin of the ADL is narrow in front of the MD but wider under in front of the AL where it forms part of an articular process.

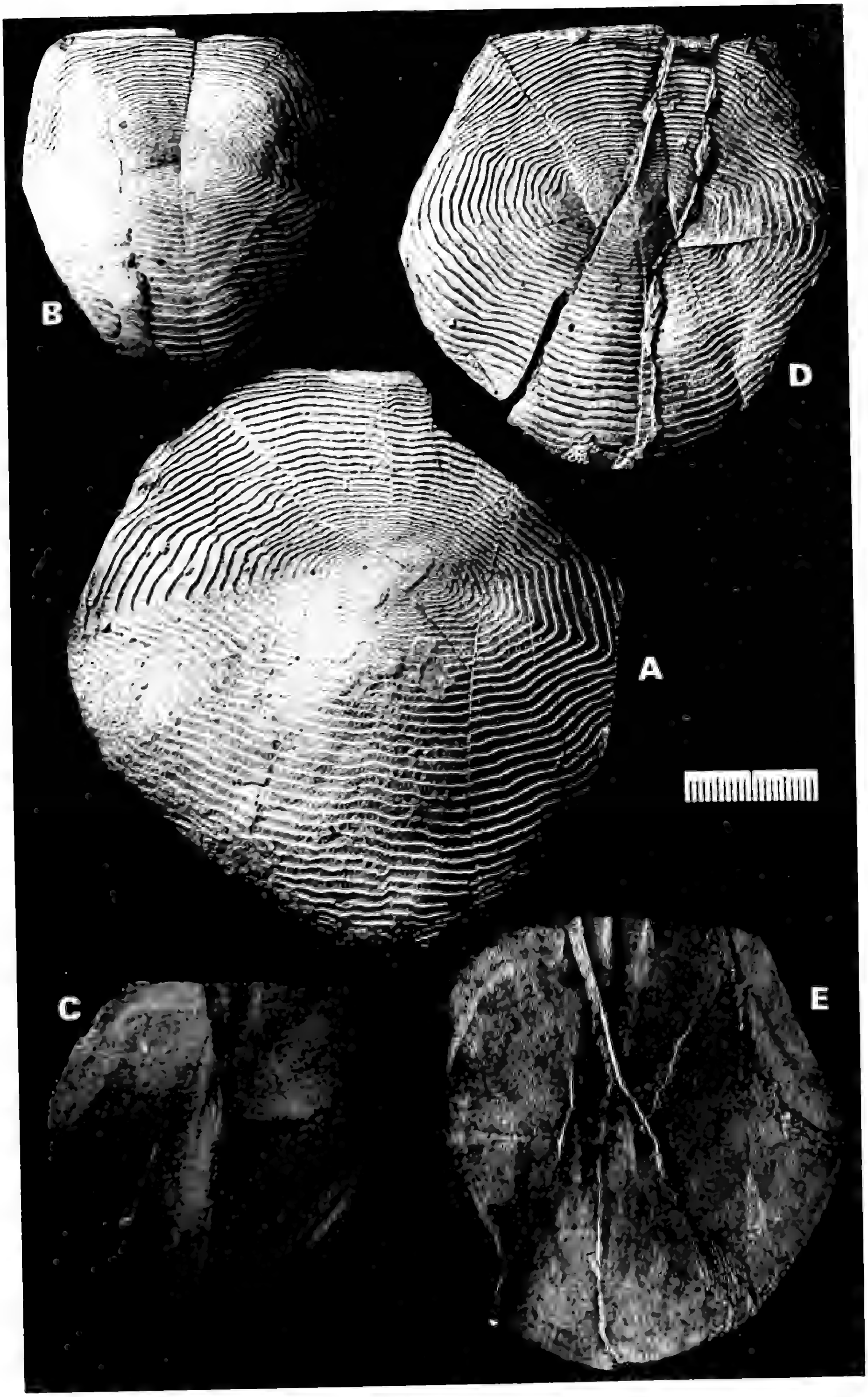
Anterior lateral (AL) — many well-preserved examples of the *Placolepis* AL plates have been recovered (Figs 3**A**, **B**, 10**D-I**). Although quite variable in shape and ornament the ALs are all longer than high with a steeply sloping anterior margin. This bears a subtriangular anterior projection which combines with, and buttresses, the anteroventral margin of the ADL to form a smooth, flattish articular lamina (Fig. 8**B**) which clearly extended under the posterior margin of the paranuchal plate of the headshield. The degree of free movement was obviously rather limited and the articulation is reminiscent of the sliding cranio-thoracic arrangement in actinolepid euarthrodires except that in the latter the glenoid process is formed almost entirely by the ADL with little involvement of the AL.

The *Placolepis* AL has an almost straight, sloping dorsal margin, a vertical, slightly concave posterior margin and a ventral margin (bordering the spinal plate) which varies from gently to strongly convex. The ornament consists of radiating longitudinal ridges which tend to converge on the posteroventral corner of the AL, as in *Phyllolepis orvini* (Stensiö, 1936: text fig. 10) and other species.

The dorsal and ventral thoracic shields are linked only by the spinal plates. Posterior dorsolateral (PDL) and posterior lateral (PL) plates were obviously absent in *Placolepis,* as in *Phyllolepis*, and the large posteriorly-directed fenestra for the pectoral fin was clearly open behind and not bridged posteriorly by the trunk shield.

Fig. 9. Placolepis budawangensis gen. et sp. nov., three isolated median dorsal plates (MD). Latex casts whitened with ammonium chloride sublimate. Scale in millimetres.

A) AM F.61766, dermal surface; **B, C**) F.61769a,b, dermal and visceral surfaces; **D,E**) F.61722a,b, dermal and visceral surfaces.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Anterior ventrolateral plate (AVL) — the AVLs of *Placolepis budawangensis* (Figs 3, 8**C**, 10**J**, **K**, 11**A**, **B**, **F**, **G**, 12**A**, **B**) are of typical phyllolepid type, large broad plates with proportions and ornament variable but not significantly different from the AVLs of *Phyllolepis orvini, P. woodwardi* (Stensiö, 1934, 1936), *P. tolli* Vasiliauskas (1963) and others. The *Placolepis* AVLs are ornamented with a variable pattern of transverse, obliquely directed, and slightly sinuous ridges. Towards the posterior margin the ridges alter direction abruptly several times and are also traversed by a prominent ridge parallel to, and a short distance anterior to the rear margin of the AVL. In this the *Placolepis* AVLs resemble those of *Phyllolepis neilseni* Stensiö (1939: text fig. 10, pl. 3) more than the AVL of *P. orvini*.

In several AVLs (Fig. 11**A**,**B**,**F**,**G**) a shallow but marked oblique groove traverses the plate from the AVL/PVL junction in the midline to the anterolateral corner of the AVL. The degree of convexity preserved in some of the *Placolepis* AVLs and the angle at which they met in the midline indicates a deeper profile than was estimated to be present in *Phyllolepis* and this is supported by the posterior ventrolateral plates.

Posterior ventrolateral plate (PVL) — the PVLs were fairly stout, subtriangular and strongly convex plates (Figs 3 **A**, **B**, 10 **L**, **M**, 11 **H**, **I**, 12 **C**, **D**). Their general proportions and ornament are so variable that many of them would be difficult to distinguish from those of various *Phyllolepis* species which are also individually variable. Some idea of the diversity of the PVLs in *Placolepis* may be obtained from Fig. 13**A**-**F**.

The oblique anterior margin displays a well developed overlap area for the AVL but the median suture is straight and non-overlapping like that of the AVLs. Experimental reassembly of the plates of the ventral trunk shield indicates that it was quite convex and that the trunk cross section immediately posterior to the thoracic shield was quite rounded (Fig. 14).

Median ventral plates (AMV, PMV) — an anterior median ventral plate has been reconstructed in various species of *Phyllolepis* (*P. orvini, P. woodwardi* Stensiö, 1934, 1936, 1939) but no such plate has been observed in *Placolepis*. The published evidence for such a plate in *Phyllolepis* appears to be based largely on the single articulated specimen of *P. woodwardi* from Dura Den, Fife, Scotland (Stensiö, 1934: text fig. 2D; 1936: text fig. 5), where a small triangular plate is identified as the AMV. The only evidence for the presence of a similar plate in *P. orvini* appears to be a slight rounding of the antero-mesial corners of the AVLs in a few of the figured specimens (Stensiö, 1936: text fig. 22, pls 19-21). It should be noted, however, that in many of the other figured specimens (Stensiö, 1934: text figs 24, 25, pl. 12; 1939: text fig. 10, pl. 3, fig. 3) there is

Fig. 10. Placolepis budawangensis gen. et sp. nov., dorsolateral, lateral, ventral and spinal plates of trunk shield and probable toothplates. Latex casts whitened with ammonium chloride sublimate. Millimetre scale for all except the toothplates (**N-Q**), which are × 2.

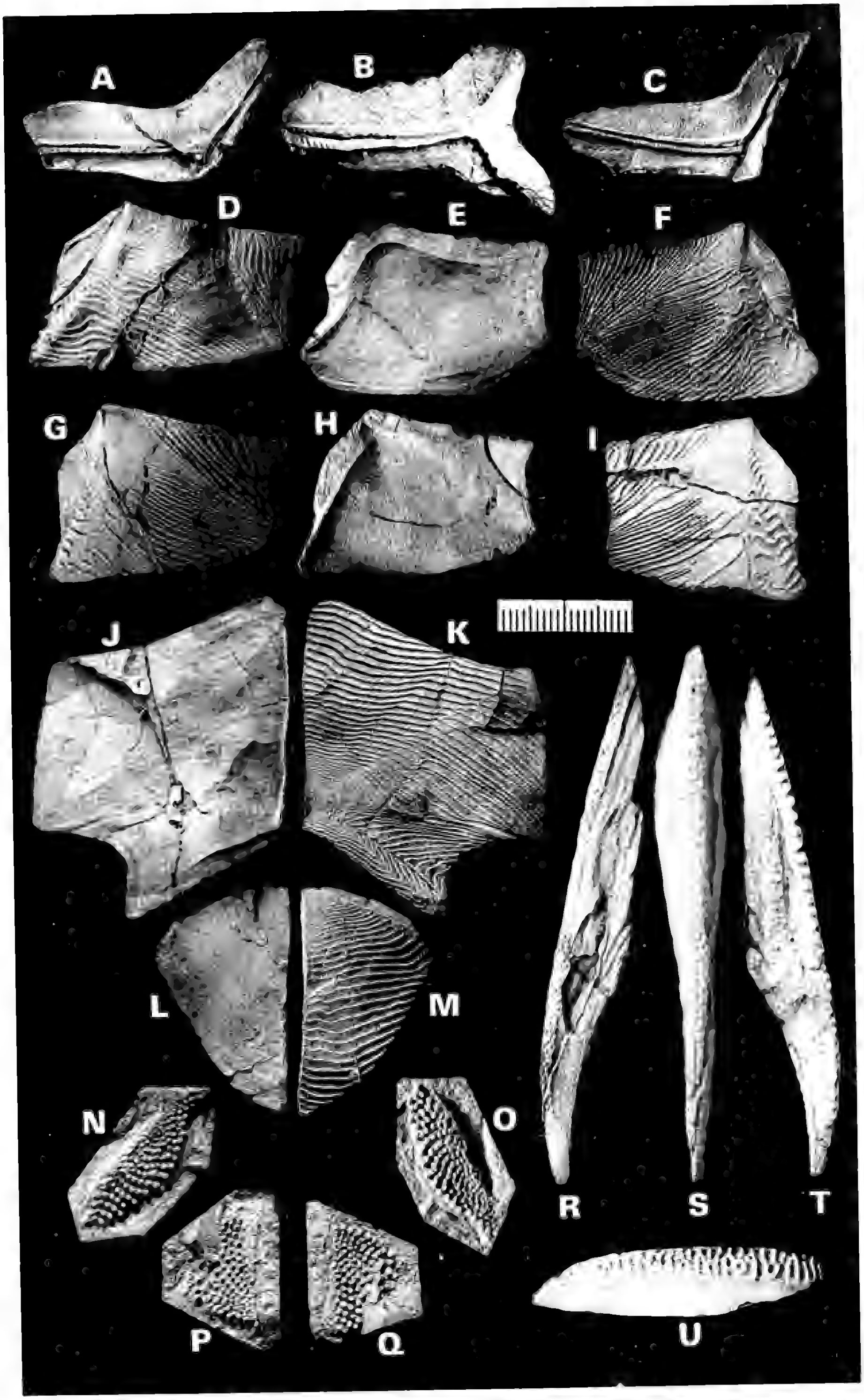
A-C) three right anterior dorsolateral (ADL) plates, in dermal view; **A**) AM F.61783, **B**) F.61782, **C**) F.61784.

D-I) anterior lateral (AL) plates; **D**) left AL, dermal surface, F.61919; **E, F**) right AL, visceral and dermal surfaces, F.61908b and counterpart, F.61908a; **G, H**) left AL, dermal surface and right AL, visceral surface, both plates closely associated on same specimen, F.61799, and probably from same individual; **I**) right AL, dermal surface, incomplete posteriorly, F.61781.

J-M) left AVL and PVL of small *Placolepis* individual, visceral and dermal surfaces; **J, K**) F.63878b, F.63878a; **L, M**) 63879b, F.63879a.

N-Q) ?inferognathal (Ig) and supragnathal (Sg) toothplates, each depicted in two possible orientations; **N, O**) Ig, F.61761, **P, Q**) Sg, F.61920; both twice natural size.

R-U) spinal (Sp) plates: **R, S, T**) ?right Sp, in ventral, lateral and dorsal views, F.61903a and counterpart F.61917; **U**) incomplete Sp to illustrate coalescence of tubercular ornament into short, transverse ridges, F.61912.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no trace of this supposed margin or of any overlap area for the AMV and the same applies to *Placolepis budawangensis* (Figs 10-12). The restoration given in Fig. 8**C** assumes that this plate is absent.

Stensiö (1934: text fig. 2D, *x*; 1936: text fig. 5, *Px*) also detected what appeared to be a small, extremely narrow, posterior median ventral plate (PMV) in the ventral shield of the holotype of *Phyllolepis woodwardi*. No trace of a PMV has been detected in any of the Greenland *Phyllolepis* material. In *Placolepis* the longitudinal median sutures are extremely straight, providing no support for the presence of such a median plate. J. Long, Monash University *(pers. comm.)* has informed the writer that the new species of *Phyllolepis* from the Mt Howitt fauna does possess a small but well-developed PMV plate. From this, and from the evidence of *P. woodwardi* described above, it would appear probable that both AMV and PMV plates formed part of the original complement of plates in the ancestral phyllolepid trunk shield and that they have been subsequently reduced and/or secondarily lost in most later representatives of the Phyllolepidae.

Interolateral plate (IL) — the single example of the IL is represented by moulds of its dermal and visceral surfaces on slabs F.63873 and F.63874 (Fig. 11**C-E**). The plate is partly obscured by a *Bothriolepis* plate but the visible portion is 37 mm long and 2-3 mm wide for most of its length. 8 mm from the distal end it flares to 5 mm wide before tapering to a point. The outer surface (Fig. 11**E**) is ornamented with extremely fine, longitudinal denticulate ridges. In general it compares closely with the IL of *Phyllolepis orvini* (Stensiö, 1936: text fig. 21, pl. 1, fig. 6, pl. 17, figs 1-3) and *P. woodwardi* (Stensiö, 1936: text fig. 5).

Spinal plate (Sp) — the spinal plate is long and well-developed, hollow throughout most of its length and with up to one third of its length projecting posteriorly and flanking the (presumed) pectoral fin (Figs 10**R-T**, 12**E,F**). The Sp is narrowest anteriorly, reaching its widest point at the posterior end of the AL and AVL junction. On the dorsal and ventral surfaces faint longitudinal ridges converge posteriorly. The outer, rounded margin is ornamented with a single longitudinal ridge flanked dorsally and ventrally by 2-3 rows of tubercles which sometimes coalesce into short, transverse ridges (Fig. 10**U**). The inner margin of the posterior spine may bear a single row of small tubercles.

Stensiö depicted the Sp as having been extensively overlapped dorsally and ventrally by the AL and AVL plates (Stensiö, 1936: 40, text fig. 20) but in *Placolepis* (and probably also in *Phyllolepis*) the AL/Sp and AVL/Sp sutures appear to have been simple, non-overlapping, edge-on contacts (Fig. 8**B, C**).

SYSTEMATIC DESCRIPTION

Order PHYLLOLEPIDA Stensiö 1934

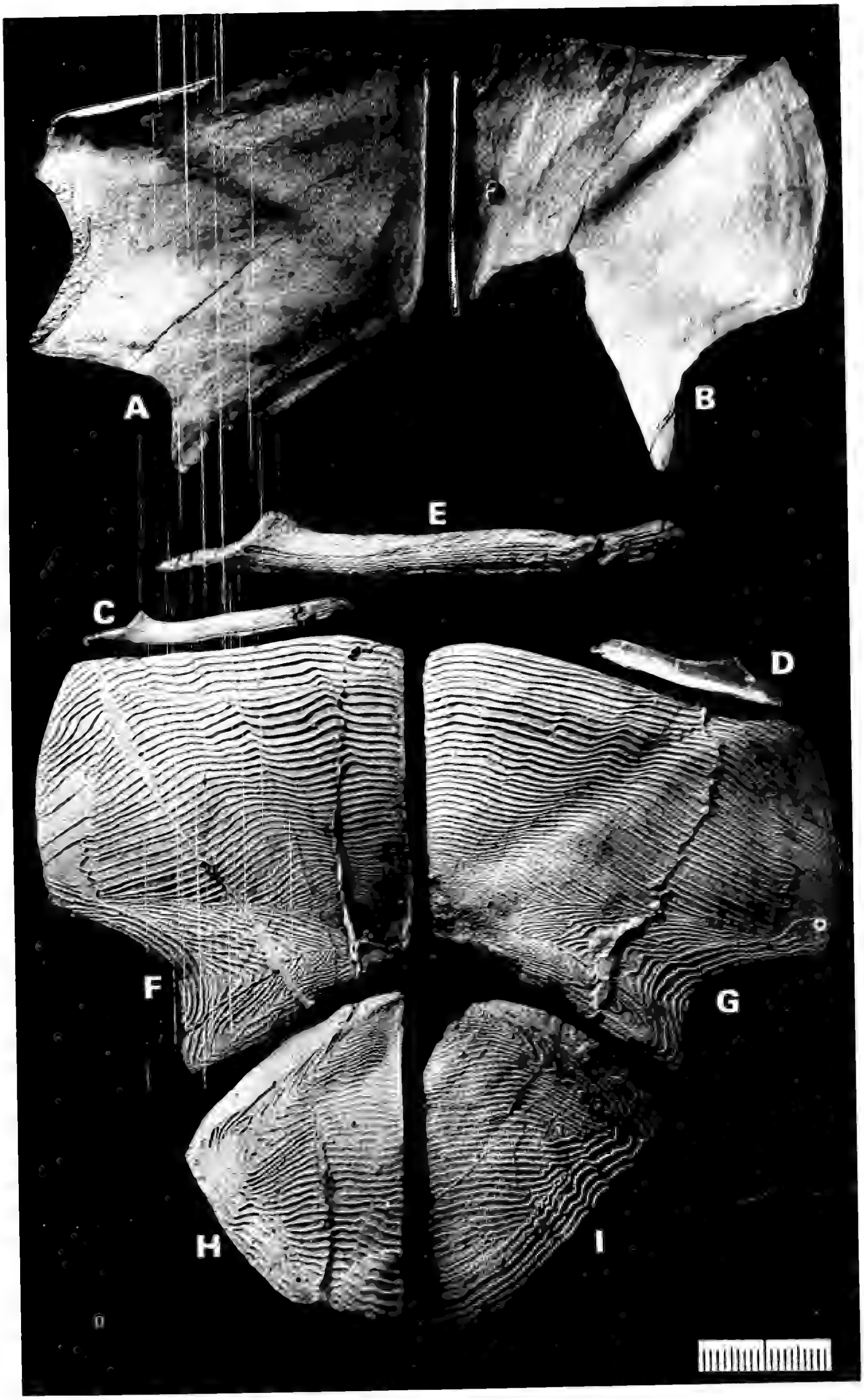
Diagnosis: cranial roof relatively flat; nuchal plate enlarged, wider than long; central plates lost; rostral and pineal plates not developed. Orbits probably small and antero-

Fig. 11. Placolepis budawangensis gen. et sp. nov., ventral trunk plates, possibly from same individual, all present on two large slabs, F.63783 (**C, E, F, G, I**) and its counterpart, F.63874 (**A, B, D, H**), in close association with a fine nuchal and paranuchal plate (cf. Fig. 6 **A, D**). Latex casts whitened with ammonium chloride sublimate.

A, G) left anterior ventrolateral (AVL) plate, visceral and dermal surface; **B, F**) right AVL, visceral and dermal surface.

C-E) right interolateral (IL) plate, in dermal (**C**) and visceral (**D**) views, with enlargement, × 2 (**E**).

H, I) right and left posterior ventrolateral (PVL) plates, dermal surfaces.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lateral. Lateral lines occupy shallow grooves; posterior pit-lines, central, supraorbital and rostral ?canals converge towards centre of nuchal. Cranio-thoracic joint formed by simple flanges. Median dorsal plate short and broad, lacking inner keel. Posterior lateral and posterior dorsolateral plates absent. Spinal plate moderately long. Anterior and posterior median ventral plates small or absent.

Family PHYLLOLEPIDAE Woodward 1891

Diagnosis: cranial shield broad and flat, nuchal wider than long, enlarged to cover much of cranial roof. Rostral and pineal plates not developed; central plates lost; marginal, postorbital and postnasal plates relatively small bordering nuchal and paranuchals laterally and anteriorly. Four pairs of shallow lateral line grooves converge on centre of nuchal. Orbits small and anterolateral, not expressed in cranial plates. Trunk shield broad and flat, moderately long; anterior dorsolaterals with long, narrow exposed face. Spinals moderately long, projecting posteriorly. Ventral shield short and broad, with large anterior ventrolaterals and shorter, subtriangular posterior ventrolaterals. Anterior and posterior median ventrals minute or absent. Ornament of concentric slightly undulating ridges, locally of elongate tubercles.

Genus *PHYLLOLEPIS* Agassiz 1844

Diagnosis: as for family with following additions. Nuchal subpentagonal, widest anteriorly. Paranuchals enlarged anteriorly, extending to widest part of nuchal, partly separating postorbitals and nuchal. Marginals small, lateral to paranuchal and bordered anteriorly by postorbital but not in direct contact with nuchal. Lateral canal diverges sharply from nuchal, traversing anterior lamina of paranuchal to meet marginal. Median dorsal subpentagonal, centre of ossification medially situated, ornament concentric, subpentagonal.

Genus *PLACOLEPIS* nov.

Name: from *plax, plakos* = broad, flat (Gr.); *lepis* = scale (Gr.).
Type species: Placolepis budawangensis sp. nov.
Diagnosis: as for family with following additions. Nuchal rounded anteriorly, widest opposite, or slightly posterior to, centre of ossification. Paranuchals relatively small, bordered anteriorly by marginals and not in direct contact with postorbitals; marginals with short but direct contact with nuchal at widest point. Lateral canal traverses paranuchals, marginals and postorbitals in close proximity to lateral margin of nuchal; paranuchal lacks lamina anterior to lateral canal. Median dorsal large, subpentagonal; ornament concentric with ossification centre situated anterior of midline. Spinals long, projecting posteriorly about one-third of total length. Anterior and posterior median ventral plates absent.

Placolepis budawangensis sp. nov.

Name: after the Budawang Range, southeastern New South Wales, Australia on the western flanks of which the type locality is situated.
Diagnosis: as for genus (only species).

Fig. 12. Placolepis budawangensis gen. et sp. nov., ventral trunk plates and spinal plates. Latex casts whitened with ammonium chloride sublimate. Scale in millimetres.
A) right anterior ventrolateral (AVL) plate, F.61505a; **B**) left AVL, F.61906a; **C, D**) right posterior ventrolateral (PVL) plate, dermal and visceral surfaces, F.61909a,b; **E, F**) spinal (Sp) plates, F.61787a, F.61748 (Holotype, cf. Fig. 3**A**,**B**).

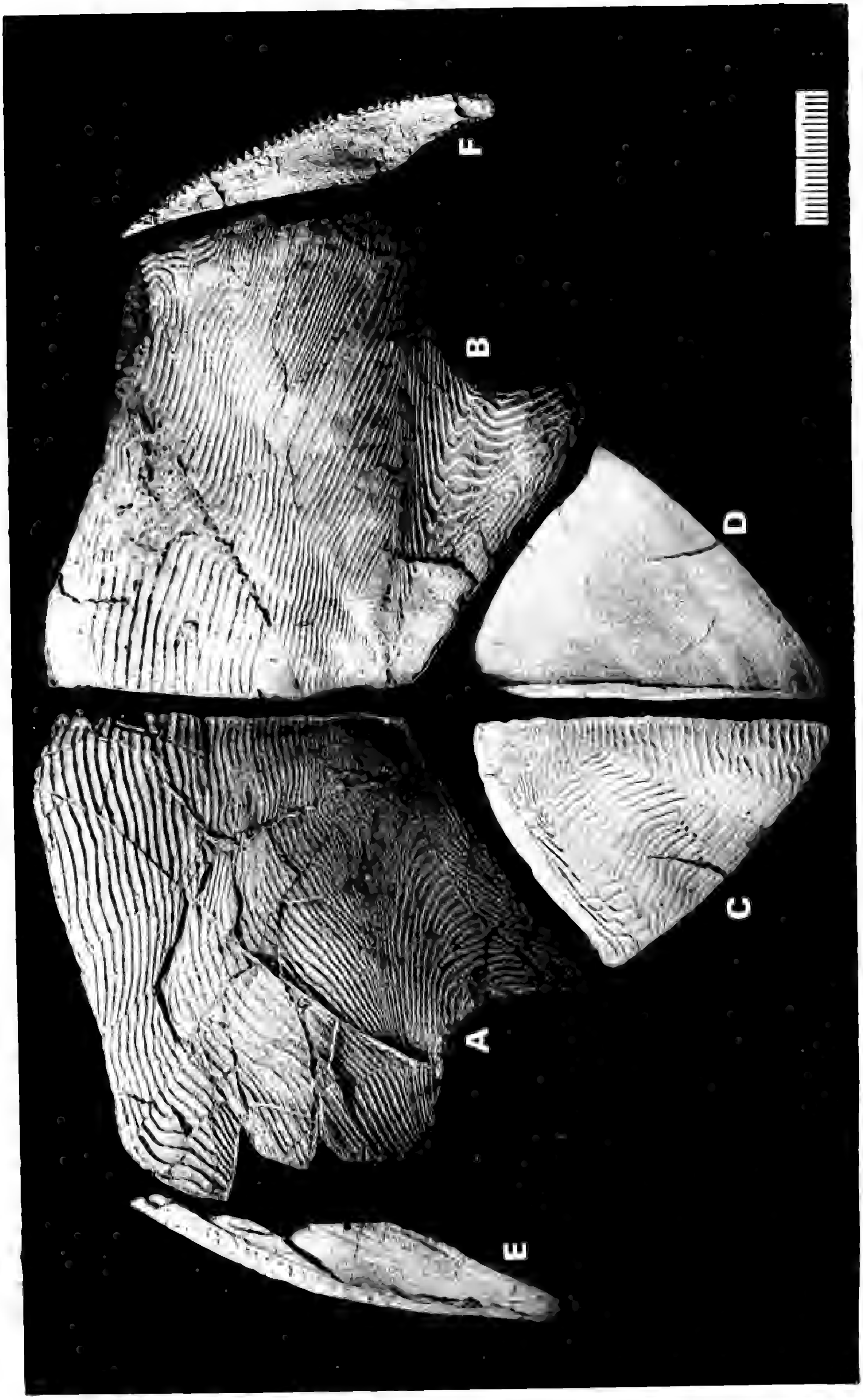
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TABLE 1

Length and width of the most complete nuchal (Nu) and the median dorsal (MD) plates of Placolepis budawangensis *gen. et sp. nov.*

Nuchal Plates	Length (mm)	Width (mm)	% L/W
F.61751	47.5	62	76.6%
F.61901	55	75	73.3%
F.61752	55	80	68.8%
F.61753	55	90	61%
F.68373-4	64	94	68.1%
F.61903	65	95	68.4%
F.61748 (holotype)	68	85	80%
F.61919	70	80	87.5%
F.61750	70	100	70%
Median Dorsal Plates	**Length (mm)**	**Width (mm)**	**% L/W**
F.61769	50	50	100%
F.61913	64	80	80%
F.61772	66	66	100%
F.61768	80	90	88.9%
F.61766	85	92	92.4%
F.61764	90	90	100%
F.63875	93	94	99%

Holotype: AM F.61748, consisting of scattered plates of a single *Placolepis* individual (Nu, PtN?, MD, 2 ALs, 2 AVLs, 2 PVLs, Sp) associated with a right PVL of another *Placolepis* and numerous plates of *Bothriolepis* sp.

Referred material: large slab, in counterpart, AM F.63873, 63874, bearing scattered remains of at least two *Placolepis* individuals (Nu, Pan, Mg, PtO, MD, AL, 4 AVLs, 2 PVLs, IL, Sp) associated with at least four individuals of *Bothriolepis* sp.

Cranial plates: nuchals (AM F.61750, 61751, 61752, 61753, 61901, 61902, 61919, 61921, 63875); postnasals? (F.61760, 61756); preorbitals (F.61915, 61916, 61918, 61921); postorbitals (F.61757, 61759, 61763); marginals (F.61756, 61758, cf. also F.63873-4) paranuchals (F.61755, 61756, 61925); superognathal (F.61920); inferognathal (F.61761).

Trunk plates: median dorsals (F.61764, 61766, 61768, 61769, 61772, 61913, 63875, 63876); anterior dorsolaterals (F.61782, 61783, 61784); anterior laterals (F.61779, 61781, 61908, 61919); interolateral (only known specimen on slabs F.63873-4); anterior ventrolaterals (F.61505, 61776, 61777, 61906, 61907, 63878); posterior ventrolaterals (F.61909, 61910, 61912, 61923, 63879); spinals (F.61787, 61912, 61903/61917, pt. and ctpt.).

RELATIONSHIPS OF PHYLLOLEPIDIDA TO OTHER PLACODERMS

Phyllolepis and *Placolepis* gen. nov. are closely related, very specialized Late Devonian placoderms characterized by a reduced complement of plates in the trunk shield and by an enormous enlargement of the nuchal plate at the expense of the other plates of the headshield, a pattern not readily comparable with that of the Arthrodira *ss.*

Phyllolepid relationships have been the subject of controversy since their discovery in the early 19th century. More recent discussions of their affinities with other placoderms are those of Westoll (1967), Stensiö (1969), Moy-Thomas and Miles

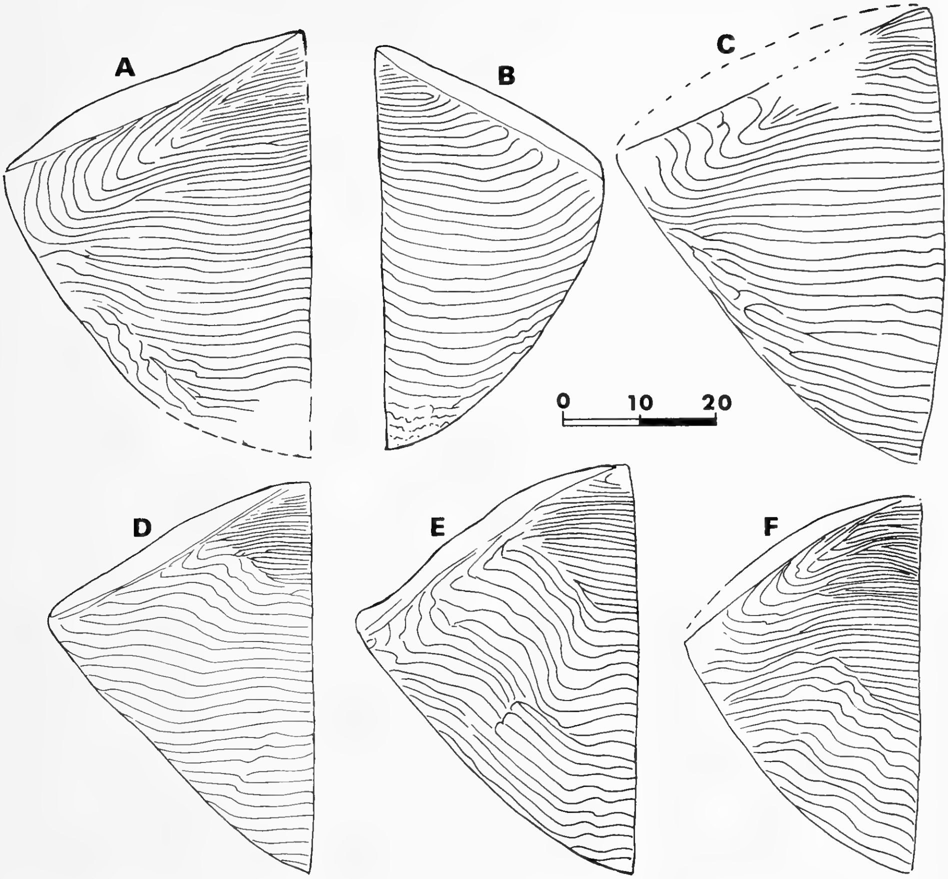

Fig. 13. Placolepis budawangensis gen. et sp. nov., six posterior ventrolateral (PVL) plates showing variation in ornament (for other examples cf. Fig. 11 **H, I**). All to same scale, shown in mm.
A) right PVL, holotype, F.61748 (cf. Fig. 3**A, B**); **B**) left PVL, F.61912; **C**) right PVL, F.61923; **D**) right PVL, F.61910a; **E**) right PVL, F.61909 (cf. Fig. 12**C**); **F**) right PVL, F.61748 (cf. Fig. 3**A, B**; extra right AVL not belonging to holotype).

(1971), Denison (1975, 1978), Miles and Young (1977), Young (1980, 1981) but it would be fair to state that a consensus is still far from being reached.

Westoll (1967: 96) suggested that placoderms formed two natural groups, divergently specialized in one important manner.

a) placoderms with a long occipital region and two pairs of paranuchals in the skull roof — petalichthyids, rhenanids and stensioellids.
b) placoderms with a short occipital region and only one pair of paranuchals — the euarthrodires (including the ptyctodontids and presumably the phyllolepids) and their probable derivatives, the antiarchs.

More recently the ptyctodontids and phyllolepids have generally been considered to belong outside the Arthrodira (or Euarthrodira) *ss.* and placed in their own separate orders.

Moy-Thomas and Miles (1971: 197) queried the use of these characters, pointing out that in most members of the first group the skull roof could not be interpreted with a high level of confidence. Since then most attention has focused on shared or derived characters in the trunk shield rather than in the headshield. Moy-Thomas and Miles (1971: 198) considered that the earliest known members of most placoderm groups already showed the typical characters of the group to which they belonged, 'thus it is not possible to say whether the trunk shield ever extended posteriorly on the flank behind the pectoral fins in petalichthyids, ptyctodontids, phyllolepids and stensioellids, as it does in arthrodires and antiarchs, and we cannot say whether the long type found in primitive arthrodires is primitive for all placoderm groups'.

Denison (1975: 12-13) proposed that an anteroposteriorly short trunk shield was primitive. He maintained that this had remained short in stensioellids, pseudopetalichthyids, rhenanids and ptyctodontids and that the first steps in lengthening it were to be seen in the Acanthothoraci (Palaeacanthaspidae and Kolymaspidae) with the addition of posterior lateral (PL) and posterior dorsolateral (PDL) plates; (but cf. also (Denison, 1978: 34) where the evidence for the PLs is questioned).

The next stage was the development of a ventral shield composed of AVLs, PVLs, AMV, PMV, and ILs; this is seen in petalichthyids and arthrodires, the early members of which had a pectoral fenestra enclosed by union of the ventral and lateral shields. The evolutionary position of the phyllolepids — with a moderately long thoracic shield but lacking PLs and PDLs — presented a problem; was this condition original or by secondary reduction?

Miles and Young (1977: 126-8) criticized Denison's phylogeny on grounds of parsimony. Whilst admitting that, at present, it is not possible to produce a convincing hypothesis of placoderm taxa relationships they suggested alternative phylogenies, starting from the basis of Moy-Thomas and Miles (1971: 198) quoted above.

Miles and Young (1977: 135-6) recognized only one genus of phyllolepid, ruling out *Antarctaspis* as a close relative. *Phyllolepis* had 'only one paired paranuchal, no tesserae and a short trunk shield with a posterior ventrolateral plate. The pattern of plates in the headshield is in some respects unique, but there are no known specializations here which link this genus with many of the groups considered so far'. They considered, but rejected, Denison's reason for linking *Antarctaspis* with *Phyllolepis*, which was based apparently on the fact that the supraorbital canal (*soc*) and central canal *(cc)* passed onto the nuchal plate. They noted that the *soc* passed onto the Nu also in petalichthyids, ptyctodontids and *Wuttagoonaspis* and that the *cc* passed onto the nuchal in *Wuttagoonaspis* and in some specimens of the arthrodire *Baringaspis*. The evidence of the sensory canals did not, therefore, provide a sound reason to link *Antarctaspis* and *Phyllolepis*.

Miles and Young also suggested (1977: 136) that the phyllolepid canal pattern was either a) primitive for placoderms or b) subject to convergent evolution. They tentatively suggested 'that phyllolepids might be most closely related to the common ancestor of arthrodires and antiarchs. These three groups are unique in having posterior ventrolateral plates'. The recent discovery of a PMV in the new Victorian phyllolepid removes another point of difference.

It was suggested (Miles and Young, 1977: 131) 'that primitive placoderms possessed median dorsal, dorsolateral, anterior lateral, interolateral, spinal, anterior ventrolateral and anterior median ventral plates. Two types of trunk shields were proposed:

a) a short shield with the plates listed above, primitive for placoderms, and in which there are no plates on the flank behind the pectoral fin; posterior laterals are absent (e.g. petalichthyids).

b) a long shield in which the ventral and lateral plates meet on the flank to enclose the

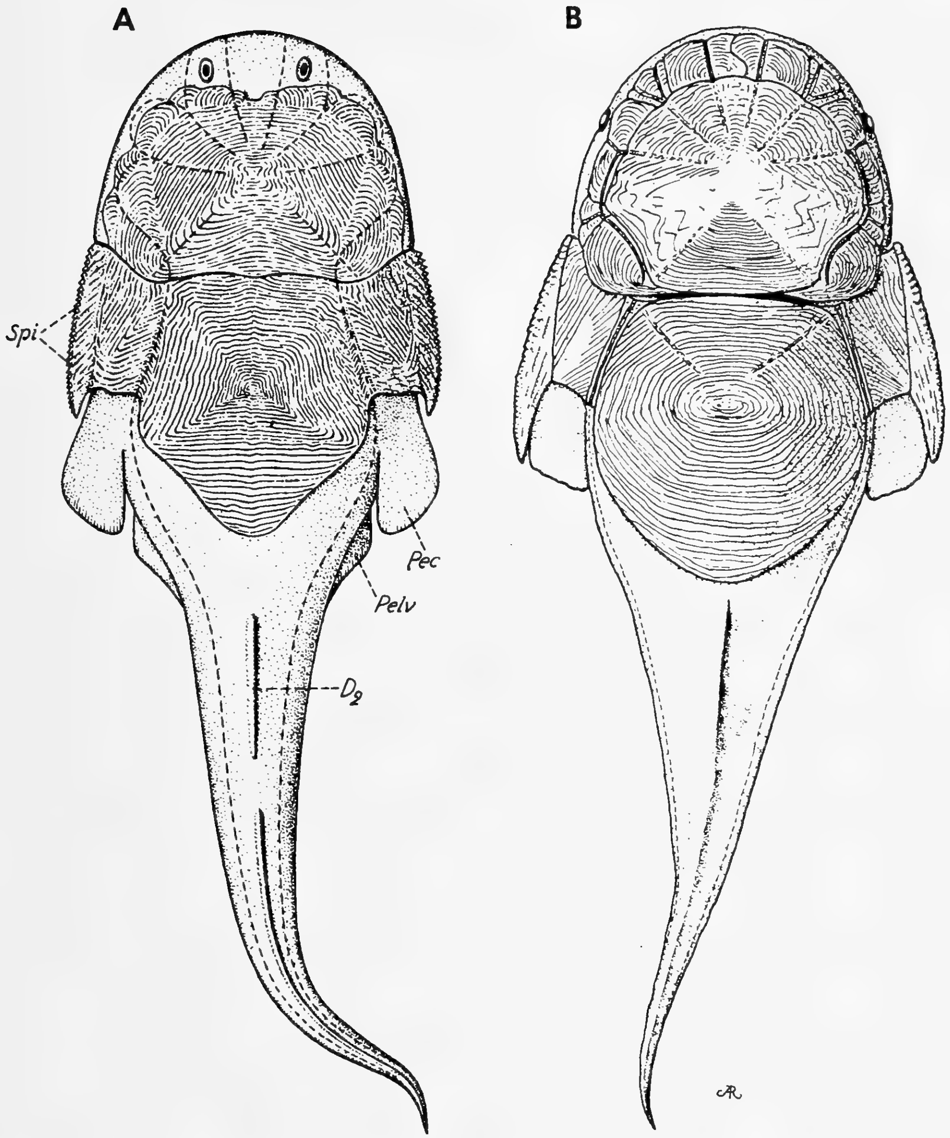

Fig. 14. Phyllolepis orvini Heintz and *Placolepis budawangensis* gen. et sp. nov. Restorations of the two genera in dorsal view illustrating alternative interpretations of the shape of the fins and trunk and the probable position of the eyes.

A. *Phyllolepis,* after Stensiö (1969: 77, fig. 3) and
B. *Placolepis* (and, it is suggested, *Phyllolepis*) by the writer.

base of the pectoral fin; posterior laterals are present, either as separate plates or combined with posterior dorsolaterals to form mixilaterals (e.g. arthrodires and antiarchs).

On this basis *Phyllolepis* (and *Placolepis*) would fall in group a) but this would be paraphyletic and would not accurately reflect its relationships, especially since we know that phyllolepids, arthrodires and antiarchs share not only posterior ventrolaterals but also posterior median ventrals.

The new genus, *Placolepis,* is not sufficiently different from *Phyllolepis* to throw much new light on the origins or relationships of the phyllolepids. Young (1980: 66, text fig. 27) included *Phyllolepis* in the Dolichothoracomorpha as the sister group of *Wuttagoonaspis,* antiarchs and euarthrodires. His analysis of the biogeography and interrelationships of placoderms 'suggests differentiation of certain more primitive placoderm taxa (*Antarctaspis, Phyllolepis* and *Wuttagoonaspis*) in the region of East Gondwana, and of more derived forms (actinolepid and phlyctaenioid euarthrodires) in Euramerica' (Young, 1981: 237).

The discovery of phyllolepids from the Middle Devonian or earlier rocks may provide a wider range of characters and a better understanding of which features are primitive; on present evidence Australia would appear to be the area most likely to yield earlier phyllolepids.

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I gratefully acknowledge the contribution made by Dr G. Gibbons, Dr R. Rogerson and the students of New South Wales Institute of Technology's Geology Department in uncovering this major find and bringing it promptly to my notice. The property on which it occurs is owned jointly by Mr and Mrs K. Aalto and Mr and Mrs V. Palasrinne of Canberra who gave us permission to excavate the site, and access to the site was provided by Mr E. Webb of 'Westwood' near Mongarlowe.

The writer was assisted in the excavations by Mr R. K. Jones, Australian Museum, Mr M. Leu, Dr R. Rogerson, Mr B. A. Ritchie and Mr T. Cogger. Mr Jones prepared and cast much of the material for study.

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The Head Shield of *Tiaraspis subtilis* (Gross) [Pisces, Arthrodira]

HANS-PETER SCHULTZE
(Communicated by A. RITCHIE)

SCHULTZE, H. P. The head shield of *Tiaraspis subtilis* (Gross) [Pisces: Arthrodira]. *Proc. Linn. Soc. N.S.W.* 107 (3), (1983) 1984: 355-365.

The head shield of *Tiaraspis subtilis* (Gross, 1933) is described. Very large orbits, large preorbital plates possibly including the postnasals, a 'fontanel' between pineal and rostral plates, and a club-shaped nuchal plate, in addition to the previously known high pointed median dorsal plate, are distinctive features of *Tiaraspis*. *Tiaraspis* is a phlyctaeniine arthrodire whose head shield resembles that of Groenlandaspididae. This resemblance supports their close relationship as suggested by Ritchie (1974, 1975) based on the trunk shield alone. This close relationship between these two genera is made tenable if the Holonematidae are not considered to be close relatives of the Groenlandaspididae.

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INTRODUCTION

Gross (1962) founded the new genus *Tiaraspis* on trunk shield parts which he described earlier (Gross, 1933a, 1937). He reconstructed the whole trunk shield with the characteristic high and narrow median dorsal plate. This median dorsal plate is easily recognized and the genus was discovered in other localities soon thereafter (Gross, 1965; Schmidt and Ziegler, 1965; and in Odenspiel, an as yet unpublished Early Devonian locality in the eastern Rheinisches Schiefergebirge). All these localities furnished only isolated parts of the trunk shield, and the head shield remained unknown until 1977 when the author together with Mr P. Brühn, Essen, West Germany, began a specific search for the head shield at the Siesel locality, east of Plettenberg, eastern Rheinisches Schiefergebirge (see Schmidt and Ziegler, 1965).

In the meantime, Ritchie (1974, 1975) allied the Early Devonian *Tiaraspis* with *Groenlandaspis* from the Middle and Late Devonian, based on features of the trunk shield. He postulated an unusual evolution from a short trunk shield with a high median dorsal plate in *Tiaraspis,* to a long trunk shield with a low median dorsal plate in *Groenlandaspis*. The new material of *Tiaraspis* described here enables Ritchie's hypothesis based on the trunk shield to be checked with data from the head shield.

MATERIALS AND METHODS

During 1977, Mr P. Brühn, Essen, and the author collected at different times in the dark-grey shales of the Lower Devonian Rimmert Formation at Siesel, east of Plettenberg, eastern Rheinisch Schiefergebirge. Remains of *Tiaraspis* are very common at this locality; only three acanthodian spines (Fig. 5**B, C**) have been discovered besides remains of *Tiaraspis*. The latter include three head shields and one isolated central plate, all in close association with trunk shield parts.

The shales of the Rimmert Formation at Siesel show cleavage oblique to the bedding, and the specimens are partly deformed. I have therefore desisted from reporting measurements. The head shield was reconstructed from the least deformed specimen (Gö 807-1). A plasticine model was built after the head shield and the trunk shield as reconstructed by Gross (1962). The author's reconstruction of *Tiaraspis* (Fig. 3) was drawn from the plasticine model.

The material is deposited in the Geologisch-Paläontologisches Institut and Museum, Universität Göttingen, West Germany (Gö 807-1 to 7), and in the private collection of Mr P. Brühn, Essen (Br. 0208).

SYSTEMATICS

Class PLACODERMI M'Coy, 1848
Order ARTHRODIRA Wodoward, 1891
Suborder PHLYCTAENIINA Denison, 1978
Family GROENLANDASPIDIDAE Obruchev, 1964
Genus *TIARASPIS* Gross, 1962
Tiaraspis subtilis (Gross, 1933)
Figs. 1-4, 5**A**

1929.	*Didymaspis*(?) Steinmann and Elberskirch, p.10.
1933a.	*Acanthaspis subtilis* n.sp. Gross, pp. 61-62, fig. 9. 2-13; pl. 4, figs. 3, 4, 8.
1933a.	*incertae sedis* (freie stachelartige Platte) Gross, p. 69, fig. 14; pl. 5, fig. 8.
1933b.	*Acanthaspis subtilis* Gross. Gross, p. 24.
1933.	*Acanthaspis subtilis* Gross. Schriel, p. 12.
1937.	*Prosphymaspis* n.gen. *subtilis* (Gross). Gross, p. 24, fig. 12D-F.
1937.	Arthrodire *incertae sedis*. Gross, p. 43, fig. 14A-C; pl. 3, fig. 1.
1962.	*Tiaraspis* n.gen. *subtilis* (Gross 1933). Gross, pp. 46-56, figs. 1-7A.
1965.	*Tiaraspis subtilis* (W. Gross). Gross, pp. 15, 16.
1965.	*Tiaraspis subtilis* (Gross). Schmidt and Ziegler, p. 226, fig. 1.
1969.	*Tiaraspis subtilis* (Gross). Miles, p. 147.
1974.	*Tiaraspis*. Ritchie, pp. 34, 35.
1975.	*Tiaraspis subtilis* (Gross). Ritchie, p. 570, fig. 1.
1978.	*T. subtilis* (Gross) 1933c. Denison, p. 65, fig. 44D.

Diagnosis: Phlyctaeniid arthrodire with a very high pointed median dorsal plate. Anterior and posterior dorso-lateral plates deep and short, curving first inward above the lateral line canal, then dorsally to be overlapped by the median dorsal. The lateral line curves strongly dorsad on the posterior dorsolateral plate. Low and small pectoral fenestra bordered posteriorly by long posterior lateral and posterior ventrolateral plates. Long, medially-barbed spinal plates. Posterior ventrolateral plates end in sharp points with a deep median embayment, the right posterior ventrolateral plate overlapping the left one anteriorly and overlapped by the left one posteriorly.

Head shield with straight posterior border and large orbits. Club-shaped nuchal plate broader anteriorly than posteriorly, with embayment posteriorly for the paranuchal plate. Small postmarginal, marginal and postorbital plates. Long preorbital plates placed laterally to a small pineal plate, a broad rostral plate, and a median space not covered by bone between the pineal and rostral. Supraorbital sensory line canal and central sensory line canal entering the central plate, postmarginal sensory canal entering the postmarginal plate, occipital cross commissure forming a canal on the paranuchal plate towards the posterior end of the nuchal/paranuchal suture, and posterior pitline running parallel to the endolymphatic duct from the growth centre of the paranuchal plate towards the point of junction formed by nuchal, central and paranuchal plates.

Holotype: Anterior ventrolateral plate (Gross, 1933a: pl. 4, fig. 8; Gross, 1962: fig. 3F), Humboldt Museum für Naturkunde, Berlin, Germany.

Type locality and horizon: Quarry Heider at Overath, southeast of Köln, eastern Rheinisches Schiefergebirge, West Germany, in Wahnbach Formation (? Late Siegenian, Early Devonian).

New material: Specimens Gö 807-1 (Figs 1**B**, 5**A**) Gö 807-2 (Figs 1**A**, 4**A**), Gö 807-3 (Figs 1**C**, 4**B**), and Gö 807-4 (an isolated central plate) from Siesel, east of Plettenberg, eastern Rheinisches Schiefergebirge, in the Rimmert Formation (? Early Emsian, Early Devonian).

Specimen Br. 0208, a skull from Odenspiel, southeast of Gummersbach, eastern Rheinisches Schiefergebirge, in the Odenspiel Formation (? Late Siegenian, Early Devonian).

Description: The posterior and central parts of the head shield are preserved in all four skull specimens. The central and paranuchal plates occupy most of the postpineal part of the skull. The paranuchal plates fill wide posterior embayments in the lateral margins of the nuchal plate, making the latter club-shaped with a three-lobed anterior portion which is twice as wide as the posterior portion. The nuchal and paranuchal plates form a straight posterior margin to the head shield. The paranuchal plate extends forward nearly half the length of the central plate and is bordered anterolaterally by the small postmarginal and marginal plates. The postmarginal (not shown in Fig. 1**B**) is represented in the counterpart, Gö 807-1b. The central plates are irregular in shape with a posterior extension between nuchal and paranuchal plates. Laterally, the central plate is bordered by marginal and postorbital plates, and by the preorbital plate anteriorly. The posterior part of the pineal plate lies between the central plates, with the anterior part between the posterior part of the preorbitals. The pineal plate is small, and is broken horizontally so that the pineal pit appears as an opening in specimen Gö 807-1a. The pineal plate does not reach the rostral plate and there is an empty space or 'fontanel' between these bones. The rostral plate forms the undulating anterior border of the head shield, and lies between the anterior part of the long preorbitals. The preorbitals may include the postnasal plates in their anterior portion; they form the dorsal and anterior borders of the large orbit, while the postorbitals occupy only a short part of the posterior margin of the orbits. The sclerotic plates are preserved in specimen Gö 807-1, and are partly superimposed on each other; I count four of them, the typical number for arthrodires (Denison, 1978).

The sensory line canals follow the usual course for phlyctaeniid arthrodires, except that the supraorbital sensory canal passes onto the central plate. The occipital cross commissure and the posterior pit line form canals on the paranuchal plate. The occipital cross commissure canal leaves the paranuchal mediad close to the posterior narrow portion of the nuchal. This could indicate the presence of a short unpaired extrascapular plate behind the nuchal plate. The middle pit line and the anterior part of the posterior pit line form distinct grooves on the central plates. The posterior part of the posterior pit line runs in a canal from the growth centre of the paranuchal plate anteriorly towards the junction formed by the nuchal, paranuchal and central plates. The endolymphatic duct presumably opened externally near the growth centre of the paranuchal, as is normal in phlyctaeniids. The canal for the duct can be seen running anteriorly within the bone beneath the posterior pitline, but its posterior end is not clear.

Reconstruction: The reconstruction (Fig. 3) of *Tiaraspis subtilis* is based on the reconstructed head shield (Fig. 2), and the trunk shield as reconstructed by Gross (1962: fig. 6). The size of the latter has been adjusted to conform to the head shield by comparison with the trunk shield parts associated with the head shields. The plasticine model shows

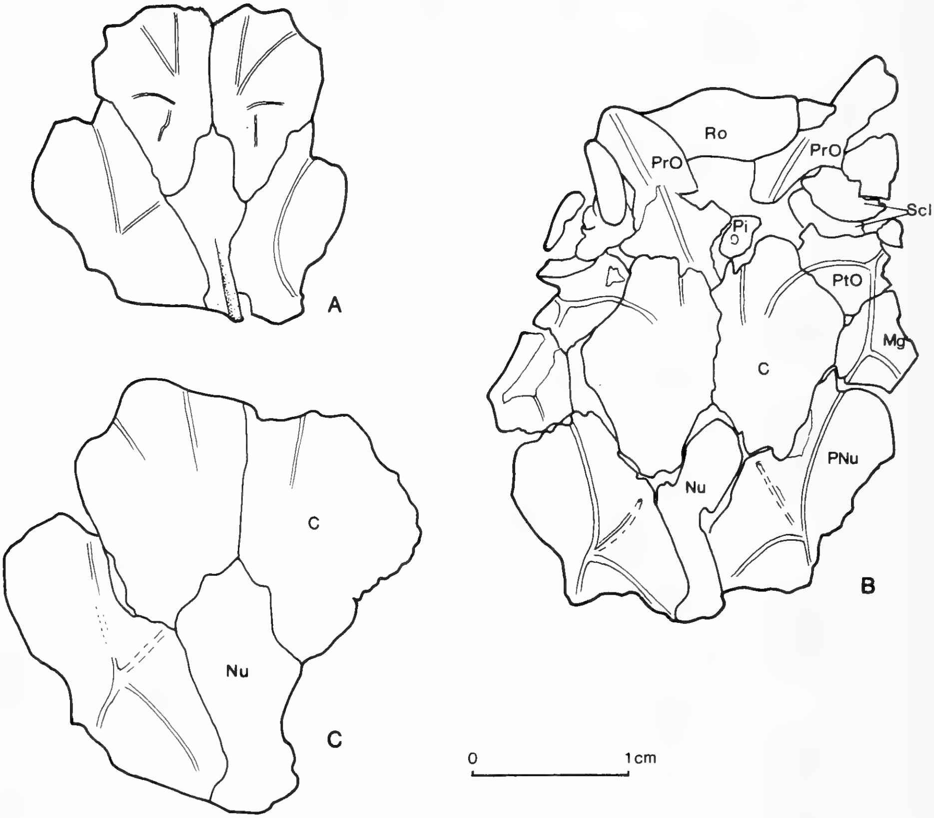


Fig. 1. Head shields of *Tiaraspis subtilis* (Gross) from the Early Devonian of Siesel, West Germany. **A**, Gö 807-2; **B**, Gö 807-1a; **C**, Gö 807-3. *C*, central plate; *Mg,* marginal plate; *Nu,* nuchal plate; *Pi,* pineal plate; *PNu,* paranuchal plate; *PrO,* preorbital plate; *Pto,* postorbital plate; *Ro,* rostral plate; *Scl,* sclerotic plate.

that the trunk shield is lower in lateral view than drawn by Gross (1962: fig. 6B) because the ventral portion of the antero-lateral plate turns horizontally so that the plate shortens dorsoventrally in lateral view. The head shield is long in comparison to the dorsal trunk shield (head shield 1.5 times the length of the trunk shield at lateral line canal level), and in comparison to relative length in other phlyctaeniines, especially holonematids. Even *Groenlandaspis* has a proportionately longer trunk shield.

The greatest difference from other phlyctaeniines can be found in the lateral side of the head. As restored, the large orbits leave little space for the suborbitals (not known), and this bone was presumably high and short. The submarginal is assumed to have occupied the normal position below the postorbital, marginal and postmarginal plates. The large orbits give *Tiaraspis* some resemblance to advanced brachythoracid arthrodires from the Late Devonian, some of which also possess 'fontanels' on the head shield, but in a more posterior position.

Geological age: The genus *Tiaraspis* is restricted to the Early Devonian (Gross, 1965). The assignment of the median dorsal plate of *Tiaraspis* sp. indet. to the Late Devonian of Modave, Belgium, was questioned by Gross (1965). At present, the genus is restricted geographically to central Europe. It is questionable that the median dorsal

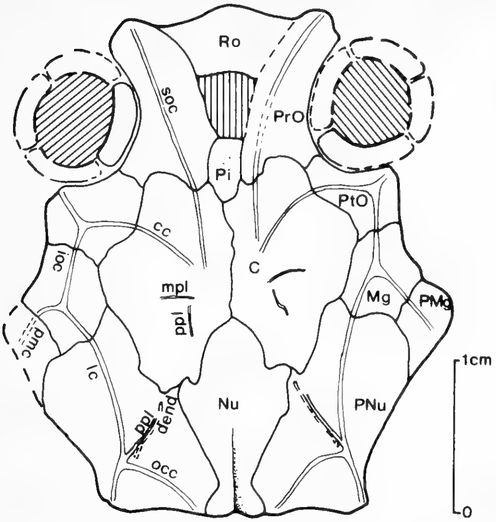


Fig. 2. Reconstruction of the head shield of *Tiaraspis subtilis* (Gross), mainly after Gö 807-1.
C, central plate; *cc,* central sensory line canal; *dend,* endolymphatic duct; *ioc,* infraorbital sensory line canal; *lc,* main line canal; *Mg,* marginal plate; *mpl,* middle pit line groove; *Nu,* nuchal plate; *occ,* occipital cross commissure canal; *Pi,* pineal plate; *pmc,* postmarginal sensory line canal; *PMg,* postmarginal plate; *PNu,* paranuchal plate; *ppl,* posterior pit line groove; *PrO,* preorbital plate; *PtO,* postorbital plate; *Ro,* rostral plate; *soc,* supraorbital sensory line canal.

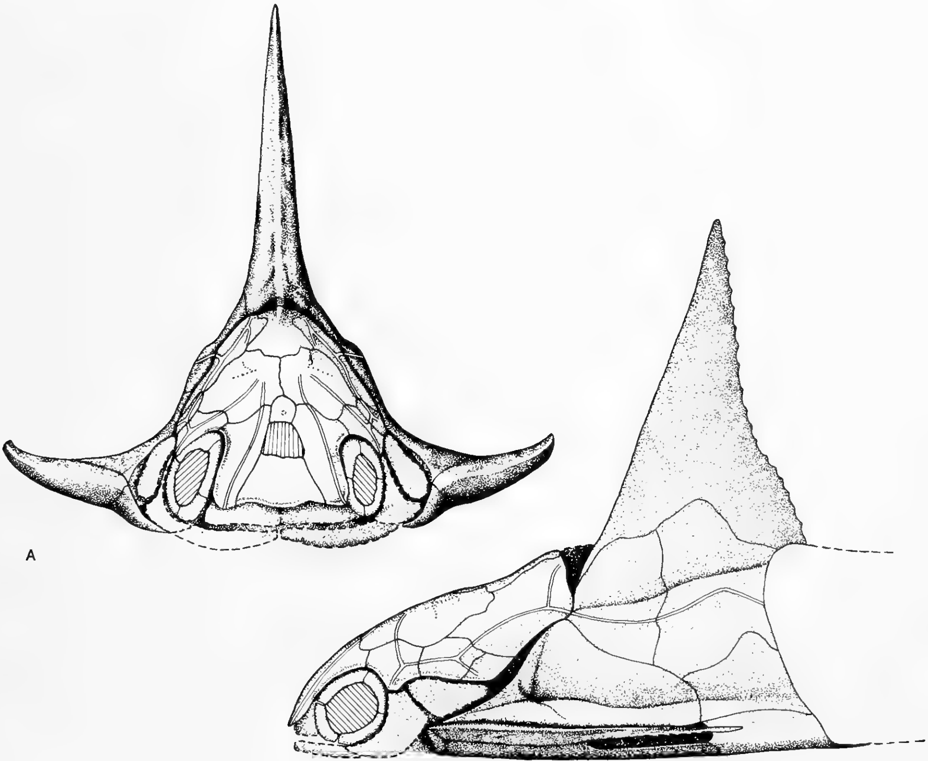


Fig. 3. Reconstruction of *Tiaraspis subtilis* (Gross). **A**, anterior view; **B**, lateral view.

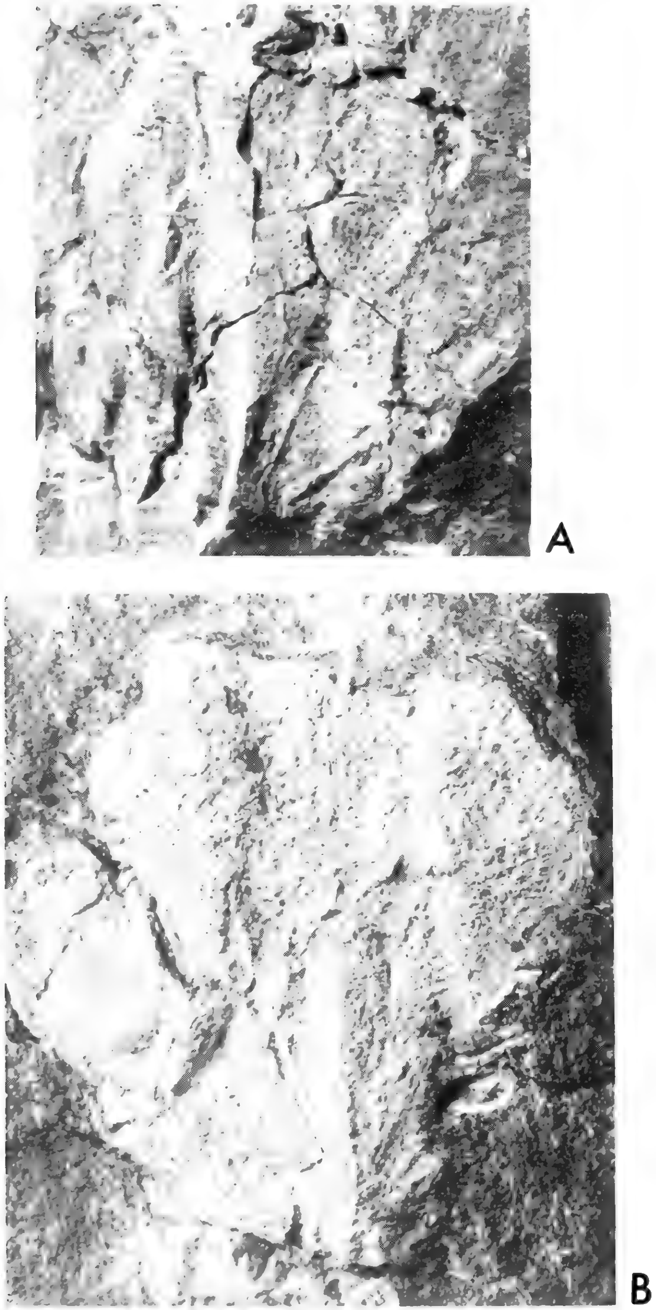


Fig. 4. Tiaraspis subtilis (Gross) from the Early Devonian of Siesel, West Germany. **A**, specimen Gö 807-2 (× 2); **B**, Specimen Gö 807-3 (× 2).

plate described by Gross (1965) from the Early Devonian of Spitsbergen belongs to this genus.

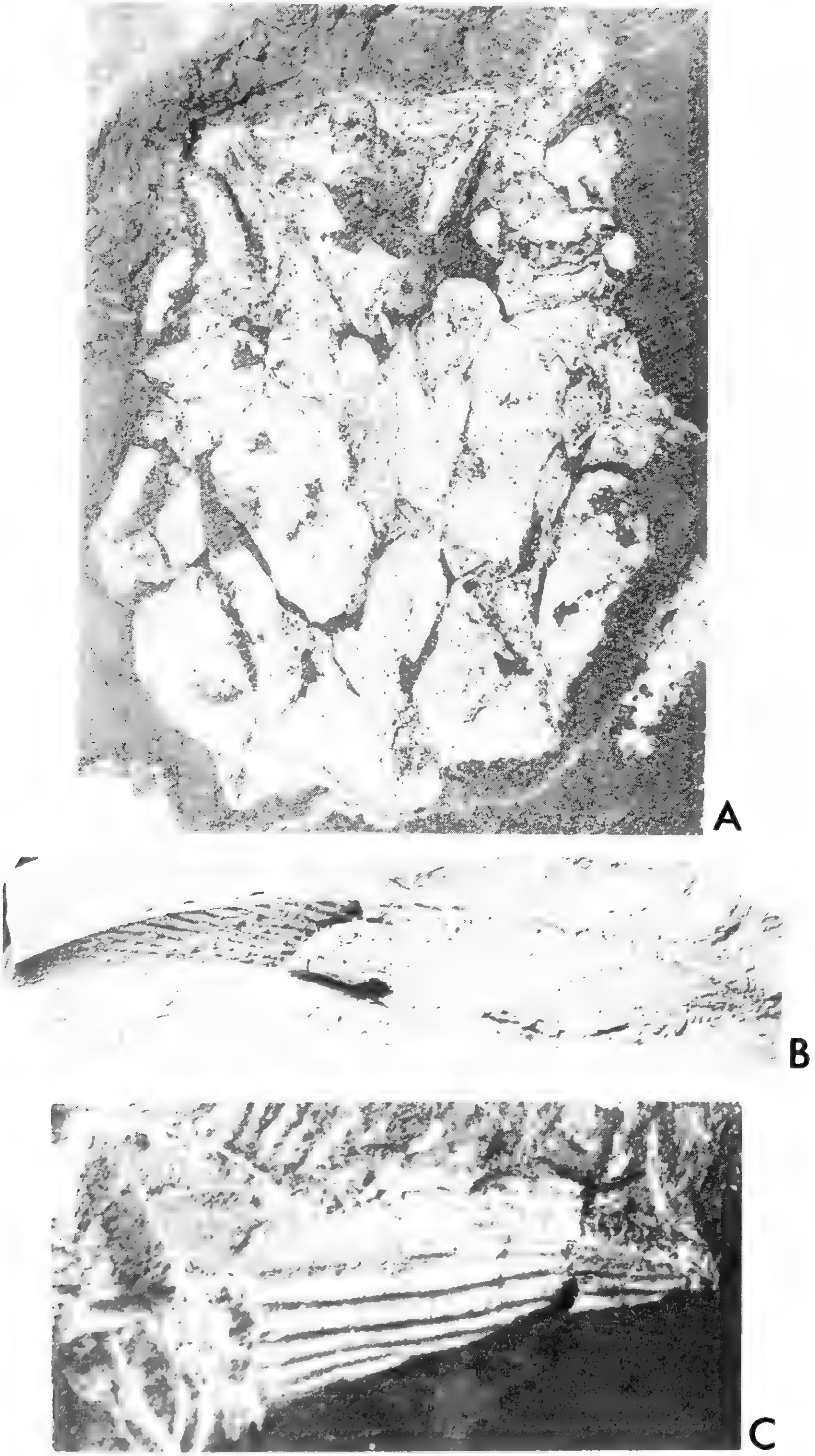
The species *Tiaraspis subtilis* occurs only in rocks of late Early Devonian age. The as yet undescribed fauna from Odenspiel is similar to that of Overath (Gross, 1933a, b, 1937, 1962). Both the Odenspiel Formation and the Wahnbach Formation of Overath are considered to be Late Siegenian (graben and Hilden, 1972; Schriel, 1933). the identification of the Siegenian index fossil *Rhenorensselaeria crassicosta* from Overath was questioned by Jux (1964). He considers the Wahnbach Formation as part of the Bensberg Formation, and the latter as Early Emsian in age. Jux (1982) correlates the Wahnbach Formation of Overath with the Odenspiel Formation, and assigns them a Late Siegenian and/or Early Emsian age. The Rimmert Formation, at least in its lower part, is of Early Emsian age according to Schmidt and Ziegler (1965), based on the occurrence of *T. subtilis*. Besides *T. subtilis, Gyracanthus? convexus* Gross 1933 occurs at Overath and at Siesel (Fig. 5**B**), and this supports the conclusion of Schmidt and Ziegler (1965). *T. subtilis* has been recorded from another Early Emsian locality in the western Rheinisches Schiefergebirge (Kahlenberg, east of Neroth; Gross, 1933b: 24), and also from the Lower Siegenian (Schmidt and Ziegler, 1965: 226). To summarize, *T. subtilis* is apparently restricted to the Siegenian and Early Emsian in the Early Devonian, but is most common in Late Siegenian/Early Emsian strata.

RELATIONSHIPS

The trunk shield of *Tiaraspis* is quite characteristic. The median dorsal plate alone makes the genus easily distinguishable from all other known arthrodires, and Miles (1969) placed it in its own family, the Tiaraspididae. Earlier, Gross (1962) noted similarities in the median dorsal plate with some antiarchs, Ptyctodontida, Arthrodira incertae sedis *(Grazosteus),* and those of *Huginaspis* and *Prosphymaspis.* Ritchie (1974, 1975) placed *Tiaraspis* with *Groenlandaspis* in the family Groenlandaspididae Obruchev, 1964, which is characterized by many primitive and some advanced features. A long, narrow median dorsal plate, no paired antero-ventral plates, an angular, dorsally directed flexure of the lateral line canal on the posterior dorsolateral plate, and a well-developed craniothoracic articulation are also characteristic of the Holonematidae. Therefore Denison (1978) united the Tiaraspididae and Groenlandaspididae with the Holonematidae, thereby following Obruchev's (1964) proposal that the latter two families be grouped together. The short, deep anterior dorsolateral and posterior dorsolateral plates distinguish *Tiaraspis* and *Groenlandaspis* from members of the family Holonematidae *sensu stricto.* Young (1981) accepted the close relationship of *Tiaraspis* with *Groenlandaspis* and *Holonema* (Fig. 6**A**), but on the other hand Dennis and Miles (1979a, b, 1980, 1982) regarded *Holonema* as a primitive brachythoracid (see also Miles, 1973).

That the Phlyctaeniidae and Holonematidae (+ Groenlandaspididae and Tiaraspididae) are closely related to each other is supported by the long trunk shield, long and narrow median dorsal plate, and the loss of anterior ventral plates as shared derived characters. A differentiated exoskeletal articulation connects the head shield with the trunk shield. *Tiaraspis* clearly belongs within Denison's (1978) suborder Phlyctaeniina, even though it may not possess a ventral ridge on the median dorsal plate, and the two pairs of superognathals are not yet known.

It is difficult to find advanced characters which separate the families within the Phlyctaeniina, as is always the case in primitive groups. The straight posterior border of the head shield is characteristic of Phlyctaeniidae, nevertheless Young and Gorter (1981) place *Denisonosteus,* a genus with a distinctly convex posterior margin, within the


A
B
C

Phlyctaeniidae. However *Tiaraspis,* with a nuchal plate similar to *Denisonosteus,* has a straight posterior margin, and no postnuchal process of the paranuchal plate as in phlyctaeniids, and is herein distinctly different from *Groenlandaspis.* Also, rostral and postnasal plates fused with each other may be an advanced character of the Holonematidae, but on the evidence of *Tiaraspis* this does not apply to the Groenlandaspididae (contrary to Young, 1981: fig. 17). Judging from the course of the supraorbital sensory canal, the postnasal in *Tiaraspis* and in *Groenlandaspis* seems to be fused with the preorbitals rather than with the rostral, unless it is a separate element lost from the skull in the available specimens. *Tiaraspis* also has a small pineal plate in the same position as the posterior part of the pineal plate in *Groenlandaspis.*

The lack of the advanced nuchal features and the straight posterior margin of the head shield exclude *Tiaraspis* from the Holonematidae in the sense of Denison (1978; *Holonema* up to *Groenlandaspis,* Fig. 6**A**). In contrast, the preorbital plate probably fused with the postnasal, the high pointed, laterally compressed median dorsal plate, and the high and short anterior and posterior dorsolateral plates unite *Tiaraspis* with *Groenlandaspis* (Fig. 6**B**). The Holonematidae are characterized by a very long trunk shield with a long, but not dorsally-pointed median dorsal plate, long anterior and posterior dorsolateral plates, long anterior lateral plate, and a very long, laterally directed pectoral fenestra. They are quite distinct from the Phlyctaeniina in these trunk shield characters and in features of the head shield (large rostro-postnasal plate, relatively small preorbital and central plates, deep cheek region with large suborbital plate). Therefore, I prefer to follow Dennis and Miles (1979a, b, 1980) and Ritchie (1975), and exclude the Holonematidae from the Phlyctaeniina; the discussion of their relationships is outside the scope of this paper. Still, the above arrangement does not eliminate the independent acquisition (Young, 1981: 269) of some characters (labelled 4 and 3c in Fig. 6**B**) within the Groenlandaspididae, and brachythoracid arthrodires including the Holonematidae. A detailed study of better-preserved skull shield material of Groenlandaspididae may reveal that these features indicate only superficial similarity. Another such independent acquisition would have to be postulated for the rostro-postnasal plate in *Arctolepis* and *Holonema.* The rostro-postnasal plate has in both forms quite a different relation to bordering plates and to the supraorbital sensory canal. In conclusion, *Tiaraspis* can be placed within the Groenlandaspididae by excluding the Holonematidae from the Phlyctaeniina. The family definition by Ritchie (1975) must be changed slightly regarding the head shield: head shield with straight or convex posterior margin, preorbital probably fused with postnasal, supraorbital sensory canal extending on to the central plate, large pineal plate or pineal plate + 'fontanel' between preorbital plates. *Tiaraspis* is more primitive in cranial features (4a-c in Fig. 6**B**) than *Groenlandaspis.* A convex posterior margin of the head shield may not be a distinctive character because it occurs also in *Denisonosteus,* an otherwise undoubted phlyctaeniid.

Finally the very high median dorsal plate and the large orbits of *Tiaraspis* could be associated with small body size; but this seems unlikely since *Groenlandaspis* with a much lower median dorsal plate is not much larger than *Tiaraspis.* Large orbits are typical for small fishes, but this is not so in arthrodires; small orbits occur not only in large, but also in small phlyctaeniines. Therefore the very high median dorsal plate and the

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Fig. 5. **A**, head shield of *Tiaraspis subtilis* (Gross) from the Early Devonian of Siesel, West Germany. Specimen Gö 807-1a (× 2). **B**, **C**, acanthodian spines from the same locality. **B**, *Gyracanthus? convexus* Gross 1933. Specimen Gö 807-5, coated with ammonium chloride (× 3); **C**, climatiid acanthodian, Gö 807-6, a left pectoral spine in ventral view (× 4).

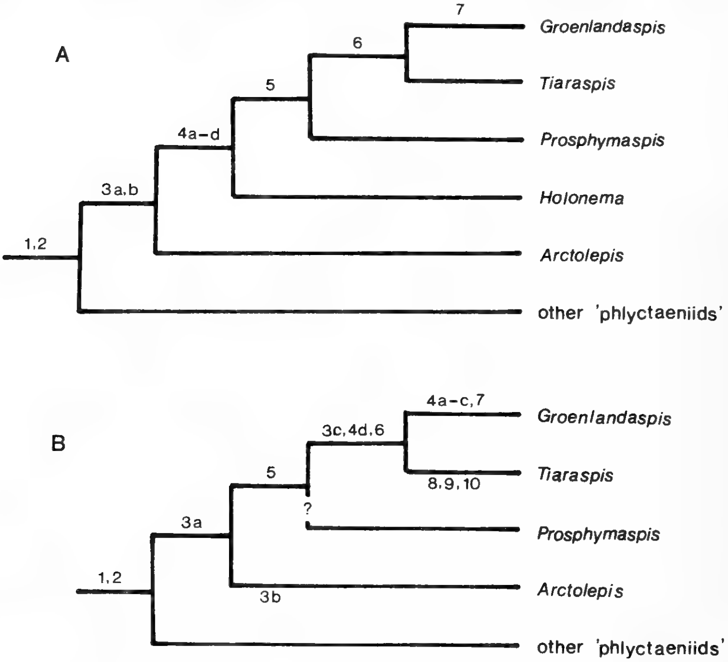

Fig. 6. **A**, Relationship scheme of Phlyctaeniina after Young (1981: fig. 16B). **B**, Here favoured relationship scheme of Phlyctaeniina without *Holonema*. Characters:
1, median dorsal plate long and narrow; 2, elongation of spinal plate; 3a, large pineal plate between preorbital plates, 3b, wide rostral plate which may incorporate fused postnasal, 3c, long preorbital plate which may incorporate postnasal; 4a, head shield with convex, angular posterior margin, 4b, paranuchal plate with postnuchal process, 4c, nuchal thickening, 4d, supraorbital sensory canal extending on to central plate; 5, high anterior and posterior dorsolateral plates, dorsally pointed median dorsal plate; 6, dorsal flexure of lateral line canal on posterior dorsolateral plate; 7, dorsal symphysis between posterior dorsolateral plates; 8, club-shaped, trilobate nuchal plate; 9, small pineal plate between preorbital plates with 'fontanel' in front; 10, large orbits.

large orbits are autapomorphies of *Tiaraspis* which may not be a common feature of the common ancestor of *Tiaraspis* and *Groenlandaspis*.

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This paper is dedicated to the late Prof. Dr W. Gross and to Dr A. Ritchie, Sydney, the two prominent students of the genus.

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Petrodentine in Extant and Fossil Dipnoan Dentitions: Microstructure, Histogenesis and Growth

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(Communicated by A. RITCHIE)

SMITH, M. M. Petrodentine in extant and fossil dipnoan dentitions: microstructure, histogenesis and growth. *Proc. Linn. Soc. N.S.W.* 107 (3), (1983) 1984: 367-407.

Twelve characters are used to define petrodentine. The proposition that 'columns of petrodentine' are a late specialization in dipnoan tooth plates is examined.

Techniques of polarized light, microradiography and scanning electron microscopy are applied to consecutive sections and surfaces of the tooth plates, from which the microstructure of petrodentine is described. Its histogenesis and growth in both extant and fossil forms are also reported. Petrodentine is found in the tooth plates of *Neoceratodus* as well as *Protopterus* and *Lepidosiren* and in all fossil forms with tooth plates that have been examined, including the Middle Devonian *Dipterus valenciennesi* and the Late Devonian *Chirodipterus australis.* The arrangement of petrodentine within the whole tooth plate is considered to be an important character in dipnoans. Specialized cells in the dental pulp secrete petrodentine in phases of growth throughout the adult life. This secretion begins in the youngest denticles in the larval tooth plate. Because of this special development petrodentine is clearly different from the interdenteonal tissue of osteodentine.

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INTRODUCTION

Recent papers by Denison (1974) and Miles (1977) have challenged the statement that a pair of tooth plates on the prearticular and pterygoid bones is the primitive condition for dipnoans. Miles (1977) concluded from his investigation on the fossil dipnoans from the Gogo Formation of Western Australia that lungfish with tooth plates are a monophyletic group. He further stated that while tooth plates are a synapomorphy of higher dipnoans the primitive dentition comprises buccal denticles and tooth ridges. Miles proposed a rudimentary form of phylogenetic analysis as a cladogram (Miles, 1977: fig. 157) using a scheme attempting to order the origin of specializations within the group. One of the characters used as a specialization, developing late within those dipnoans with tooth plates, is the arrangement of the types of dentine into columns of petrodentine surrounded by trabecular dentine. This character is confined to the lepidosirenids.

The term petrodentine was proposed by Lison (1941) to describe one of the component tissues in the tooth plates of an extant lepidosirenid. This referred to the hypermineralized dentine developing in close proximity to trabecular dentine, but contrasting in the degree of mineralization. However, Ørvig (1976b) has compared dentine in other genera of dipnoans with petrodentine as defined by Lison (1941) and concluded that a type of hypermineralized dentine, with structural features equivalent to those in petrodentine, is present in forms as far back as the Devonian. Denison (1974) also described hypermineralized dentine, although he did not refer to it as petrodentine, in many other genera including the Devonian form *Dipterus fleischeri.* From these reports it was apparent that the tissue type 'petrodentine' needed to be clearly defined, and that if equated with specialized hypermineralized dentine it was apparently more widespread amongst tooth plate-bearing dipnoans than was recognized by Miles (1977). It is clearly implicit in the statements of all three authors (Lison, 1941; Denison, 1974; and Ørvig, 1967) that a type of dentine can exist, within dipnoan tooth plates, in which the mineral content is considerably greater than normal dentine. A comparable tissue with a high percentage of mineral and a low percentage of organic matrix, derived by modification of dentine matrix, is the enameloid cap in the teeth of elasmobranchs and teleosts (Smith, 1980). However, the arrangement of petrodentine within the tooth plate and its histogenesis throughout ontogeny imply that it is a special type of dentine with clearly defined characters different from enameloid. Published accounts make it difficult to establish what these characters are and, therefore, difficult to compare the tooth plate structure of both fossil and extant genera.

With these objectives I have attempted to derive a set of criteria to characterize the tissue type petrodentine as first described in *Protopterus aethiopicus* Owen (Lison, 1941). This has involved a critical survey of the literature and new observations on both extant and fossil dipnoan tooth plates. The current study is concerned with three aspects of hypermineralized dentine in dipnoan dentitions. These are 1) the arrangement, microstructure and growth of petrodentine in tooth plates of extant forms; 2) the characters used to identify petrodentine from observations in polarized light, microradiography, and scanning electron microscopy; and 3) an analysis of the distribution of petrodentine amongst forms with tooth plates throughout the fossil record.

Information on the structure of tooth plates, their component tissues and their pattern of growth is of no value in assessing relationships between dipnoans, tetrapods and crossopterygians if it is accepted that tooth plates are a synapomorphy of higher dipnoans. However, it is of some value to establish characters of the dentition in any consideration of dipnoan interrelationships and in any study which seeks to distinguish primitive from derived characters of dipnoans as a prelude to recognizing characters synapomorphous with tetrapods or crossopterygians.

CRITICAL REVIEW AND TERMINOLOGY

The tissue in dipnoan tooth plates called 'petrodentine' (Lison, 1941) was first described by Owen (1839) in *Protopterus annectens* Owen as 'clear substance' because of its obvious translucence relative to dentine and bone. Prior to the suggestion by Lison (1941) that a new term should be used for this special category of dentine, both Kerr (1903) and Nielsen (1932) acknowledged that it is characterized by extreme hardness. They termed it vitrodentine and enamel respectively. Subsequent to those accounts Ørvig (1967) and Schmidt and Keil (1971) have discussed the structural similarity of the tissue in dipnoan tooth plates with durodentine (synonymous with enameloid, Poole, 1967) in elasmobranch and actinopterygian teeth, although they correctly recognized that histogenesis of this tissue is different in dipnoans from that of enameloid. All these terms are based on the composition of only one of the structural components of the tooth plate and its properties of hardness and translucency. Other terms for the dental tissues are derived from the composite arrangement of the hard and soft tissue components; these are syndentine (Thomasset, 1928, 1930), tubular dentine (Nielsen, 1932; Moy-Thomas, 1939), pseudohaversian osteodentine (Lison, 1941), compact or vascular pleromin (Ørvig, 1976b), trabecular dentine (Denison, 1974), central columnar dentine (Kemp, 1979).

The term tubular dentine is based on the parallel arrangement of vascular canals running through the tooth plate from the formative surface to the tritural surface. Denison (1974) used this term in his general review of the structure of teeth in lungfishes, believing that this regular arrangement of vascular canals was derived from the primitive type of trabecular dentine, with irregular vascular canals, as a specialization. The difficulty of using this term has been previously discussed (Radinsky, 1961; Smith, 1979a). The term syndentine (Thomasset, 1930) is another one based on overall structure, implying that it is derived in ontogeny from separate parts now joined together. This is not a feature that could be recognized in the mature tissue and most subsequent workers have rejected the term (Smith, 1977). Denison's concept of the tissues in lungfish tooth plates is slightly ambiguous. He stated that both trabecular dentine, found in many of the tooth plates, and tubular dentine are highly mineralized. However, Denison (1974) chose to recognize as petrodentine only the hypermineralized dentine arranged as columns as in the lepidosirenids. Nowhere does he state that all the examples of hypermineralized dentine may be equivalent to petrodentine. As it is one of the objectives of this paper to consider the evidence for the distribution of highly mineralized dentine (petrodentine) within tooth plates of dipnoans, Denison's observations will be included in the next section.

Ørvig (1951) in a comprehensive study of tissues in placoderms and elasmobranchs recognized that 'tubular dentine' is a distinctive tissue, different from trabecular dentine (osteodentine) found extensively in teeth of fishes. He reached this conclusion because he regarded 'tubular dentine' as having a different ontogenetic pathway and, more importantly, a different structure. The main reason for this statement is the different cellular origin of the interstitial tissue, although Ørvig (1951) regarded the tubular component as analogous with dentinal osteons of osteodentine. Lison (1941) was faced with the same difficulty of a general terminology for the tissue around the petrodentine in the whole tooth plate. He called it 'pseudohaversian osteodentine'. This is an unnecessarily complicated term because once it is accepted that the component of dentine arranged in concentric layers around the vascular canal can be compared with an osteon (denteon), then by analogy with compact bone the denteons can form either with or without prior resorption of the interstitial tissue. In both cases the denteons compare with the true Haversian systems, both primary and secondary ones. Many different categories of osteodentine are illustrated by Ørvig (1951: figs 1, 2) and again his term osteodentine (Ørvig, 1967: 102) includes all dentines which start as trabecules of mineralized tissue (woven-fibred, coarse-bundled) and become compact by growth around the blood vessels of concentric dentine layers (denteons). In this category he included as osteodentine the tissue at the margins of the tritural columns in holocephalan and dipnoan tooth plates. Again, Ørvig had accepted that the columnar tissue forming the wear-resistant ridges (triturators) of the tooth plate is different from any of the other osteodentines. In his 1967 review Ørvig decided to recognize a new category, columnar pleromic hard tissue, for these hypermineralized tissues forming initially in a superficial position and growing continuously in a basal direction.

Essentially this pleromic hard tissue, or pleromin, is the main component of the ridges of the tooth plate and is equivalent to petrodentine. I reach this conclusion because Ørvig still felt it necessary to have two terms for the different composite tissues. Where the composite tissue is formed of tritural columns of pleromin separated by parallel denteons, he referred to it as vascular pleromin and still rejected the term 'tubular dentine'. Hence Ørvig (1976a,b) proposed the recognition of two types of pleromic hard tissue: vascular pleromin (synonymous with tubular dentine) typified by the tissue in *Neoceratodus* and *Ceratodus,* and compact pleromin, blocks or columns of petrodentine without vascular canals except at the margins of the tritural column, typified by *Monongahela* and *Lepidosiren.* Kemp (1979) rejected all previous terms and referred to 'central columnar dentine' in toothplates of *Neoceratodus forsteri.*

By this stage of the review we have identified the main problem, that is, are Denison (1974) and Miles (1977) correct in considering the most significant features of the tooth plates to be the arrangement of the component tissues, i.e. columns of petrodentine with or without vascular canals, or should emphasis be primarily on whether there is a special histological type of dentine that is hypermineralized and of continuous growth from the basal surface? Some conflict of opinion can be found in Denison's (1974) account because, as Miles (1977) observed, he described the tooth plates of *Monongahela,* a gnathorhizid, as showing a distinctive histological structure comparable with that of *Protopterus,* while those of *Gnathorhiza,* were claimed to be sufficiently different not to support a close relationship with lepidosirenids.

Most people searching for homologies in the tissues have been faced with this plethora of names and been unable to reach agreement. Ørvig (1951, 1967, 1976a,b) recognized the special type of dentine in dipnoans (and holocephalans), principally for two reasons — it is extremely hard and lacks collagenous matrix, and it grows continuously at the basal surface by elongation into the tissues supporting the tooth plate. After consideration of all the possibilities for a comparison between dipnoan tissues and osteodentine in general, we are left with the statement that the interstitial tissue between the denteon systems in dipnoan tooth plates is different in its development, structure and growth from the 'inter-denteonal' tissue of osteodentine. It is this statement that we must examine.

If we accept that tooth plates are a specialization in dipnoan dentitions (Denison, 1974) and that they evolved only once (Miles, 1977), then petrodentine would be an additional specialization confined only to those forms with tooth plates. It is also apparent that we must decide whether or not it is another specialization to have the petrodentine arranged into columns (compact pleromin) or interspersed with regularly arranged vascular canals (vascular pleromin). Ørvig (1976b) also claimed that the pleromin of holocephalan tooth plates is arranged in columns in some forms, although he noted that it differed from that in *Lepidosiren* in a detail of the histological structure (Ørvig, 1983). It is implicit in both Denison's (1974) and Miles's (1977) statements that arrangement into columns of petrodentine is the significant advanced character. If this is in fact so then we must look for the pattern in the distribution of these tissues amongst the genera of dipnoans.

REVIEW OF THE DISTRIBUTION OF PETRODENTINE WITHIN DIPNOANS

Characters of the tissue

It is quite clear from the literature that all dipnoan tissues described by Ørvig (1967, 1976a,b) as pleromin have the properties of the tissue first described by Lison (1941) as petrodentine. In the review of dental tissues by Schmidt and Keil (1971) they equated the petrodentine with durodentine (enameloid, Poole, 1967) of elasmobranchs and actinopterygians, although Schmidt and Keil (1971) noted that the petrodentine forms out of contact with the dental epithelial cells, and is therefore, quite different from enameloid. Ørvig (1967a,b) had recognized that a special population of cells, pleromoblasts, is responsible for the production of pleromin in all groups that he studied and that this method of histogenesis is a significant difference from that of enameloid. Lison (1941) had originally also described two populations of cells developing within the pulp cavity — petroblasts secreting petrodentine and odontoblasts the dentine. All the characters that may be used to describe the tissue petrodentine are listed in Table 1. The important ones to distinguish it from enameloid are numbers 10 and 11; both are difficult but not impossible to demonstrate in fossil material. In many adult tooth plates new material, in the form of denticles, is added at the labial margins and these provide examples of tissue histogenesis as in earlier on-

TABLE 1

*Characters used to identify petrodentine in extant and fossil tissues**

1. not diagenic, not stained during fossilization
2. translucent in transmitted, non-polarized light
3. few tubules, or if present, very thin and confined to margins
4. hypermineralized relative to normal dentine and bone
5. birefringence due to mineral component, bands crossed at right angles
6. opposite signs of birefringence in adjacent regions; each band inclined 45° to the vertical axis
7. assumed formation from fibre-based matrix, with crystals in groups retaining the fibre orientation
8. continuation of crystal-fibre bundles with collagen-fibre bundles at margins
9. extreme reduction of organic matrix, concomitant with mineralization
10. continuous sequential growth at abtritural surface from pulpal cells
11. develops late in histogenesis of the tissues in each denticle or region
12. forms in earliest ontogenetic stage of the tooth plate

* compiled from publications by Lison (1941), Ørvig (1967, 1976), Schmidt and Keil (1971), Smith (1980).

togenetic stages. In the denticles at the labial margins of the tooth plates of *Sagenodus inaequalis* (Smith, 1979), petrodentine develops later than the peripheral dentine (Table 1 — character 11). Identification of forming surfaces roofing a pulp chamber, and sequences of growth lines parallel to this surface in many fossil genera show that growth is continuous and extensive (Table 1 — character 10). The pattern of growth in dipnoan tooth plates has been investigated by new methods (Smith, Boyde and Reid, 1984) and an analysis of this is in progress (Smith, MS).

Extant genera

The translucency, lack of tubules and non-diagenic properties of petrodentine (Table 1 — characters 1-3) were the only characters referred to by the early workers; both Schmidt and Keil (1971) and Ørvig (1976) cite these references. The first description of the histology of any tooth plate was by Owen (1839, 1841, 'clear substance') in *Protopterus annectens* and also in *Lepidosiren paradoxa* (Owen, 1845: 159, fig. 4). Günther (1871) first described the 'clear substance' between the vascular canals in *Neoceratodus forsteri*.

In the larval stages of the extant forms Parker (1892) noted what he called 'infilling dentine' in *Protopterus aethiopicus*, later used by Jarvik (1967) as an example of pleromin (Ørvig, 1967). Ørvig (1967: figs 45a,45b) figured Lison's findings as examples of the ontogenetic development of pleromin. Kerr (1903) described the dentine in this position in *Lepidosiren paradoxa* as vitrodentine (after Röse, 1892). Semon (1899) studied the early stages of *Neoceratodus forsteri* and described intrapulpal dentine in the position of the infilling dentine of Parker (1892). The account of tooth plate development in larval stages of *Protopterus aethiopicus* by Lison (1941) clearly demonstrates that this infilling dentine is petrodentine in the early ontogenetic stages (Table 1 — character 12). An account of the growth of petrodentine in larval stages of *Protopterus aethiopicus* by Smith (1984) shows how continuous extensive growth of petrodentine contributes to the structure of the larval tooth plate. Both these studies show that petrodentine is secreted from pulpal cells after a cone of primary dentine is formed (Table 1 — character 11). Similarly, recent studies on *Neoceratodus forsteri* (Kemp, 1979) show that petrodentine (central columnar dentine) starts to form from pulpal cells within the primary dentine and that continuous growth from this surface contributes to the main tissue mass of the tooth plate.

Lison (1941) figured the adult tooth plates of *Protopterus aethiopicus* with the translucent columns of petrodentine without tubules contrasting with the dentine with tubules surrounding the vascular canals. Growth lines are not mentioned although he did suggest that growth is continuous from special pulp cells (Table 1 — character 10) and that a differential rate of growth allows the vascular canals to be included at the margins of the petrodentine. Lison concluded that it is exactly the same tissue between the vascular canals of *Neoceratodus forsteri*. Schmidt and Keil (1971) described the polarized light appearance of petrodentine of *Protopterus aethiopicus* and concluded that the bands crossing at right-angles are due to crystals following the course of the collagen fibres. These crystal-fibre bundles are continuous with the collagen fibres of the dentine (Table 1 — characters 5, 7, 8) and at the junction between the two tissues there is a neutral, or apparent isotropic zone. In a study of the growth of tooth plates in *Protopterus annectens* (Smith, 1984) it is shown that petrodentine is added to the abtritural surface and that this increases in extent not only at the labial and posterior margins but also at the lingual or palatal margins (Table 1 — character 10). Also demonstrated are the lines of low mineral density, in sequence and parallel to the formative surface; these are interpreted as lines of growth.

A section through a tooth plate of *Lepidosiren paradoxa* is figured by Tomes (1904) showing apparent superimposed layers of the petrodentine (translucent material). Denison (1974: fig. 14) illustrated a similar section through the tooth plate of *Lepidosiren paradoxa* and described the same region as hypermineralized, also showing growth lines, although these were not described. Scanning electron micrographs of *Lepidosiren* sp. from the Upper Miocene are figured by Ørvig (1976b: figs 22-25) and these show the distinctive microstructure of woven crystal-fibre bundles between the vascular canals.

Ørvig (1976b: figs 13, 14) figured Günther's illustrations of *Neoceratodus forsteri* and referred to the petrodentine (pleromin) as the tissue between the vascular canals, as Lison (1941) had also previously concluded. He also illustrated, in horizontal sections (Ørvig, 1976b: fig. 19), the typical birefringence of the petrodentine and the characteristic microstructure in polarized light, of radial bundles around the vascular canals. This is contrasted with osteodentine in which there is no hypermineralized interstitial matrix, formed of radially oriented crystal-fibre bundles between the denteons (see Ørvig, 1951). The ultrastructure of petrodentine in ceratodontids is shown by Ørvig (1976b: figs 15, 16) in a Triassic genus and, as in lepidosirenids, this shows the crystal-fibre images of coarse intertwining fibre bundles. Kemp (1979), referring to this part of the tissue as central material, decided that it had not formed following the loss of a collagen fibre matrix as it first appears with only scant reticulin fibres, but she offered no alternative explanation of the basis for the crystal-fibre bundle images. As I have also concluded (Smith, 1980) the basis for the orientation of the crystallites is not established. It could be determined by the matrix or by the cell processes at the formative front.

The fact that petrodentine is hypermineralized has been assumed from its translucency, hardness and appearance in acid-etched scanning electron micrographs. The degree and extent of this hypermineralization has only recently been demonstrated using microradiographic information (Smith, 1980, 1984). From these studies it is apparent that the degree of mineralization is very high indeed, of the same order as enamel in the teeth of tetrapods, and enameloid in elasmobranchs and actinopterygians (Table 1 — character 4). Preliminary studies on quantitation of microradiographs show that petrodentine is 4½ times as dense as dentine. This compares with human enamel which is 5 times as dense as dentine. This is true of all three extant genera of dipnoans. The reduction of the organic matrix with progressive mineralization of the tissue has been shown by Lison (1941) and James (1957), (Table 1 — character 9).

The arrangement of the hypermineralized dentine in *Protopterus* and *Lepidosiren* is described by Denison (1974) as alternating columns of petrodentine and trabecular dentine. Ørvig (1976b) termed this compact pleromin. Both regarded such tissue as an advance on the type called hypermineralized trabecular dentine (Denison, 1974) or vascular pleromin (Ørvig, 1976b). Compact pleromin is the advanced character in dipnoan tooth plates referred to by Miles (1977b) as 'columns of petrodentine'. Although, as Ørvig (1976b) stated, in all forms the tissue starts off as compact pleromin in the larval tooth plates.

Fossil genera

Petrodentine is a major part of the tritural columns of the ridges of the tooth plate in *Lepidosiren* sp. from the Miocene (Ørvig, 1976b). Günther (1871) figured sections of *Ceratodus runcinatus* Pleininger, a Triassic form showing petrodentine between the vascular canals, which he compared with *Neoceratodus forsteri.* He also showed growth lines parallel to the tritural surface; a sequence of growth lines is also figured by Stromer and Peyer (1917) and the ultrastructure of these lines is recorded by Smith, Boyde and Reid (1984). Schmidt and Keil (1971) concluded that the histological features of *Ceratodus kaupi* Agassiz, another Triassic ceratodontid, are similar to those of *Protopterus.* They recorded the non-diagenic, unstained character (Table 1 — character 1) of the tissue between the vascular canals and contrasted this with the dentine surrounding the canals (Schmidt and Keil, 1971: fig. 181). The other features noted by them are a matted feltwork of fine tubules, and a pattern of birefringence, typical of petrodentine, in which the birefringent fibre bundles are organized radially adjacent to the vascular canals. Ørvig (1976b: figs 15, 16, 17) has also produced scanning electron micrographs of this tissue, clearly petrodentine, in a Triassic ceratodontid. Stromer and Peyer (1917) figured sections of *Ceratodus parvus* Agassiz from the Upper Triassic and these show that the organization of petrodentine is such that it is beneath each crest of the ridges in these radiate tooth plates. Denison (1974: fig. 8) illustrated a section through two denticles of a juvenile tooth plate of *Ceratodus parvus* and commented that this tissue is unspecialized, highly mineralized, trabecular dentine.

Since these early reports, only Denison (1974) and Ørvig (1976b) have commented further on the types of dentine in fossil dipnoan tooth plates and they have produced conflicting opinions on the significance of the distribution of petrodentine amongst these groups. It is apparent that all forms assigned to the families Lepidosirenidae and Ceratodontidae possess petrodentine as a major component of the tooth plate. In the former group it is arranged as columns (compact pleromin; Ørvig, 1976b) and in the latter petrodentine is frequently interspersed amongst parallel vascular canals (vascular pleromin; Ørvig, 1976b). The proportion and arrangement of trabecular dentine (osteodentine) at the margins of the petrodentine varies considerably amongst the genera, and it may be that this feature is as significant as the presence or absence of petrodentine. The morphology of the tritural surface of the tooth plate is affected by the distribution of petrodentine and trabecular dentine, with their inherently different rates of wear. This variation is shown by Tabaste (1963) in the Lower Cretaceous ceratodontids in sections of *Ceratodus tuberculatus* Tabaste and *Ceratodus africanus* Tabaste. Schultze (1981) compared the histology of flat-surfaced Lower Cretaceous tooth plates of *Ceratodus frazieri* Ostrom with that of *Ceratodus africanus* and described patches of osteodentine (trabecular dentine) between large areas of petrodentine. These patches of osteodentine were observed to correspond with the circular depressed areas on the tritural surface.

Amongst the genera of dipnoans possessing radiate tooth plates (Denison, 1974), there are only a few in which the histology has been investigated. Denison (1974: fig.

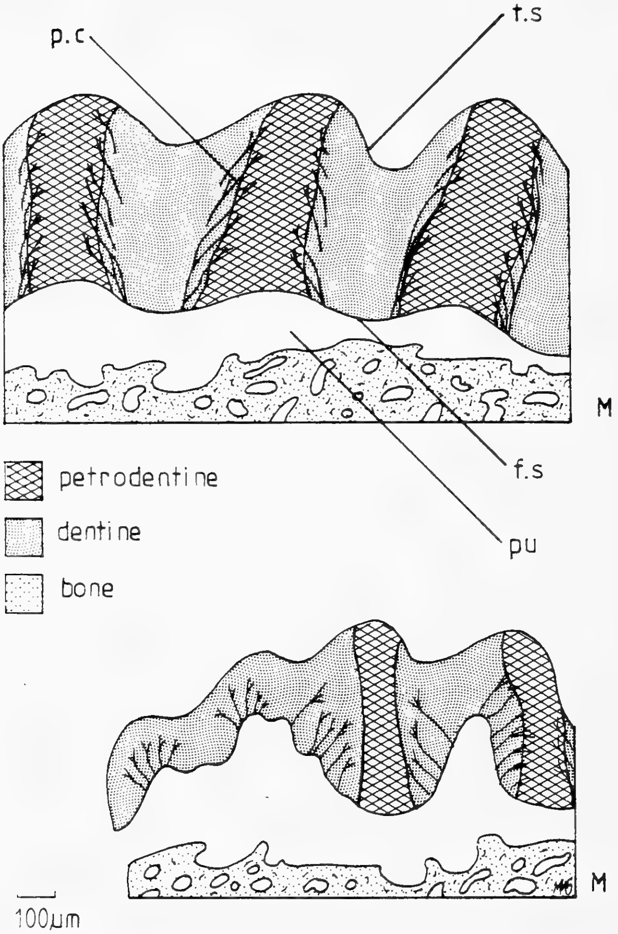


Fig. 1. Monongahela dunkardensis Lund. Juvenile tooth plate, vertical sections along one ridge (Prev. figs 12 & 13, Denison, 1974; F.M. 5507, 5505). Regions of petrodentine separated by dentine. Pulp canals terminating in dentine tubules pass across the border between tissues. Labial margin of tooth plate, no petrodentine in youngest denticles. Key to this figure is the same for all subsequent drawings (see p.407).

12) described young tooth plates of *Monongahela dunkardensis* Lund, an example of a Permian form, and illustrated the arrangement of columns of hypermineralized dentine (petrodentine), alternating with trabecular dentine. Ørvig (1976b) later referred to this as compact pleromin. I was fortunate to be able to examine the same section (Field Museum 5502) in polarized light and found that the column of translucent dentine showed alternating signs of birefringence either side of an isotropic zone (Table 1 — character 6). This together with other features confirmed my opinion that there is petrodentine in this genus. I was also able to observe in a section through the youngest tissue at the labial margin of one ridge (Fig. 1), that these columns of petrodentine develop late in the histogenesis of each denticle of the tooth plate.

The tooth plates of *Gnathorhiza serrata* Cope were described as consisting of ordinary trabecular dentine (Denison, 1974: fig. 15). However, examination of the same section in polarized light convinced me that part of this tissue is petrodentine. Of the

Carboniferous forms, Denison (1974) described the tooth plate of *Sagenodus* sp. as a thick layer of highly mineralized 'tubular dentine' (vascular pleromin of Ørvig, 1976a,b) and commented that the newest denticles at the labial margin show how this tissue was initially formed. The growth of the tooth plates of *Sagenodus inaequalis* was studied (Smith, 1979) and this confirmed Denison's observations that growth is continuous beneath the tritural surface and areal growth is by extension at the labial margins. It was concluded that the major part of the tooth plate is petrodentine and that this forms late in histogenesis of the newly-added denticles.

Devonian dipnoan genera are of the greatest importance in determining the stratigraphic record of the distribution of petrodentine. Denison (1974) has stated that the specialized dentine (tubular dentine/vascular pleromin) only occurs in post-Devonian dipnoans. However, on this point, Denison also states that both the simple trabecular dentine and the tubular dentine are highly mineralized. So, once again, we find that statements are made about the interstitial component being hypermineralized but the arrangement of vascular canals is either irregular and branched, or regular and parallel. Ørvig (1967) has used the embracing term pleromin for both categories, but Denison (1974) and Smith (1979a) rejected this usage. However, Ørvig is almost certainly correct in assuming that a special kind of hypermineralized dentine (petrodentine) forms in many of the genera of Devonian dipnoans, and he gives *Scaumenacia* and *Rhinodipterus* as examples. (Examination of Ørvig's material, generously made available to me, both s.e.m.'s and slides, confirmed that this is a valid conclusion.) Denison (1974) also decided that the dentine in *Scaumenacia* is highly mineralized, because of the translucency and relative lack of odontoblast tubules. (I have examined the section figured by Denison (1974: fig. 5) but it is very difficult to interpret because the mounting medium has begun to crystallize.) Of the other Devonian dipnoans examined by Denison, a section of *Dipterus valenciennesi* is illustrated in which patches of hypermineralized dentine are in the centre of each denticle cusp, (Denison, 1974: figs 2,4) but this is regarded as pleromic dentine *sensu* Tarlo and Tarlo (1961) (for discussion see Smith, 1977). Smith (1977: figs 70,71) figured the tooth plates of the Late Devonian *Chirodipterus australis* but she made no decision about the type of dentine forming the interstitial tissue between the vascular canals.

From this review of the literature it is immediately apparent that there has been little agreement, either on the type of dentine or its mode of growth in Devonian forms. However, as a basis for further investigation, the general statement can be made that a type of hypermineralized dentine, petrodentine, probably occurs in a variety of Devonian dipnoans with radiate tooth plates.

There are still divergent views on the primitive condition of the dentition in dipnoans and the statements made by Denison (1974) and Miles (1977) that tooth plates are a derived character has been challenged by Campbell and Barwick (1983). They have stated that amongst early Devonian dipnoans there were already two different types of dentition, crushing plates of dentine on the pterygoid and prearticular as in *Dipnorhyncus sussmilchi* Etheridge and *Speonesydrion iani* Campbell and Barwick and a shagreen of small denticles with marginal dentine ridges as in *Uranolophus wyomingensis* Denison. They have argued that Denison (1974) did not define the term tooth plate precisely and the exclusion of *Dipnorhynchus* from the tooth plate-bearing group is not justified. Prior to the statements made by Denison (1974) the view that *Dipnorhynchus* represented the primitive condition was widely accepted (White, 1965; Thomson, 1967). If petrodentine is regarded as a feature of tooth plates, and *Dipnorhynchus* and *Speonesydrion* are accepted as members of the group with tooth plates, it becomes important to establish if they have petrodentine in the dental tissues. Moreover, the examination of the dental tissues in early denticulated genera such as *Uranolophus* and *Griphognathus* for petrodentine also becomes of some importance.

MATERIAL-TECHNIQUES

MATERIAL

Protopterus aethiopicus Owen

Serial, coronal sections through larval stages of 27.5 mm, 54 mm and 57 mm. BM(NH) P10362-P10839.

S.e.m. blocks as cut, polished and etched surfaces; either 0.1NHCl for 1 min. or 1NHCl 10-30 sec., S45, S46: Consecutive ground sections, vertical labio-lingual, M47: Lower jaw segment RCS/OM-A449.3.

Decalcified serial sections, vertical labio-palatal, through upper tooth plate, stained H & E, Mallory, Masson, WJ 5/49.

Lepidosiren paradoxa Natterer

S.e.m. blocks as cut, polished and etched surfaces; 0.1NHCl for 1 min, 10 min 10% NaOCl, Critical point dried, S65, 66, 67: Consecutive ground sections M65: Lower jaw segment from specimen supplied by Dr N. A. Lockett from the 1977 Amazon ∝ Helix Research Expedition.

Lepidosiren sp.

Upper tooth plate, Miocene, La Venta Formation, Colombia, South America; collected by Dr Kubet Luchterhand, on loan from the Field Museum of Natural History, Chicago. PF9005.

Protopterus sp.

Upper tooth plate, Eocene, Mali, Africa; collected by Ms Alison Longbottom, joint expedition 1981 BM(NH) and Kingston Polytechnic, Dr Cyril Walker.

Neoceratodus forsteri Krefft

Decalcified, vertical sections through upper tooth plate, H & E, Alcian Blue & Safranin, BM(NH) 5005, 5006. S.e.m. blocks (prepared as *Protopterus*) S41-44: Consecutive ground sections vertical and horizontal M41-43. Specimen from Warwick James Collection, Royal Dental Hospital.

Ceratodus madagascariensis Priem

Upper Cretaceous, NW Madagascar, upper tooth plate, vertical, ground sections, BM(NH) P15660.

Ceratodus runcinatus Pleininger

Triassic, Lettenkohle, locality Hohenech; upper right tooth plate vertical ground sections and s.e.m. block S137, S139 from specimen PV 19270; s.e.m. block S145 from specimen PV 19279.

Ceratodus kaupi Agassiz

Triassic, Lettenkohle, locality Bibersfeld; lower right tooth plate vertical ground sections and s.e.m. block S140 from specimen PV 4460.

Sagenodus inaequalis Owen

Carboniferous, Coal Measures, Northumberland; upper tooth plate, vertical ground sections, BM(NH) P7326, P3381.

Dipterus valenciennesi Sedgwick and Murchison

Middle Devonian, Caithness; upper tooth plates, vertical and horizontal ground sections through specimens BM(NH) P 44671, P 53537.

Chirodipterus australis Miles

Middle Devonian, Gogo, Australia; vertical labio-lingual section and consecutive s.e.m. blocks, through upper and lower tooth plates; BMR 22592-4, BM(NH) P 52561.

TECHNIQUES

Photomicrographs

Ordinary light, polarized light and phase contrast, Zeiss Photomicroscope III; Camera Lucida drawings on Zeiss Universal.

Microradiographs

X-ray generator, Phillips PW 1720, copper anode, fine focus 300μm beryllium window; PW 2213/20. Kodak high-resolution spectroscopic plates 649-0; 30kV 33mA, 10 mins.

Scanning electron micrographs

SE-mode, Cambridge Mark 2A, operated at 30kV; Coates and Welter Kwikscan, field emission cathode, operated at 15kV; St. George's Hospital Medical School. Cambridge Stereoscan 180, operated at 30kV, Electron Microscopy Unit, ANU. BSE-mode, Cambridge Stereoscan S4-10, operated at 20kV, Hard Tissue Unit, Anatomy Department, University College, London.

OBSERVATIONS

The histology and microstructure of the dental tissues of the extant genera and several fossil genera have been investigated using the four techniques previously described by Smith (1979b, 1980) and Smith, Boyde and Reid (1984). The methods which use ground sections, decalcified sections and blocks of tissue, some made anorganic by the removal of cells and organic matrix, are:

i) the level of hypermineralization by microradiographic analysis;
ii) optical properties by polarized light;
iii) the ultrastructure by s.e.m. of polished and etched surfaces, or anorganic surfaces;
iv) histogenesis by comparison of mature regions with forming surfaces in all types of preparation.

The terminology of Smith (1979), which Schultze (1981) also adopted, will be used. Where the vascular canals ascend in the direction of the tritural surface they will be called pulp canals. Gross (1956) described the narrow branching tubes running through the dental tissues of *Dipterus* and *Rhinodipterus* as pulp canals (Fig. 2). This

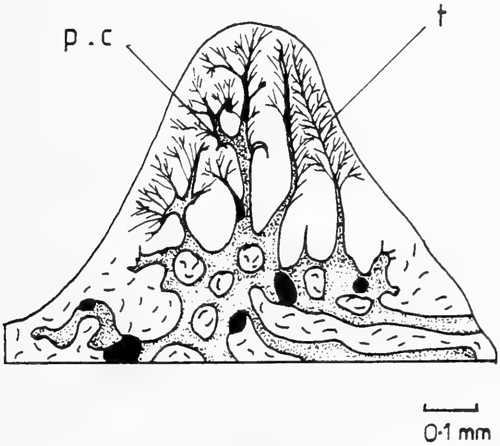


Fig. 2. Rhinodipterus secans Gross. Drawing from Gross (1956: fig. 122B). Vertical section through one denticle of the tooth plate. Pulp canals run into the dentine from the tissue spaces in the bone, finer tubules penetrate the dentine from the pulp canals.

seems entirely justified as many fine tubules, housing the odontoblast cell processes, lead out of the pulp canals and permeate the dentine in the adjacent region. Where the dentine surrounding the pulp canals is clearly a distinct tissue on the basis of its fibre organization, level of mineralization and content of tubules, it is termed circumpulpal dentine.

The observations that follow attempt to show in each form, both extant and fossil, as many of the characters of petrodentine as possible within the limits of the available material. The characters used are those given in Table 1.

1. *PROTOPTERUS AETHIOPICUS* — Larval

Detailed aspects of the growth of tooth plates in larval stages are discussed by Smith (1984). Sufficient additional information is given here to comment on the ontogenetic development of petrodentine in the early development of the dipnoan tooth plate. Serial, coronal sections through the head of a 57 mm larva of *Protopterus aethiopicus* provide examples of many stages of development from separate to integrated denticles in each ridge of the tooth plate.

The first stage of development in which discrete denticles can be recognized is for convenience termed stage (0) where a cone of pallial dentine is formed at the margins of the dental papilla. In stage (i) of denticle development (Figs 3**a**, 4) two populations of cells are established within the pulp: those secreting the primary dentine forming the walls of the cone, the odontoblasts; and those forming a distinct tissue inside the cone, the petroblasts, secreting petrodentine. This differs from the dentine in retaining little of the organic matrix and for this reason is presumed to have a higher proportion of

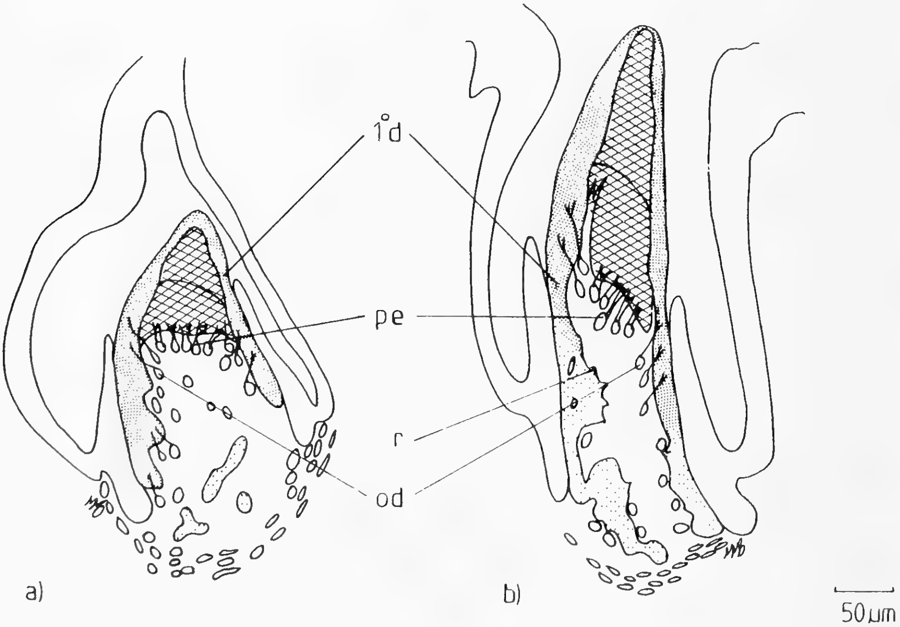
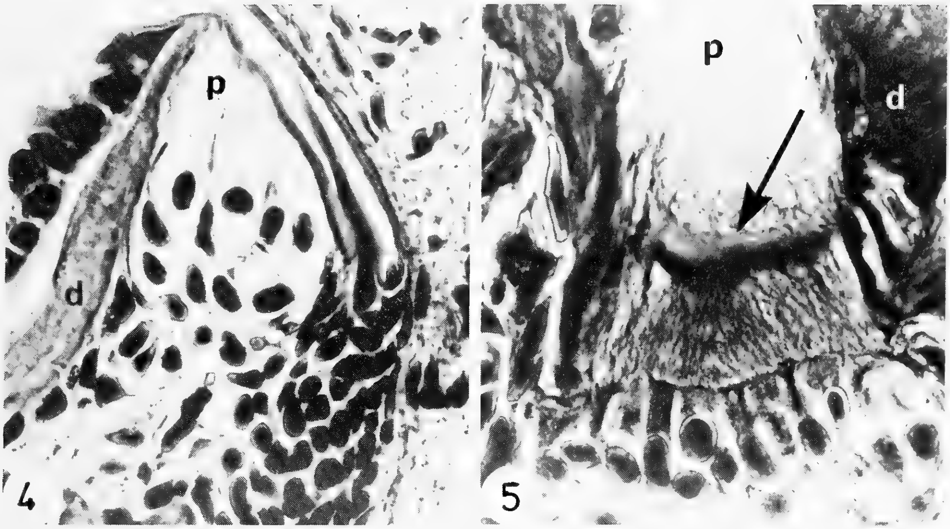


Fig. 3. Protopterus aethiopicus Owen. 57 mm larva; stage (i) and stage (ii) denticles from the prearticular tooth plate, distribution of dentine and petrodentine (Key as in Fig. 1). (**a**) early formation of petrodentine from petroblasts at the pulp surface. Primary dentine formed earlier in development is extended at the margins from odontoblasts, in advance of petrodentine (**b**) later stage, ankylosis of dentine to bone of the pedestal, and extension of the height of petrodentine by continued secretion from petroblasts. Space for this growth created by resorption of bone.



Figs 4, 5. Protopterus aethiopicus. 57 mm larva H & E Decalcified, coronal section (P10500). *Fig. 4.* Slightly earlier stage than (3**a**), pale stained matrix of petrodentine containing cell processes from petroblasts. These are distinct from odontoblasts related to the forming front of dentine. Field width — 150μm. *Fig. 5.* Forming front of petrodentine beneath tritural surface in oldest region of tooth plate. New matrix of petrodentine has a high level of organic matrix in contrast to the mature tissue (p). Petroblasts form an integrated layer at the forming surface, with cytoplasm indicative of secretory activity. Growth line with a concentration of organic matrix separates the new tissue from that formed earlier (arrow). Field width 120μm.

mineral. As growth occurs to increase the height of the denticle the odontoblasts continue to secrete the primary dentine, extending the pallial dentine into that of the pedestal (Smith, 1984), which is in part formed by bone (Fig. 3**b**). Within this structure petrodentine is added at the formative front by a well organized row of cells (Fig. 5). Beyond the formative front, and parallel to it is a growth line (arrow, Fig. 5) with a greater concentration of organic matrix. This contrasts with the earlier formed petrodentine now devoid of organic matrix, this having been replaced by hydroxyapatite. Resorption of the pedestal tissue occurs in advance of the forming front of petrodentine (r, Fig. 3**b**), so that new dentine and petrodentine grow into a resorption space in the basal bone of the tooth plate. In this way continuous growth of petrodentine will replace that lost by wear at the tritural surface. The pattern of this replacement growth and its contribution to the changing morphology of the tooth plate is reported elsewhere (Smith, 1984).

2. *PROTOPTERUS AETHIOPICUS* — Adult

Vertical sections through one ridge of the tooth plate show the composition of all the tissues that contribute to the whole structure (Fig. 6). These include the bone of the pedestal or bone of attachment, the dentine enclosing the pulp canals, the petrodentine and the superficial layer of enamel (Smith, 1979b). A comparison is easily made in each section between the mature tissue at the tritural surface (Fig. 7) and the new tissue at the forming surface (Figs 8, 9), situated deep within the bone (character 10, Table 1).

i) MATURE TISSUE STRUCTURE — Microradiographs of ground sections show the extremely high degree of mineralization of the petrodentine (character 4, Table 1)

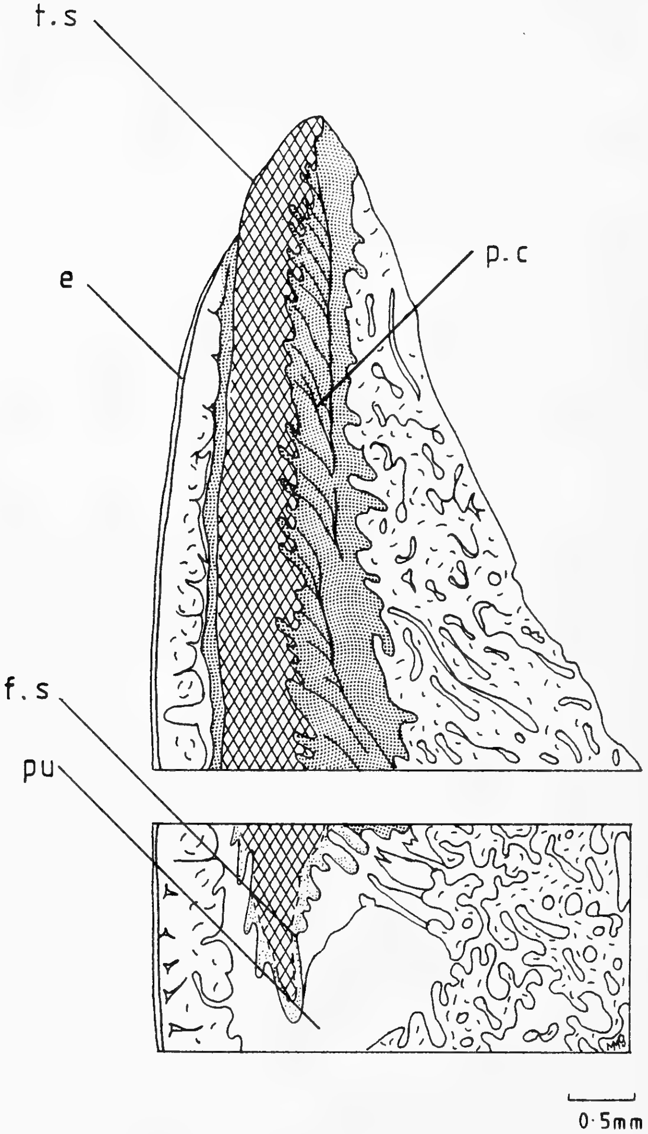


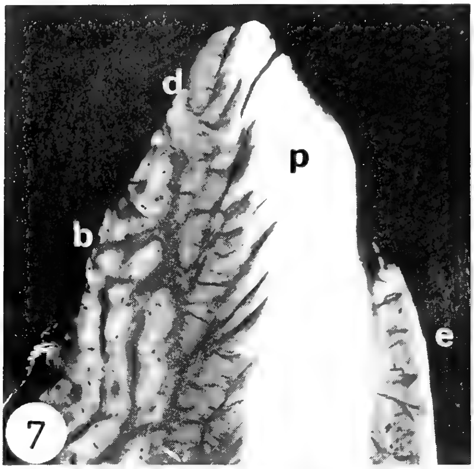
Fig. 6. Protopterus aethiopicus — (G.S., M.R, 47-6, A.449.3) Vertical section through ridge 3 of lower jaw tooth plate. Ridge of petrodentine supported by dentine and bone with a growth surface (f.s) deep to the tritural surface. Pulp canals run from the pulp cavity through the dentine and terminate close to its border with petrodentine. Enamel on the labial margin covers dentine and bone (1/3 of the total height is omitted in the drawing).

relative to the adjacent dentine and bone (Figs 7, 8, 10). This is approximately four and a half times greater in density than the dentine and bone. The only tissue of equivalent opacity to X-rays is the very thin layer of enamel (Figs 7, 8) on the labial and lingual margins of the bone. Decalcified sections (Fig. 9) show that the major part of the petrodentine is removed during processing by the dissolution of calcium salts, leaving only traces of organic matrix at the junctions with the dentine of the pulp canals and a substantial amount of matrix at the forming surface (character 9, Table 1). None of this organic matrix of the petrodentine is birefringent (character 5, Table 1) in contrast with that of the dentine and bone which shows the birefringence typical of collagen fibre bundles (Fig. 9). The same features are shown in the sections of larval tooth plates (Figs 4, 5). At the tritural surface the major part of the ridge is petrodentine (Fig. 7), supported on either side by bone and linked to this by dentine containing pulp canals (for convenience of description termed trabecular dentine). The pulp canals, each surrounded by dentine (circumpulpal dentine) run into the petrodentine at an angle to the vertical axis of the ridge. In the same position collagen fibre bundles of the trabecular dentine pass into the petrodentine (character 8, Table 1). At this junction the sign of birefringence changes from positive due to the collagen fibres, to negative due to crystals of hydroxyapatite parallel to the fibre bundles. In the petrodentine, the birefringence is due to organized crystal-fibre bundles (shown in s.e.m.'s, Fig. 13) and shows an isotropic zone in the mid-vertical line, with either side of this, positive and negative signs of birefringence in the NW and NE positions relative to crossed polars (character 6, Table 1). Tubules do not extend for any distance into the petrodentine; the bulk of the tissue is atubular (character 3, Table 1).

A block of tissue cut adjacent to the vertical sections (as in Fig. 10) and including also the labial growth margin (Smith, 1984) allows a comparison of the same regions, mature and forming surfaces at a higher level of magnification, using the s.e.m. (Fig. 11). The major part of the tissue between the pulp canals is petrodentine (high mineral density in Fig. 10) and this appears as a basket-weave of crystal-fibre bundles (c.f.b.) (Fig. 12) in which all the crystals lie parallel to each other in one c.f.b. and are at an angle to the adjacent one (Fig. 13). The circumpulpal dentine which contains tubules has a homogeneous appearance (crystals too small to resolve) and has etched to a lower level than the petrodentine. It produces the low density regions in the microradiograph.

ii) FORMING TISSUE STRUCTURE — In the microradiograph (Figs 8, 10) the high degree of mineralization of the petrodentine is reached within a very short distance of the formative front (Fig. 8). The forming tissue is low in mineral and high in organic matrix and is secreted by cells (petroblasts) lining both surfaces of the downward growing ridge of petrodentine (Figs 8, 9). Numerous processes from the petroblasts penetrate the forming tissue (Figs 8, 9) and these can be seen as spaces in s.e.m.'s of an anorganic preparation of the forming surface (Figs 14, 15). The organization of the crystal-fibre bundles is established in this region but the individual crystals (presumed smaller) are not as easily resolved as in the mature tissue at the same magnification (Figs 13, 15).

The large pulp canals passing into the petrodentine from the pulp chamber are not, at the initial formative stage, lined with circumpulpal dentine (Fig. 14). The microradiograph (Fig. 10) and the block of tissue in the s.e.m. (Fig. 11) are of equivalent regions (the section being adjacent to the cut face of the block). They show the extent of hypermineralized tissue in this region, and the way in which pulp canals are gradually incorporated into the growing front of petrodentine by a differential cessation in growth of petrodentine at this point. The incorporation of pulp canals later in growth at the formative front is also seen in Figs 8 and 9. In all these regions the new tissue, petrodentine and trabecular dentine, is forming against a resorption surface of the bone, marked by a reversal line or scalloped border (r, Fig. 8). In the same way resorption precedes new growth in the larval tooth plate. More detailed presentation of this information on the relationship between resorption and growth will appear in two papers in preparation.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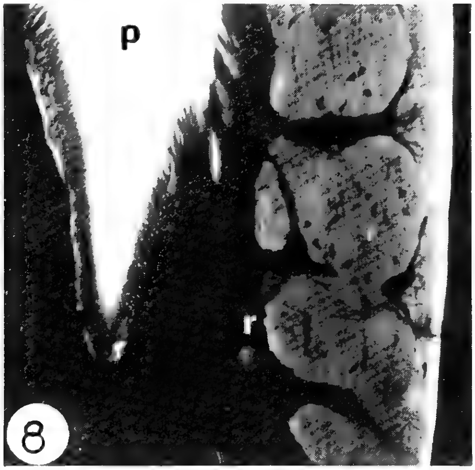
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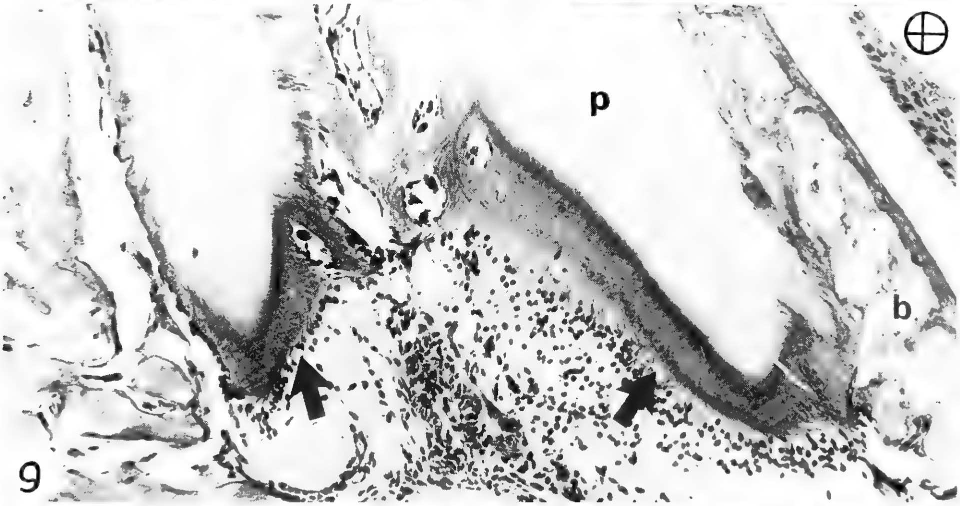
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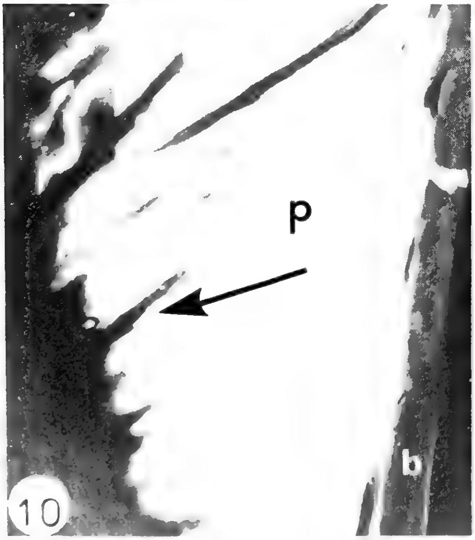
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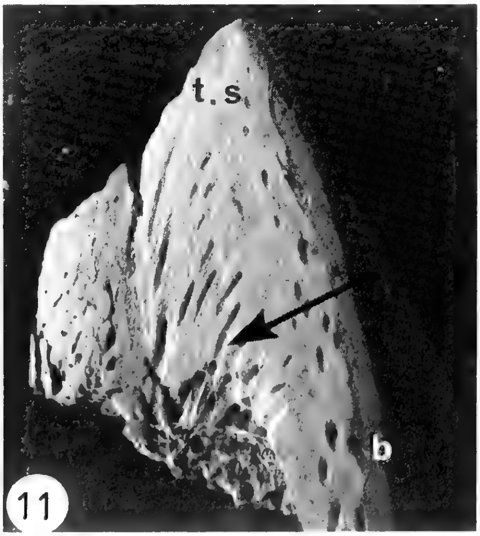
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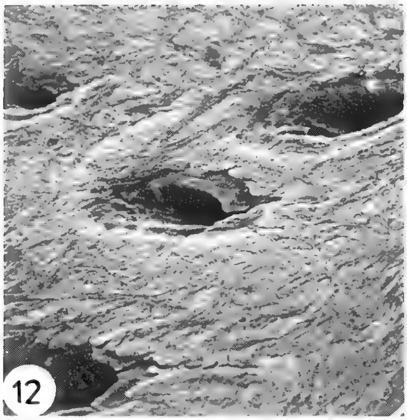
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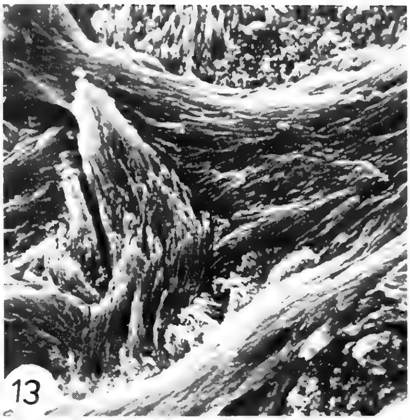
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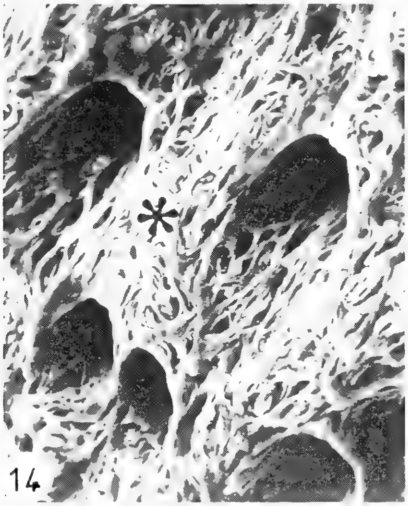
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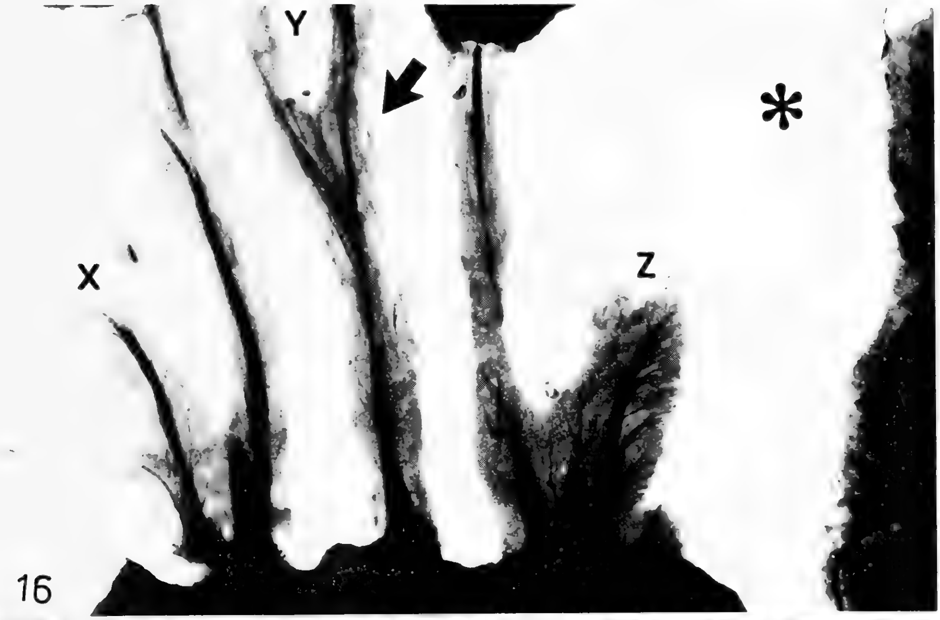
Figs. 7, 8. Protopterus aethiopicus (MR 47/6, A449.3) Microradiographs of vertical section through ridge 3 of lower jaw tooth plate. Opacity of petrodentine to X-rays, equivalent to that of enamel (100 μm section, 30kV, 33mA, 10 mins). *Fig. 7.* Tritural surface of abraded petrodentine, dentine and bone. Pulp canals of dentine pass into petrodentine from lingual border. Field width 2 mm. *Fig. 8.* Forming surface (as in Fig. 6, but labial margin on reverse side). Fringe of less mineralized tissue with many tubules at both borders of petrodentine indicates growth from both surfaces. Space for pulp chamber by resorption of bone (r). Field width 0.8 mm. *Fig. 9. Protopterus aethiopicus* (WJ5/49-36) Decalcified section H & E, ½ PL vertical, labio-palatal. Forming surface (arrows) of petrodentine in two adjacent ridges. High content of organic matrix compares with low mineral content in Fig. 8. Petroblasts linked to this surface with short cell processes. Birefringent collagen in the adjacent dentine and bone and the dentine around the pulp canals. Absence of organic matrix in older petrodentine (p). Field width 2 mm. *Figs 10, 11. Protopterus aethiopicus* (45/4a, A.449.3) Microradiograph and adjacent surface as s.e.m block. Labial margin of ridge 2. Lower jaw tooth plate. Many pulp canals from forming surface (arrow) and extensive area of hypermineralized dentine (p) within a shell of bone as in Fig. 9. S.e.m's in Figs 12-15 from this surface. Field widths 1.7 mm and 3 mm. *Figs 12-15. Protopterus aethiopicus* Anorganic specimen s.e.m's of cut, polished, etched surface (0.1NHCl for 1 min) and forming surface lining the pulp cavity. *Fig. 12.* Petrodentine near tritural surface (t.s. Fig. 11), circumpulpal dentine (c.p.d) lining each pulp canal. Field width 310 μm. *Fig. 13.* Parallel crystals in each domain or crystal-fibre bundle from petrodentine in field of Fig. 12. Field width 30 μm. *Fig. 14.* Forming surface from field near arrow (Fig. 11). Many large pulp canals, none with a lining of c.p.d. Numerous small spaces in petrodentine, occupied *in vivo* by organic fibres and cell processes from petroblasts. Field width 310 μm. *Fig. 15.* Field from between pulp canals in Fig. 14 (asterisk). Tubule (t) could be occupied by either cell process or fibre bundle. Same magnification as Fig. 13, but crystallites smaller and not individually resolved. Field width 30 μm.

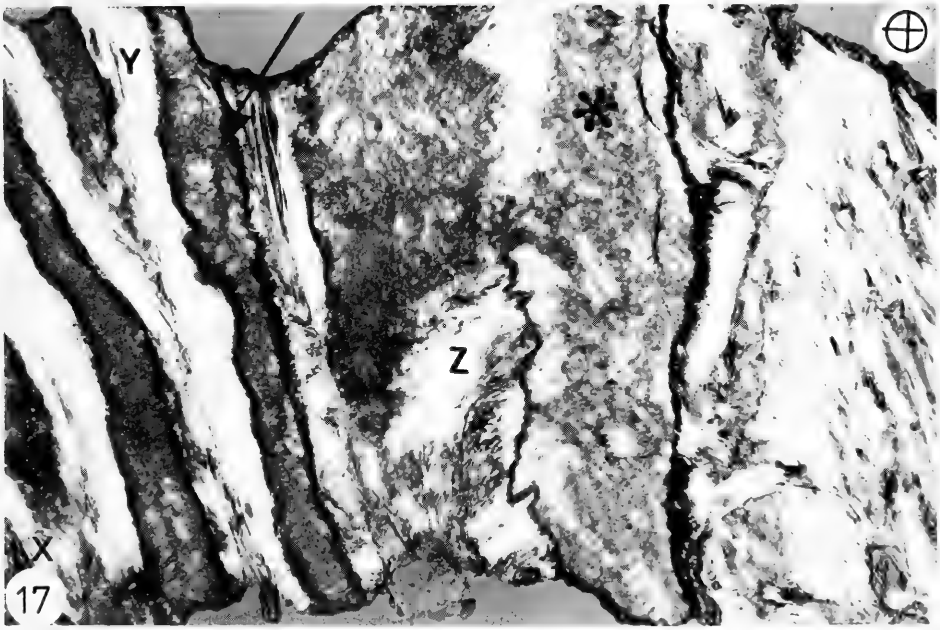
3. *LEPIDOSIREN PARADOXA*

Microradiographs of vertical labio-lingual sections through the central region of the tooth plate, between ridges two and three, show a much more extensive region of hypermineralized tissue (Fig. 16) than sections through only one ridge of the tooth plate (Fig. 18). The amount of this petrodentine is considerably greater and reaches across the whole width of the tooth plate in this region. It is only interrupted by pulp canals traversing the thickness of the tooth plate from the pulp chamber to the tritural surface (Figs 16, 17 Y). The microradiograph of a vertical section through ridge three (Fig. 18) shows a much narrower region of petrodentine, comparable with that in ridge three of *Protopterus* (Figs 6, 7), and proportionally fewer pulp canals entering from the pulp chamber. All of the pulp canals are walled by dentine that has many branching tubules and a much lower mineral density than the petrodentine. In phase contrast microscopy (Fig. 19) of the same ground section as the microradiograph (Fig. 16) the tubules are seen to radiate from the pulp canal (X in Figs 16, 19), branch, and terminate in fine extensions of the tubules within the petrodentine. Some of these in the petrodentine may be spaces between the crystal-fibre bundles and not necessarily tubules containing cell processes from the odontoblasts. The circumpulpal dentine, tapers to a thin layer at the forming front of the petrodentine and the most recently formed canals are not lined with this form of dentine. S.e.m.'s of the block of tissue adjacent to the section show the typical interlacing crystal-fibre bundles of petrodentine (Figs 20, 21). Some of these crystal-fibre bundles run into the dentine at the junction with the petrodentine (Figs 20, 21). In the s.e.m. of a region of petrodentine near the forming front many fine fibrils, of presumed organic matrix, are associated with the crystal-fibre bundles (Fig. 21). In polarized light microscopy (Fig. 17) of the same ground section as the microradiograph (Fig. 16), the circumpulpal dentine along the length of the pulp canals (X, Y, Z), shows the strong birefringence due to collagen fibres. An isotropic line occurs at the junction between circumpulpal dentine and petrodentine (Fig. 17) where the birefringence due to the mineral cancels out that due to the collagen fibres. In the narrow regions of petrodentine, birefringent bands (due to crystal-fibre bundles) of opposite sign of birefringence, run at 45° to the vertical axis. Also in the larger masses of petrodentine the birefringence appears as a basket-weave of opposite signs of birefringence (asterisk, Fig. 17).

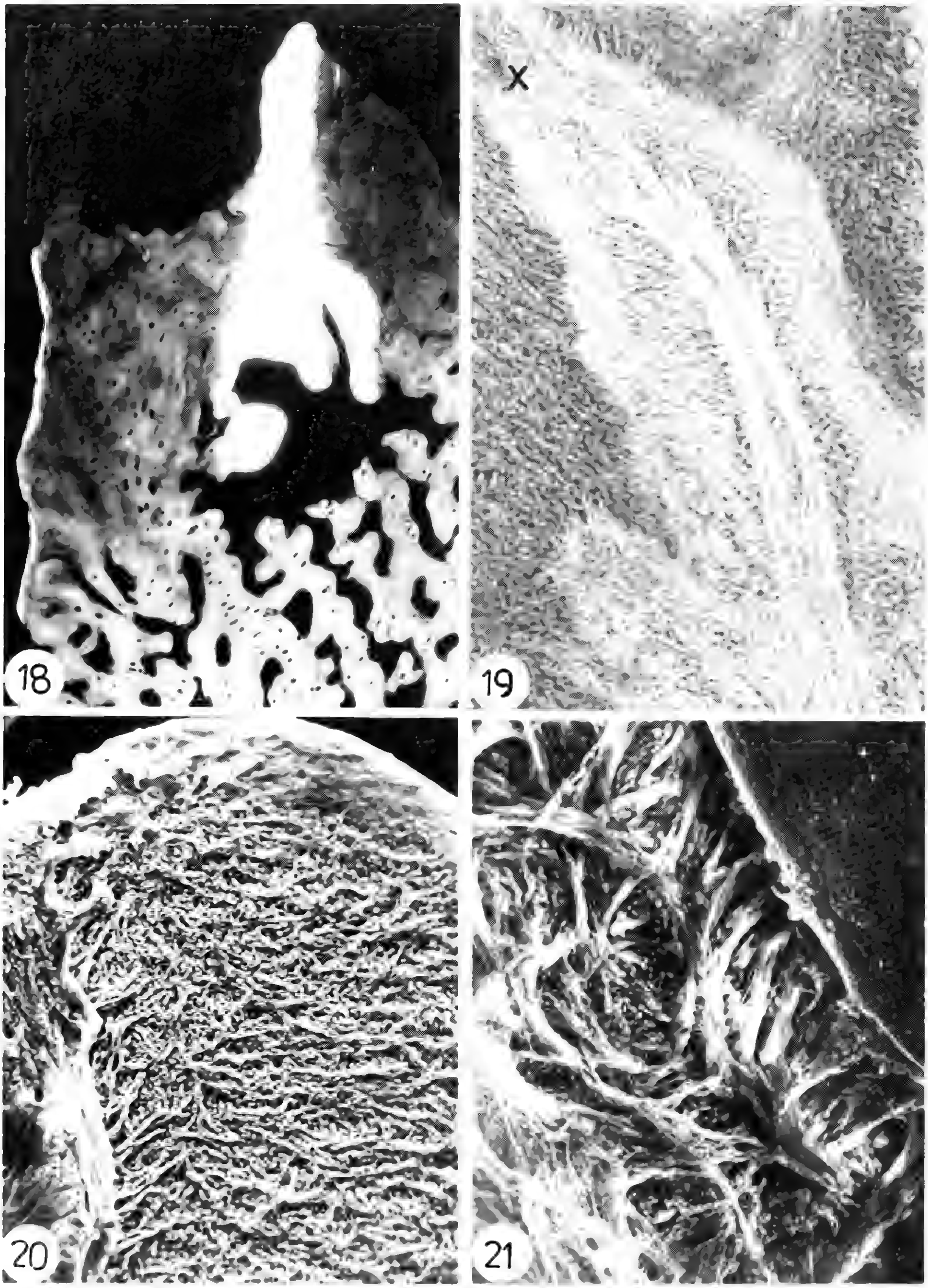
4. LEPIDOSIRENIDS — **Fossil forms**

Two examples of tooth plates from fossil species of *Protopterus* and *Lepidosiren* have been sectioned — *Lepidosiren* sp. (Fig. 22) from the Upper Miocene in Colombia, from the same locality as the specimens figured as whole tooth plates and s.e.m.'s by Ørvig (1976b: figs 20-25), and *Protopterus* sp. from the Eocene in Mali. The distribution of the tissues petrodentine, trabecular dentine and bone as they appear within the sections (Figs 22, 23) depends to a great extent on both the individual age of the tooth plate, and the position in the tooth plate through which each section was cut. The tissue contributing to the wear-resistant parts of the ridges on the tritural surface is petrodentine: the histology and ultrastructure is similar to that described in the extant forms. In both *Lepidosiren* sp. and *Protopterus* sp. distinct growth lines can be recognized, parallel to the forming surface and spaced out at regular intervals, at a steep angle to the tritural surface (Figs 22, 23). Pulp canals run from the pulp chamber towards the margins of the petrodentine branching initially within the trabecular dentine; finer branches continue into the petrodentine. The section of *Lepidosiren* sp. (Fig. 22) is vertical through the tooth plate and is the first one adjacent to the medial symphysis. It illustrates an unusual feature of growth in these genera, viz. that growth can occur from both labial and medial or palatal aspects (Smith, 1984). The section of *Protopterus*





Figs 16, 17. Lepidosiren paradoxa Natterer (65/4) Labio-lingual, vertical ground section through central area joining R_2 and R_3, corresponding pulp canals (X, Y, Z) pass from the forming surface to the tritural surface. Typical area of petrodentine (asterisk, Fig. 16) shown as alternate bands in polarized light (Fig. 17) and as opaque to X-rays in microradiographs (Fig. 16). c.p.d. strongly birefringent, with tubules and less dense to X-rays. Field width 1.5 mm.



Figs 18-21. Lepidosiren paradoxa.
Fig. 18. Microradiograph of adjacent sections to Figs 16 & 17, shows petrodentine of R_3, and enamel layer. Tissues compare with Figs 7 & 8. Field width — 2 mm. *Fig. 19.* Phase contrast of pulp canal X in Figs 16 & 17, tubules from pulp canal pass through c.p.d. and stop at junction with petrodentine. Field width — 280 µm. *Fig. 20.* S.e.m. of adjacent cut, polished, etched surface, shows petrodentine near tritural surface, of the same ridge as in Fig. 18. Field width — 310 µm. *Fig. 21.* S.e.m. of same ridge only near forming surface. Shows crystal-fibre bundles of petrodentine merging into dentine. Field width — 62 µm.

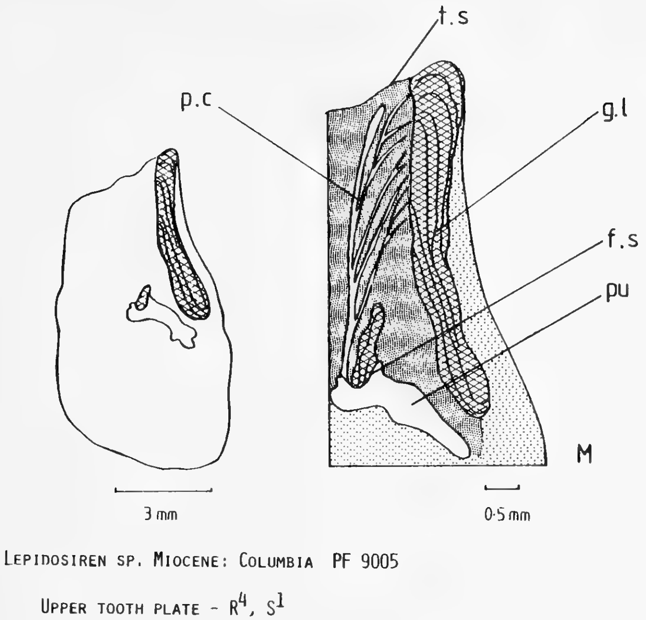


Fig. 22. Lepidosiren sp. Vertical section through the entire upper tooth plate and bone parallel to the medial symphysis, shows amount of petrodentine relative to bone and dentine. Detail of growth lines and pulp canals.

sp. (Fig. 23) shows the main region of growth of ridge one at the labial margin. Here there is an extensive forming surface of petrodentine and a free margin not attached to the bone. This is directly comparable with the part of the tooth plate of *Protopterus aethiopicus* shown in Figs 10 and 11. In both these sections (Figs 22, 23) patches of petrodentine are found separated from the main region by trabecular dentine and bone. They relate to the side-ribs of the other ridges (ridge 2,3) and to new, smaller regions of growth on the medio-palatal aspect.

5. *NEOCERATODUS FORSTERI*

Vertical sections along one ridge of the tooth plate (Figs 24, 25, 26) together with horizontal sections across two ridges (Figs 27, 28, 29) show the distribution of the tissues, the arrangement of the pulp canals and the composition of the two types of dentine. These can be compared with Ørvig (1976b: figs 13, 14, 19), of which two figures were redrawn from Günther (1871). The hypermineralized dentine, labelled as pleromin by Ørvig (1976b), is all of the tissue between the parallel, evenly-spaced pulp canals passing from the formative surface to the tritural surface. In microradiographs the appearance is similar to that shown in *Lepidosiren* (Fig. 16). In a horizontal section showing the bifurcation between two ridges (Fig. 29) the petrodentine is the entire amount of tissue between the pulp canals and adjoins the bone at the labial and medial margins. The bone is most extensive at the mid-point between two ridges (Fig. 29) and is confined to a very thin border at the labial extremities of each ridge. Kemp (1979: figs 13A, E) has illustrated a similar distribution of tissues in a horizontal section through the adult tooth plate. In the decalcified sections most of the matrix of petrodentine has been removed leaving only thin strands staining with alcian blue (Figs

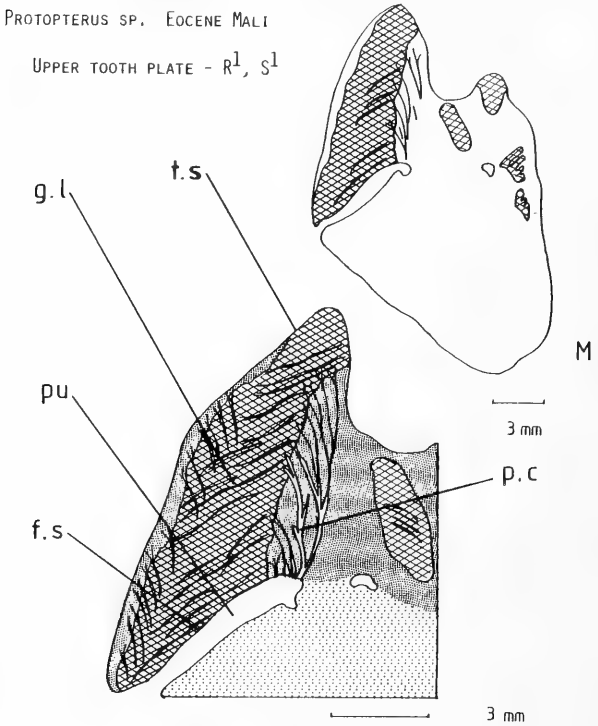


Fig. 23. Protopterus sp. Vertical section through bone and petrodentine, labio-palatal plane, of first ridge (R^1) in upper tooth plate; patches of petrodentine in medial part. Detail of growth lines and pulp canals.

24, 26). In the horizontal ground sections (Figs 27, 28) the petrodentine is translucent, lacks tubules, and in polarized light shows a high degree of preferred orientation of the crystal-fibre bundles in a radial arrangement relative to the pulp canals (Fig. 28). This observation is in agreement with Ørvig (1976b: fig. 19). In the equivalent s.e.m.'s of the block adjacent to the ground sections (Fig. 30) the petrodentine etches less deeply than the circumpulpal dentine and is composed of the typical large crystals (Fig. 34) arranged as crystal-fibre bundles, some arranged radially and some at an angle to these, lying in the vertical plane of the section (Figs 30-33).

The pulp canals are lined with dentine some of which completely infills the canal towards the tritural surface (Fig. 24). This circumpulpal dentine is less opaque to X-rays (Fig. 29), and retains a high proportion of organic matrix in decalcified sections (Figs 24, 26); this remaining organic matrix is strongly birefringent in contrast to the matrix of the petrodentine (Fig. 25). In horizontal ground sections the birefringence of the circumpulpal dentine is delineated by an isotropic line at the junction between the

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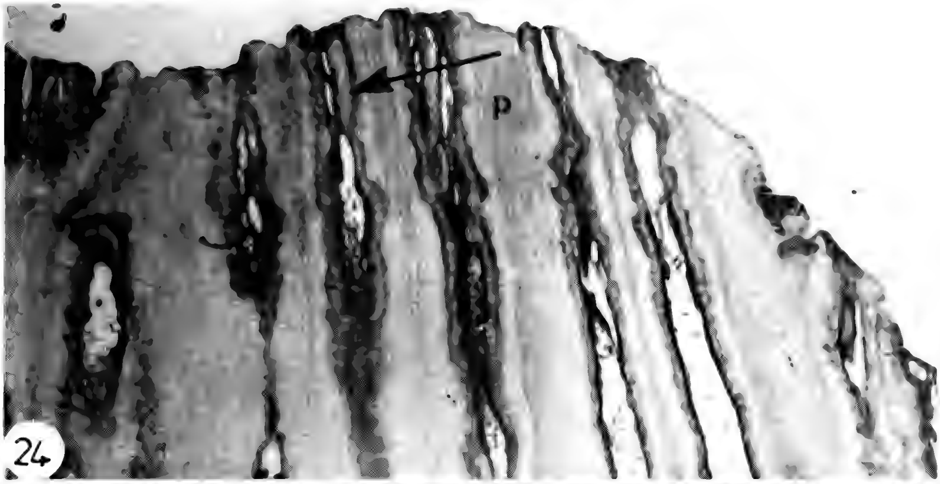
Figs 24-26. Neoceratodus forsteri Krefft (BM(NH) — 5005) Decalcified, Alcian Blue and Safranin (fig 3, pl 2, LP Plan, White, 1966). Vertical section through upper tooth plate in central region of tritural surface.
Figs 24, 25. Thin strands of organic matrix remain in the petrodentine. In contrast, much organic matrix remains around pulp canals, strongly birefringent in polarized light (arrows). Field widths — 3 mm. *Fig. 26.* Phase contrast of two pulp canals near tritural surface, tubules for odontoblast cell processes in c.p.d. and infilling dentine (asterisk) in pulp canals. Some organic fibres link into petrodentine/dentine (c.p.d.) junction. Field width — 0.5 mm.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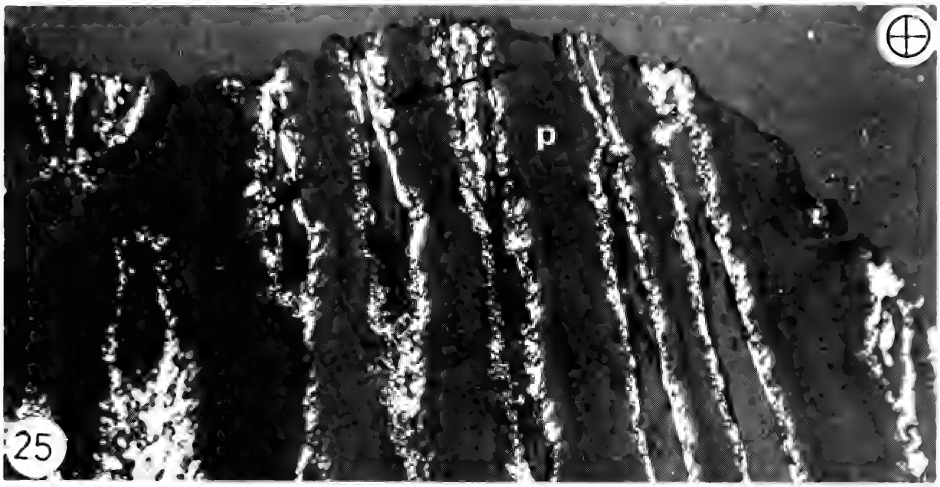
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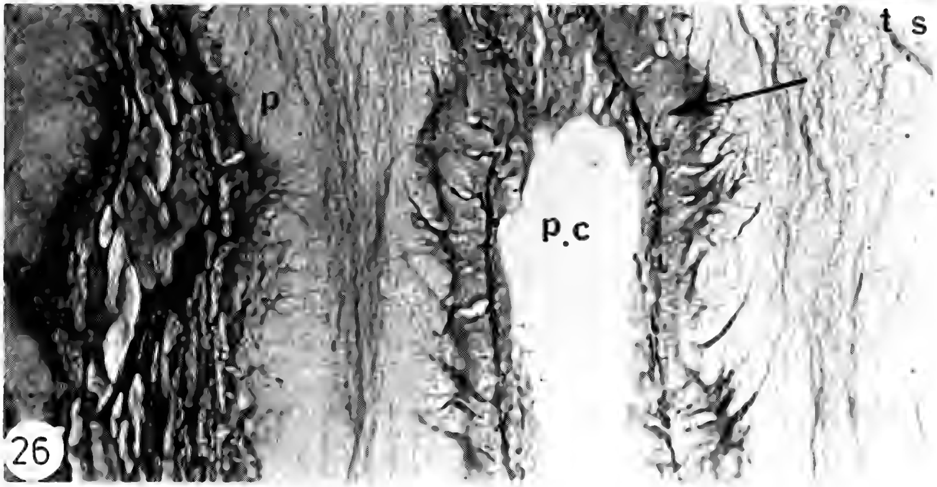
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tissues (Fig. 28) where the sign of birefringence changes. This dentine shows a dark polarization cross in the position of the polarizer and analyser, reflecting the radial or concentric arrangement of the collagen fibres. Spaces housing cell processes from the odontoblasts run through the circumpulpal dentine, ending as fine processes in the adjoining petrodentine (Fig. 26). Other fine fibrils lie parallel to these tubules and run into the petrodentine as continuations of the collagen fibre bundles. Both these structures provide links across the junction between circumpulpal dentine and petrodentine. Comparing a younger region of the tooth plate with an older one (Figs 31, 32), the difference in the surface of the pulp canals is apparent; in the mature tissue only is there a lining of circumpulpal dentine and this is shown both by the microradiographs and by the longitudinal sections. In the younger tissue the surface to the pulp canal is petrodentine (Figs 31, 33), and several tubules assumed to contain cell processes are present (Fig. 33). The large-sized crystals are arranged in groups, lying parallel to each other and at an angle to the next adjacent group (Fig. 34).

In this way the pattern of development of the tissues in the tooth plate is shown to be characterized by (1) the formation of petrodentine from the surface lining the pulp chamber, leaving spaces for vascular pulp canals, and (2) by the narrowing of each canal by the secretion of a lining of circumpulpal dentine over the original surface of the petrodentine. At a lower level in the tooth plate the surface of petrodentine continues to grow deeper into the bone as space is created by resorption of bone (Smith, 1984). This process of histogenesis is the same as in *Protopterus* and *Lepidosiren*.

6. CERATODONTIDS — **Fossil forms**

The tooth plates of several species of *Ceratodus* have been investigated and the structure compared with those of *Neoceratodus*. Material has been examined optically in thin sections and by s.e.m. whenever both have been possible.

i) *Ceratodus madagascariensis* Priem. Sections, figured as low-power plans of the tooth plate by White (1966: fig. 2, pl. 2), are of a tooth plate from the Upper Cretaceous. The pulp canals are as regularly arranged as in *Neoceratodus* (White, 1966: pl. 2, figs 2, 3) and the tissue between the pulp canals shows a very regular arrangement of crystal-fibre bundles when viewed in polarized light (Figs 35, 36). There is a neutral zone at the mid-point between adjacent canals and either side of this the crystal-fibre bundles show opposite signs of birefringence, features typical of the high degree of organization of crystals in petrodentine. Sections viewed in phase contrast allow the tubules to be clearly identified (Figs 37, 38), and these are shown running into the petrodentine from the pulp canals; it is assumed from their shape and size that they contained cell processes from the body of the odontoblast cell in the pulp canals. Comparison of a forming surface (Fig. 37), with a more mature region situated towards the tritural surface (Fig. 38) shows that in the forming region the pulp canal is not lined with circumpulpal dentine. The pulp canals in the older zones of the tooth plate have a lining of circumpulpal dentine; this tissue is not birefringent, has become stained during fossilization, and the tubules run through it into the petrodentine from the surface of the pulp canal. The arrangement and proportion of these tissues in the tooth

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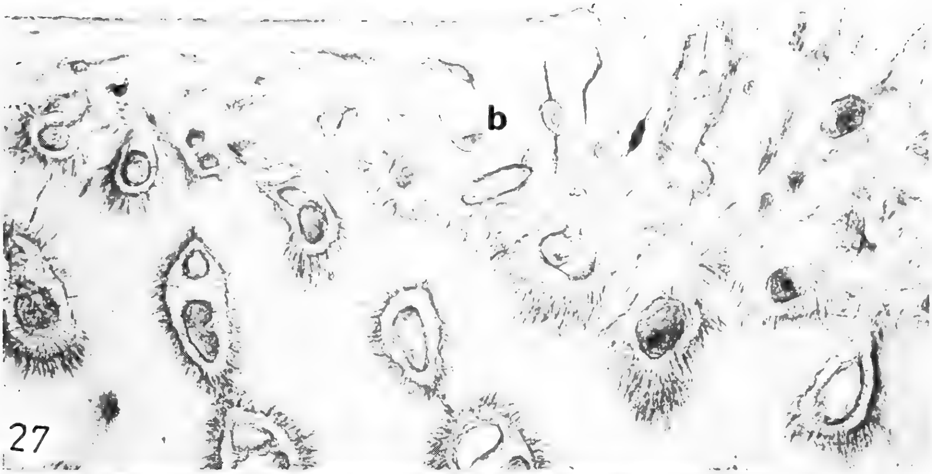
Figs 27-29. Neoceratodus forsteri (41/1-3). Horizontal ground section across two ridges of upper tooth plate. Field of region of indentation between ridges at labial margin.
Figs 27, 28. Same area in ordinary and polarized light. Very thin layer of bone merges into thicker bone (top right) at junction between ridges. Isotropic lines mark junctions between c.p.d. and petrodentine, where the sign of birefringence changes as mineral exceeds collagen fibres. Field widths — 2.5 mm. *Fig 29.* Microradiograph of adjacent section, bone at deepest point of indentation between ridges. Petrodentine evenly opaque to X-rays, some canals lined by less dense circumpulpal dentine. Field width — 4.2 mm.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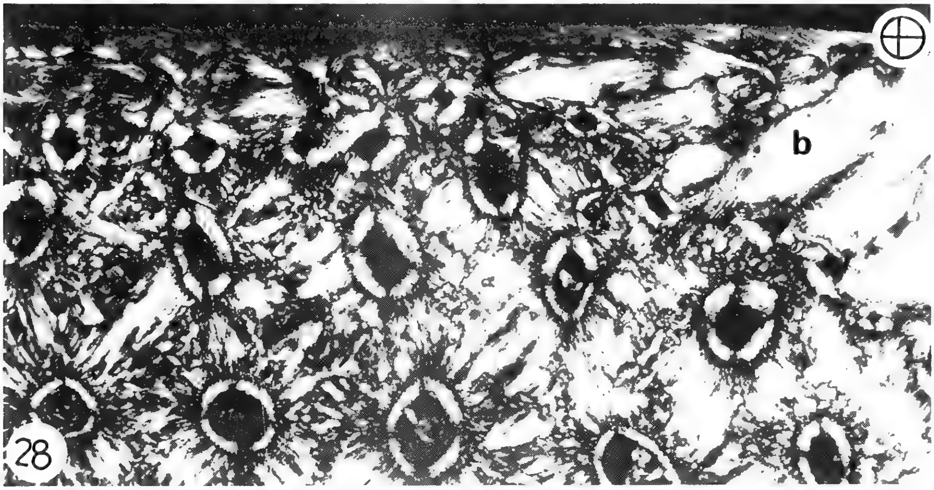
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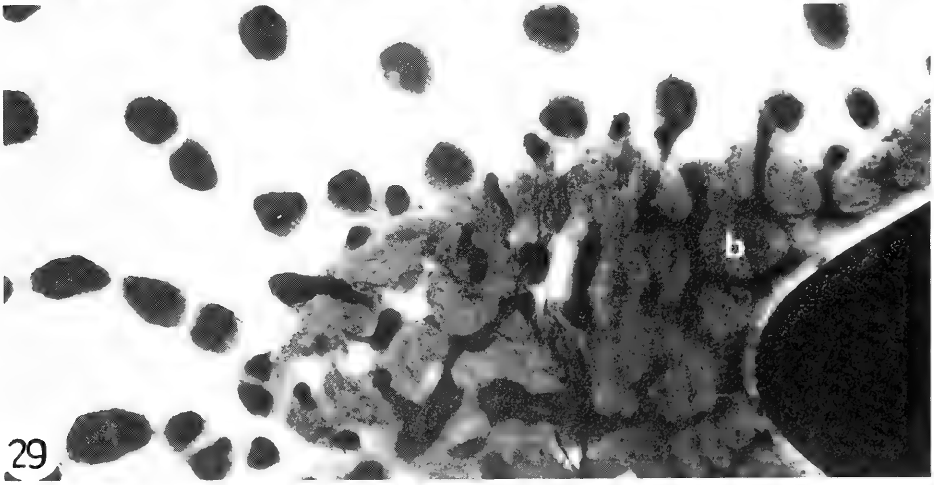
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plate of *Ceratodus madagascariensis* is compared with that of *Neoceratodus, Lepidosiren* and *Protopterus* in the final diagram (Fig. 57).

ii) *Ceratodus runcinatus* and *Ceratodus kaupi.* Tooth plates of specimens from the Triassic of West Germany have been sectioned and s.e.m.'s made from the adjacent block surfaces. The arrangement of the pulp canals throughout the tooth plate is very regular as in most ceratodontids and they run from the forming surface to the tritural surface (Smith *et al.,* 1984: fig. 1). Growth lines are very conspicuous and form a series in the petrodentine parallel to the forming surface. This, and other aspects of growth are discussed in Smith *et al.* (1984). The arrangement of pulp canals in these tooth plates was compared with those of *Neoceratodus.* Both horizontal and longitudinal sections of *Ceratodus runcinatus* have been illustrated by Günther (1871: figs 4-6, pl. 33). In polarized light the properties of the tissue between the pulp canals are identical with those described for *Ceratodus madagascariensis* — that is, strong birefringent bands at 45° to the pulp canals with opposite signs of birefringence. There is a difference between *Ceratodus runcinatus* and *Ceratodus kaupi* in that the latter shows more interwoven crystal-fibre bundles.

In s.e.m.'s the tissue between the pulp canals etches less deeply and has larger crystals than the circumpulpal dentine, and is arranged as a felt-work of crystal-fibre bundles (Figs 39, 40, 43, 44). Ørvig (1976b: figs 15, 16, 17) has also illustrated these features in Triassic ceratodontids, in which he refers to denteons around the vascular canals and pleromin as the interstitial tissue. Etching of the surface by a different acid reveals the organization of the crystals within the crystal-fibre bundles (Fig. 41), each one with many parallel crystals and variation in the orientation of adjacent bundles. These are all features of petrodentine. Confirmation of the differences in mineral density is given by the back-scattered electron image of the same tissue surface (Fig. 42). The density of petrodentine, being much greater than circumpulpal dentine, results in the lighter appearance of the petrodentine. The darker regions are those around the pulp canals and these are due to less dense packing of the mineral phase. This circumpulpal dentine is added in concentric layers to the surface of the petrodentine as a lining to the pulp canal (Smith *et al.,* 1984: figs 11, 12).

The fine details of organization of the crystals into crystal-fibre bundles appear to be slightly different in the two species, but the specimens of *C. kaupi* examined with the s.e.m. are of tooth plates from a young individual. However, the polarized light appearance is also different in many sections and it could reflect a real difference between the species in the organization of the matrix and crystals. Further observations using s.e.m. preparations are needed.

7. *SAGENODUS INAEQUALIS* Owen

The growth of tissues in the tooth plates of this genus from the Carboniferous has been previously discussed (Smith, 1979a) and the conclusion reached that petrodentine is present in the tooth plates of *Sagenodus inaequalis.* It is, however, worth including

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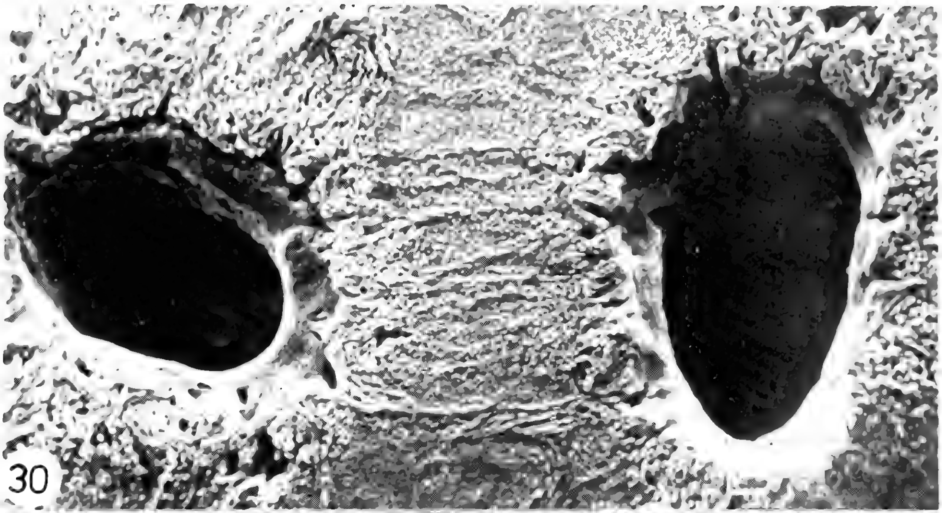
Figs 30-34. Neoceratodus forsteri S.e.m.'s of block of tissue adjacent to sections in Figs 27-29 (etched 1 min. 0.1 NHCl). *Fig. 30.* Crystal-fibre bundles of petrodentine in radial arrangement between pulp canals. Lining of dentine (c.p.d. — deeper etch depth) around older pulp canals. Field width — 625 µm. *Figs 31, 32.* Comparison between pulp canal near to forming surface, without a lining of c.p.d. and canal in older region in which petrodentine is lined with dentine (c.p.d.) with tubules, around the pulp canal. Field width 130 µm. *Fig. 33.* Higher magnification of Fig. 31 shows tubule in petrodentine (arrow) and crystals of c.f.b.'s lining the wall of the pulp canal. Field width — 32.5 µm. *Fig. 34.* Domains of crystals, parallel in each c.f.b. but opposite directions in adjacent bundles. Field width — 13 µm.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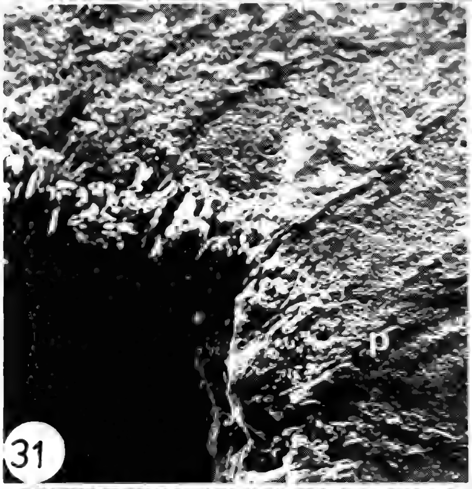
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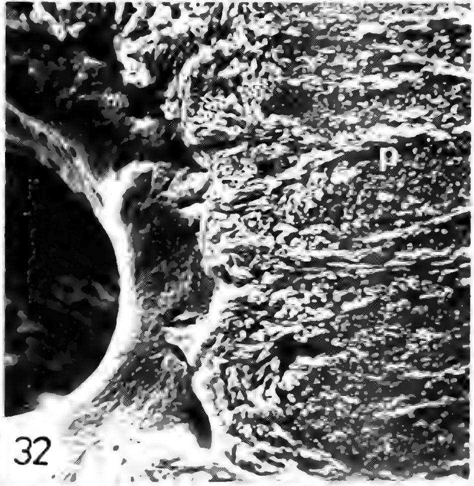
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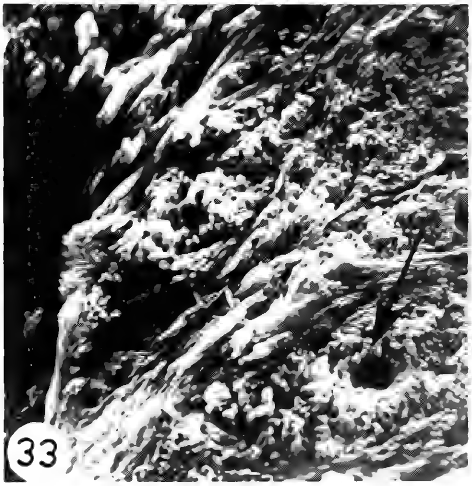
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some additional information. The arrangement of the pulp canals in each denticle of the ridges is very irregular relative to those in the ceratodontids (Fig. 45). Only the central part of each denticle along each ridge has tissue with some of the properties of petrodentine (Fig. 47) and this region grows at a forming surface bordering a small pulp chamber. The tissue between the pulp canals is translucent, and was unstained during fossilization, but is relatively weakly birefringent, showing the same sign of birefringence over larger areas than is typical for petrodentine. The organization of this tissue is clearly different from the circumpulpal dentine lining each pulp canal (Fig. 48), but only s.e.m.'s will show how the crystals are arranged. Tubules run through the circumpulpal dentine passing into the petrodentine for a short distance. At the ends of the pulp canals the main tubules branch freely and terminate in many fine extensions within the petrodentine (Fig. 46). As in the lepidosirenids, large areas of bone and trabecular dentine separate the regions of petrodentine both along each ridge, and between the ridges (Fig. 47, and Smith, 1979a: fig. 9).

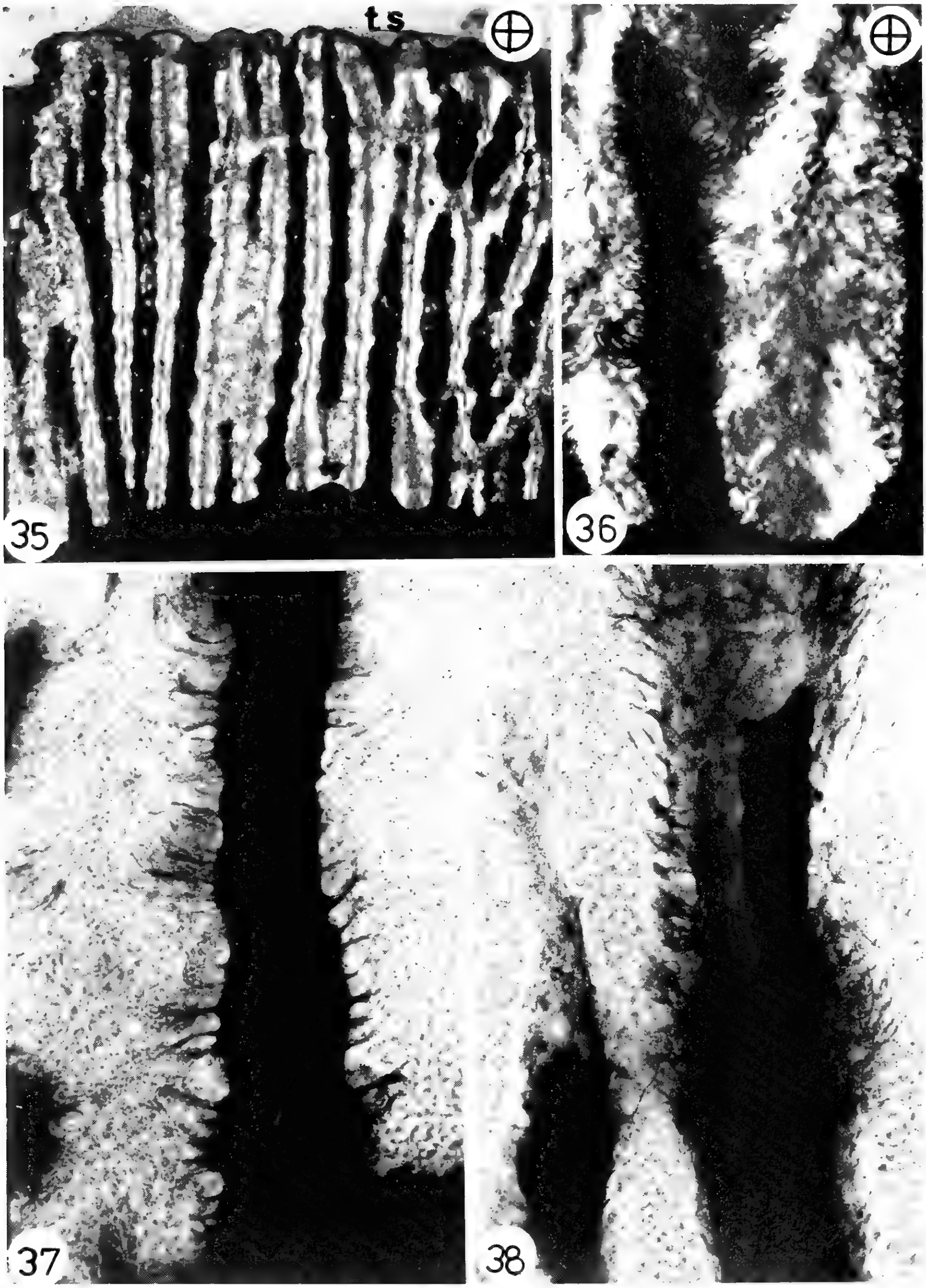
8. *DIPTERUS VALENCIENNESI*

Two sections have been examined. One is in a vertical plane through one denticle of the tooth plate (Figs 49, 50). The same section is figured as a low-power plan by White (1966: pl. 1, fig. 2). The second is in a horizontal plane through the base of one denticle of the tooth plate (Fig. 51). The pulp canals have an irregular arrangement and run from a small pulp chamber into the denticle where they branch towards the tritural surface (Figs 49, 50). This is the type of arrangement shown in the diagram from Gross (1956) in Fig. 1. In some regions the pulp canals merge with the medullary spaces of the spongy bone; in others a slightly enlarged space occurs beneath the dentine. For convenience this is called a pulp chamber (pu, Fig. 50). The tissue constituting the central part of each denticle is different from that at the margins and at the base. It has many of the properties of petrodentine, being translucent, unstained, and without tubules (Fig. 49). Bands of birefringence of opposite signs produce a woven appearance in polarized light (Fig. 50). In the horizontal section at the base of a denticle, birefringent bands, also of opposite signs and assumed to be crystal-fibre bundles, lie between the tissue surrounding the pulp canals. These are crystals with a preferred orientation in the horizontal plane. In the tissue surrounding the pulp canal the preferred orientation of the crystals is in the vertical plane, parallel to the pulp canals. Only a very thin region of circumpulpal dentine is observed surrounding the pulp canals towards the tritural surface. This has tubules and growth lines concentric with the canal. Growth lines are not observed within the petrodentine, although growth appears to result in the addition of petrodentine to the basal surface. It is also apparent that invasive growth of petrodentine occurs within the adjacent spongy bone (pleromic dentine, Smith, 1977).

The s.e.m. appearance of this tissue in *Dipterus* sp. is typical of petrodentine in that crystal-fibre bundles are arranged in a basket-weave throughout the tissue (Ørvig, pers. com.) with two distinct zones of preferred orientation as described from the observations in polarized light.

9. *CHIRODIPTERUS AUSTRALIS*

The tooth plates of *Chirodipterus australis* Miles from the Late Devonian have been studied and figured previously (Smith, 1977: figs 16, 70-75). The structure of the dentine and arrangement of the tissues in sections through the tooth plate and s.e.m.'s of the tritural surface of a worn part of the tooth plate were described. It was shown that growth lines separate regular segments of the tooth plate and that these are parallel to the forming surface, lining one surface of an extensive pulp chamber (Smith, 1977: fig.



Figs 35-38. Ceratodus madagascariensis Priem P15660, BM(NH) (fig. 2, pl. 2, White, 1966) Upper Cretaceous. Vertical section, upper tooth plate.

Fig. 35. Regular arrangement of parallel pulp canals from pulp chamber to tritural surface. Field width — 5 mm. *Fig. 36.* Birefringent tissue between pulp canals has arrangement typical of petrodentine, bands at 45° to pulp canals. Field width — 0.6 mm. *Fig. 37.* Forming surface, tubules pass into petrodentine from pulp canal. Field width — 0.3 mm. *Fig. 38.* Older parts of canal are lined with c.p.d. and tubules pass through this into petrodentine. Field width 0.3 mm.

16). Pulp canals run into the dentine from the pulp chamber and branch irregularly throughout the dentine (Smith, 1977: fig. 70). Although it was reported that the major part of the dentine between the pulp canals is probably equivalent to petrodentine in other dipnoan tooth plates, the relatively limited observations made such a statement inconclusive. Further sections of specimens prepared while the tooth plate was still in the limestone matrix have made possible s.e.m. observations of dentine at all levels from the forming surfaces through to the mature tissue. These have allowed more accurate interpretation of the tissue components of the tooth plate.

The tritural surface is relatively unworn at the labial margin of the tooth plate where it carries a number of rounded tuberosities on the surface. In a section of this region (Fig. 52) the pulp canals are wide at the pulp surface, then branch, anastomose and taper to become very thin at the tritural surface. The tissue between the canals is strongly birefringent and in some regions this birefringence is assumed to be due to parallel orientation of crystals as crystal-fibre bundles. These are arranged in alternate directions, with each c.f.b. showing an opposite sign of birefringence. This is particularly apparent in the younger tissue at the labial margins. In other regions there is principally one preferred orientation of the crystal-fibre bundles.

In an s.e.m. of the surface adjacent to the sections, both forming tissue and mature tissue are observed (Fig. 53). The growth lines are accentuated by etching and appear similar to those described in *Ceratodus runcinatus* (Smith *et al.,* 1984). The lower border of the petrodentine has also etched more deeply (Fig. 53) than the rest and this is interpreted as a less highly mineralized growth zone where a new layer of petrodentine is forming from cells lining the pulp cavity. The pulp canals are wide invaginations along this margin, each bordered only by petrodentine. In the regions near the tritural surface a thin lining of circumpulpal dentine has formed around the canals. The petrodentine between the canals has an intricately woven arrangement of crystal-fibre bundles with many small tubular spaces between them (Fig. 55). The same appearance is seen on the etched tritural surface (Fig. 54) where the circumpulpal dentine is etched more deeply. At higher magnifications the individual crystals can be resolved (Fig. 56) and although in some regions they are all parallel in bundles, in others they appear to be relatively disorganized. It may be found that the detailed crystal arrangement varies between the dental tissues of different dipnoans. This could be attributed to the different responses of the cells forming each tissue to the functional requirements of the tooth plates.

CONCLUSIONS

From the critical review of the literature and from new observations on both extant and fossil dipnoan tooth plates, a clear definition of petrodentine has emerged and a set of criteria proposed — Table 1. Because petrodentine is a term first used for dipnoan tissues (Lison, 1941), and because it is not ambiguous, it is preferred to the term pleromin. Both vascular and compact types of pleromin have been described (Ørvig, 1967, 1976a,b). It is possible also to describe the arrangement of petrodentine as vascular or compact.The combination of methods used in this investigation is

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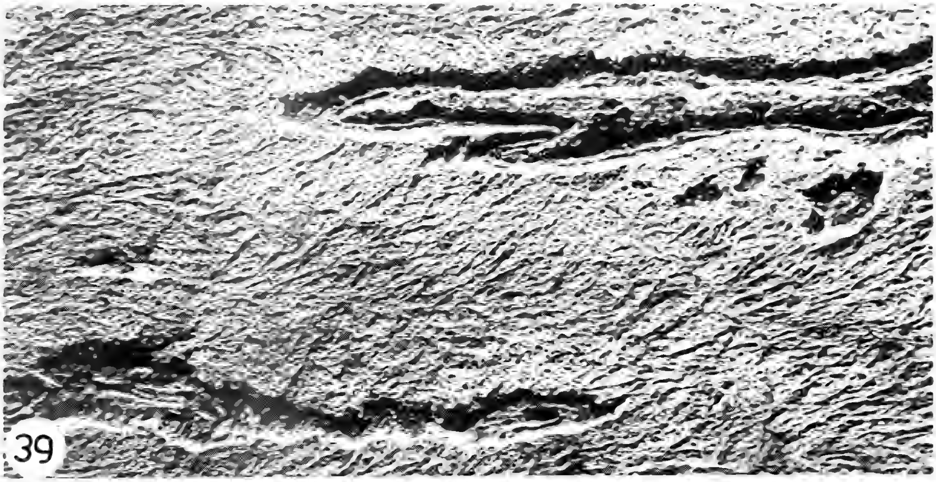
Figs 39-41. Ceratodus runcinatus Pleininger. Spec. No. PV 19270 IMGP — Tübingen. Triassic. S.e.m.'s of cut polished and etched surfaces, vertical through tooth plate (N HCl, 10 sec.).
Fig. 39. Crystal-fibre bundles of petrodentine many at 45° to the long axis of the pulp canals. Deeper etch depth to c.p.d., infilling fossil matrix in centre of pulp canal. Field width — 1.1 mm). *Fig. 40.* Oblique surface through junction between petrodentine and c.p.d. shows larger crystals of the petrodentine organized into crystal-fibre bundles. Field width — 130 μm. *Fig. 41.* Etch 10% Formic acid, 30 mins. reveals domains of parallel crystals in each c.f.b. Field width 45 μm.



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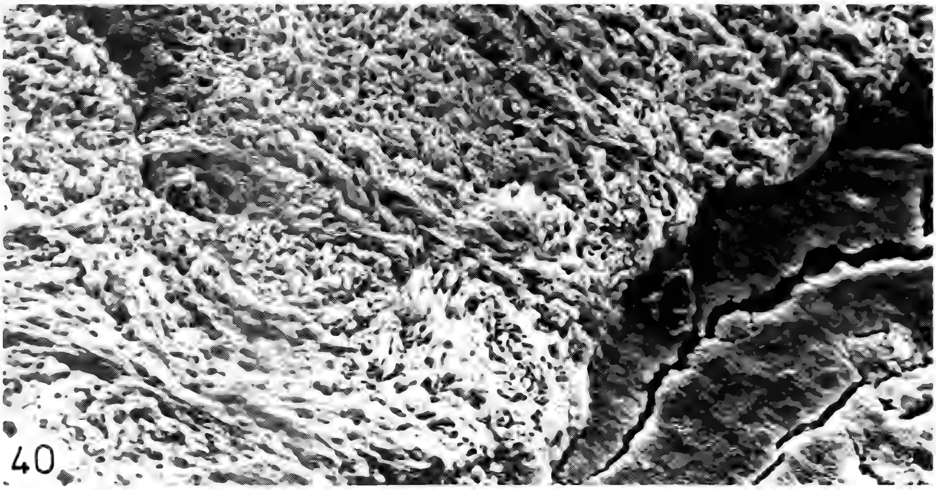

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essential to decide whether the dentine of a tooth plate is in part composed of this special type of extra-hard tissue. Quantitation of the degree of mineralization would, obviously, add to the descriptive data presented in this paper. At present only approximate values can be given for radiological density from the microradiographs of extant forms, petrodentine being 4.5 times as dense as dentine and bone. The nominated criteria can be successfully applied to both extant and fossil forms.

Petrodentine as defined here is not confined to advanced dipnoans, but is present in forms such as *Dipterus* and *Chirodipterus* which extend back to the Middle Devonian. Both Denison (1974) and Ørvig (1976) suggested that a type of hypermineralized dentine is present in some Devonian forms. In *Dipterus valenciennesi* petrodentine is confined to the denticles of each ridge but in *Chirodipterus australis* it forms a larger part of the tooth plate, being extensive beneath the tritural surface. It has not been possible to enlarge upon the comments made previously on the tooth tusks of *Holodipterus gogoensis* Miles (Smith, 1977), where the tissue type is not certain.

From the observations presented here and those in previous publications it is concluded that petrodentine is present in all the extant forms. The only real differences between forms are the arrangements of the vascular pulp canals within the petrodentine and the angle that the formative front of petrodentine presents to the tritural surface. Most of the general features of histogenesis and growth are shared by the extant and fossil forms. That is, growth of petrodentine occurs at the surface deep to the tritural surface within a space created by resorption of bone. This growth surface may be extensive or very narrow but in either case growth of petrodentine is differential. Where a vascular pulp canal becomes included in the surface as an invagination, growth of petrodentine in that region has ceased. This canal then becomes narrower by a lining of circumpulpal dentine laid down by odontoblasts, each one leaving fine branches in the petrodentine and tubules connecting these with the pulp canal. Lison (1941) suggested two possible methods by which the canals at the centre of the trabecular dentine might have originated; the first by resorption, and the second by localized absence of growth of the roof of the pulp chamber. The latter is supported by the present investigation. Denison (1974) thought that the pulp canals had migrated from a position beneath the centre of the denticles to a position at the sides. This was suggested to him by the arrangement of tissues in *Monongahela,* and by the position of the pulp canals in *Protopterus* at the margins of the ridges.

The arrangement and growth of petrodentine in Tertiary lepidosirenids is similar to that in the extant forms, and its arrangement and growth in fossil ceratodontids as old as the Triassic is similar to that in the extant *Neoceratodus.* Genera differ in the microstructure of their tissues, that is in the arrangement of the vascular canals, and in the proportions of petrodentine to trabecular dentine. These differences include the pattern of the crystal-fibre bundles which may be dependent on function, as well as the branching and extent of penetration into the petrodentine of the tubules from the cells in the pulp canals.

Figs 42-44.

Fig. 42. Ceratodus runcinatus Spec. No. PV19279 IMGP — Tübingen. Polished, non-etched surface, back-scattered electron image. No topography on surface (except scratches from polishing and holes where pulp canals are empty). Contrast shows differences in mineral density, petrodentine being more densely mineralized than dentine around pulp canals. Field width — 177 μm.

Figs 43, 44. Ceratodus kaupi Agassiz PV4460 IMGP — Tübingen. Triassic. *Fig. 43.* Vertical, cut surface through small tooth plate. Forming surface of petrodentine (arrow) pulp canals with very thin lining of c.p.d. Most of tooth plate is formed from interwoven crystal-fibre bundles. Field width — 730 μm. *Fig. 44.* High power of central area of petrodentine shows many alternating crystal-fibre bundles. Field width — 45 μm.


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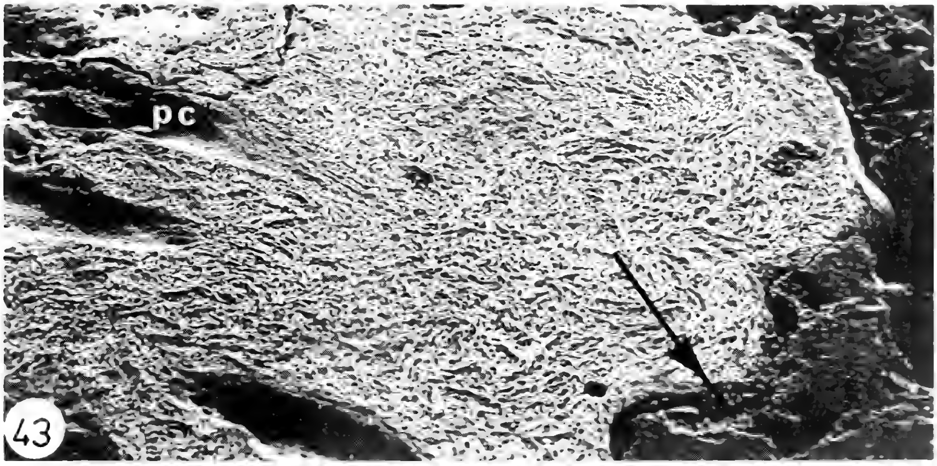
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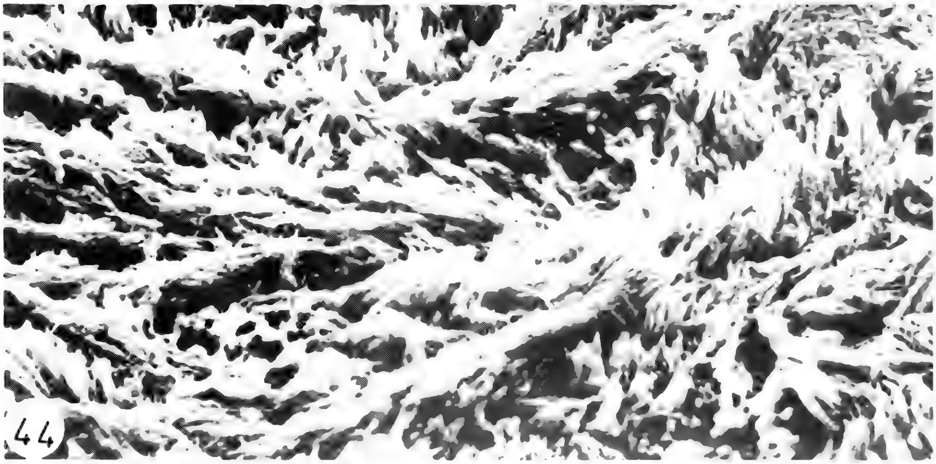
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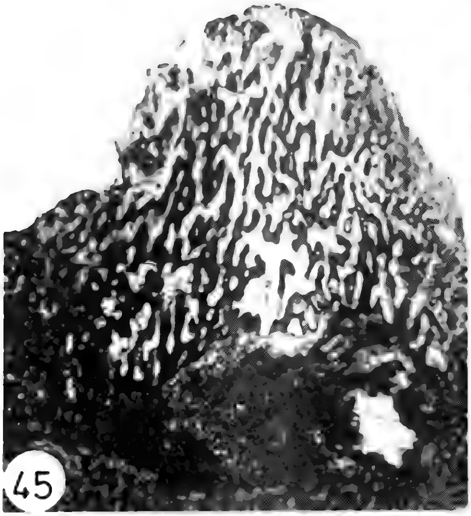
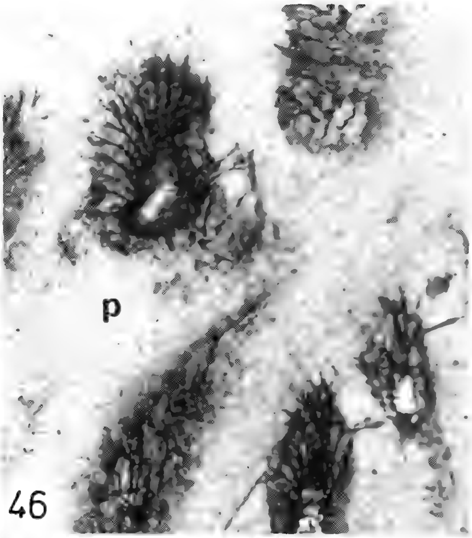
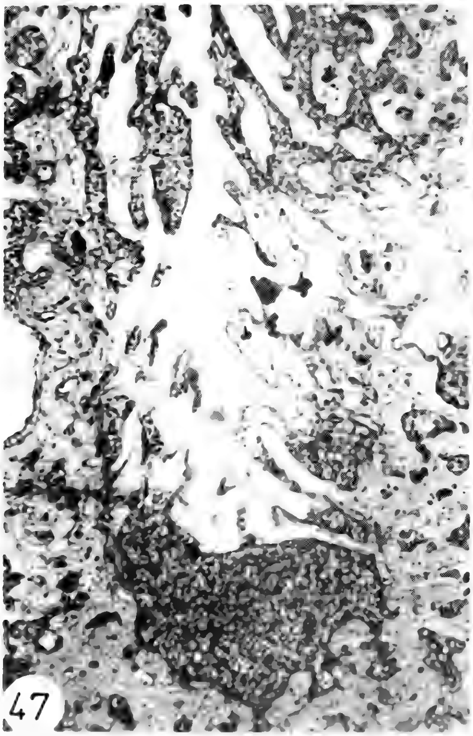
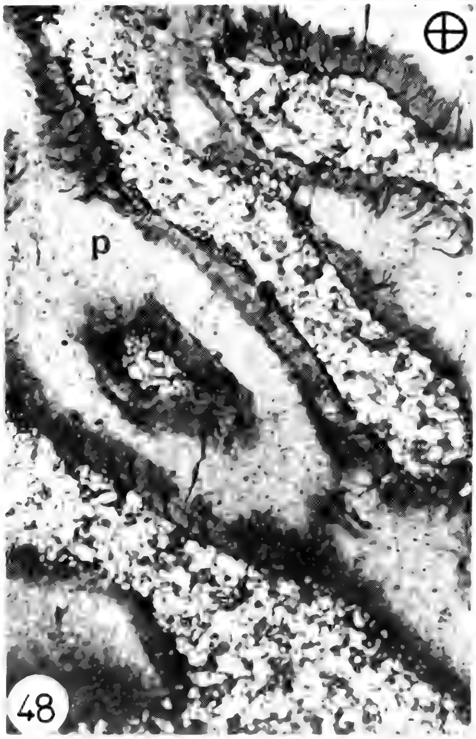
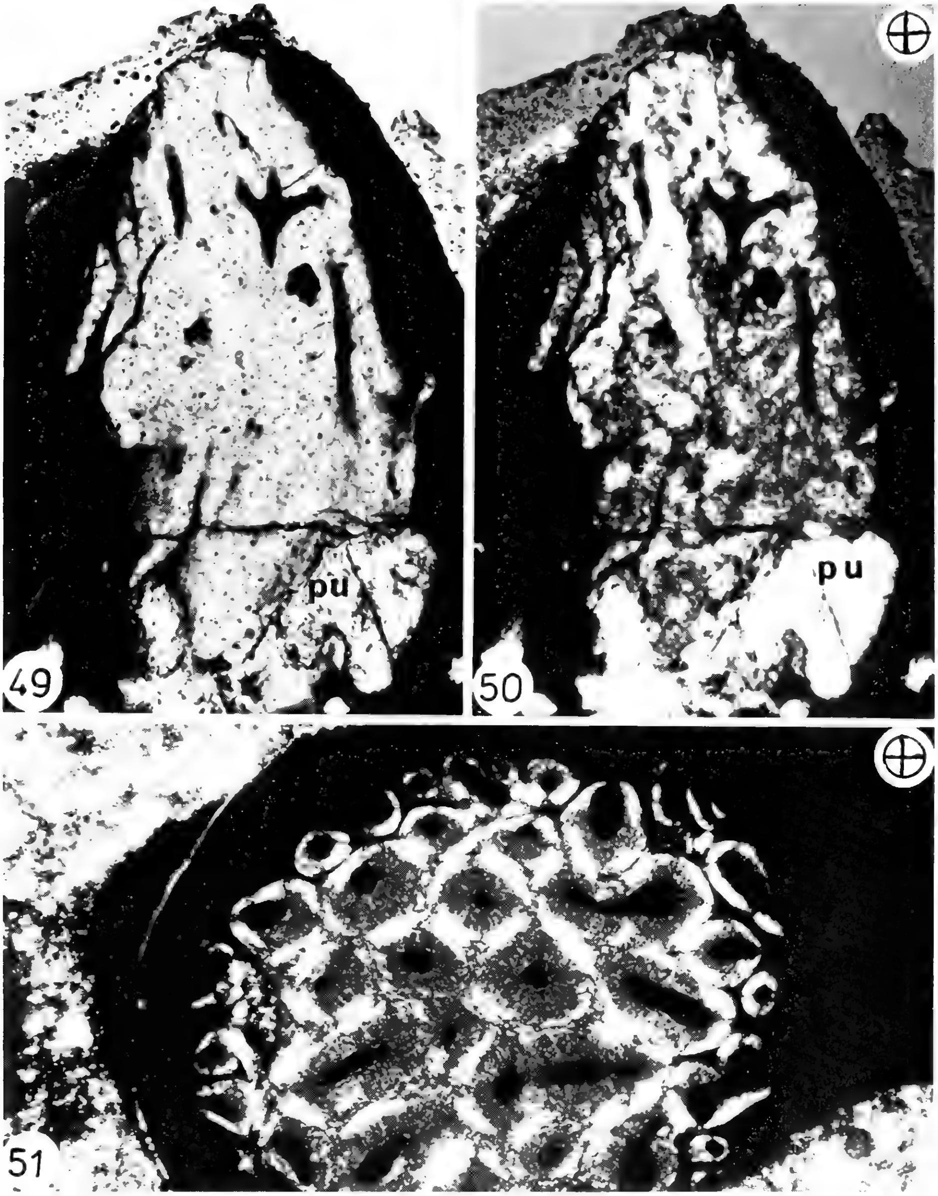








Figs 45-48. Sagenodus inaequalis Owen P7326 & P3381, BM(NH). Carboniferous (fig. 1, pl. 2 & fig. 3, pl. 1, White, 1966, LP Plan).
Fig. 45. Vertical section through anterior cusp of upper tooth plate, irregular arrangement of pulp canals and translucent petrodentine. Field width 52 mm. *Fig. 46.* ½ PL of pulp canals near tritural surface with multibranched tubules emerging from pulp canal into petrodentine. Field width 0.4 mm. *Fig. 47.* Vertical, antero-posterior section through upper tooth plate; one column of petrodentine with many pulp canals beneath one ridge, small pulp chamber. Field width — 35 μm. *Fig. 48.* ½ PL of pulp canals in central region and lining of c.p.d. distinct from petrodentine. Field width — 0.4 mm.



Figs 49-51. Dipterus valenciennesi S & M P44671, P535373 BM(NH). Middle Devonian (fig. 2, pl. 1, LP Plan, White, 1966).

Figs 49, 50. Vertical section through one denticle of upper tooth plate in O.L. and P.L. to show translucency and birefringence of petrodentine. Small pulp chamber separates petrodentine from bone. Irregular arrangement of pulp canals through the petrodentine. Field width 0.6 mm. *Fig. 51.* Horizontal section through one denticle P.L. shows birefringent bands of opposite sign in tissue between the dentine adjacent to pulp canals. Translucency and arrangement of crystal-fibre bundles indicative of petrodentine. Field width 1.2 mm.

Petrodentine differs from trabecular dentine by its extreme hardness which results from high levels of mineralization and reduction of organic matrix. Its production by specialist cells at the pulp surface (whether a pulp chamber or a pulp canal) in a relatively continuous sequence of growth makes petrodentine a unique tissue. The microstructure of mature petrodentine, with domains in which relatively large crystals are grouped in parallel bundles but tubules housing odontoblast cell processes are absent, is very similar to enameloid or acrodin in the separate teeth of elasmobranchs and actinopterygians. However the production of these tissues is entirely different and, therefore, they are considered not to be homologous. In dipnoans a specialist cell population has developed from a presumed single population of dentine-producing cells of the mesodermal dental pulp. Studies of larval tooth plates show that petrodentine is produced by a distinct group of cells from those producing the outermost, primary dentine. Petrodentine forms in this way in the smallest separate denticles which fuse together to make the radiate ridges of the tooth plate. It is beyond the scope of this paper to discuss whether the specialist cells, petroblasts, are derived from one or two populations of progenitor cells, or by dedifferentiation of odontoblast cells. However, some petrodentine surfaces are subsequently lined by dentine with tubules, and circumstantial evidence suggests that some petroblasts revert to odontoblasts in these regions of slower growth, although adjacent cells continue to form thicker petrodentine. Details of the formation, development and growth of petrodentine are not known. Kemp (1979) has stated that petrodentine (central material) does not stain for collagen and that it does not become hypermineralized as a result of loss of collagen. She has suggested that fine reticulin fibres may be the basis of this tissue matrix. Clearly agreement can only be reached when more information is available at the ultrastructural or biochemical level. It is generally stated that fine tubules from the odontoblast cells do not remain in the petrodentine. However, during the first stage of its production there are cell process spaces. These are probably polarized cell processes temporarily trapped in the first formed secretion. Cell processes withdraw as more petrodentine is secreted and the first-formed tissue becomes completely calcified throughout. It will be interesting to know whether the cell process controls the orientation of the crystals or whether the type of organic matrix is the controlling factor.

Some of the Carboniferous forms examined, for example *Sagenodus,* have very irregular arrangements of the pulp canals but it is concluded that the tissue between them in the central part of the ridges is probably petrodentine. *Scaumenacia* also has petrodentine (Ørvig, 1983, pers. comm.) dispersed between numerous pulp canals. The pattern of change that produced different types of tooth plates is not understood. The arrangement of the tissues in lepidosirenids clearly differs from that in ceratodontids, but whether the arrangement in *Sagenodus* was modified to give either

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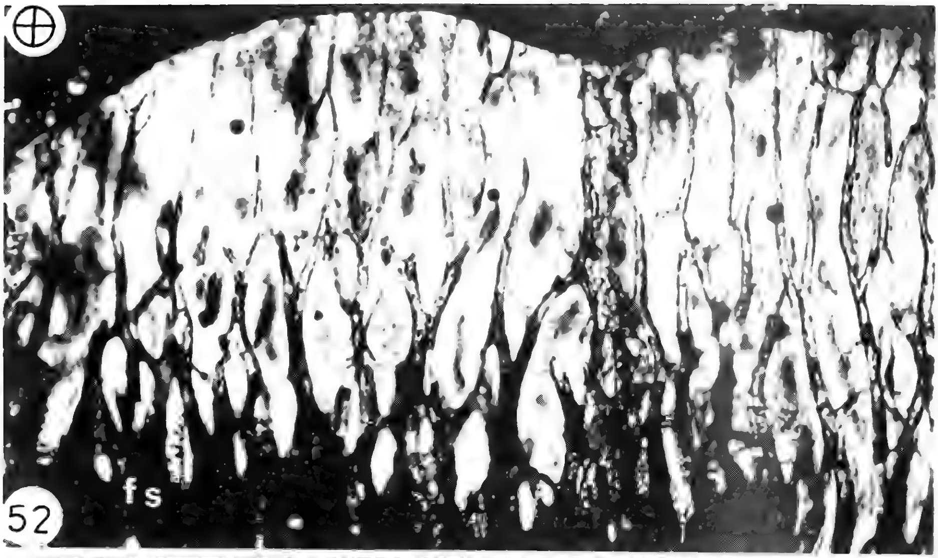
Figs 52-56. Chirodipterus australis Miles BMR 22592-4, P52561 BM(NH). Middle Devonian.

Fig. 52. P.L. of vertical section through labial margin of lower tooth plate, shows extent of birefringent petrodentine and irregular arrangement of pulp canals. These anastomose and taper markedly from forming surface to tritural surface. Field width — 3.13 mm. *Fig. 53.* S.e.m. of section adjacent to Fig. 52 prepared as polished, etched surface (1NHCl, 30 secs). Fringe of deeper etched material at lower border where petrodentine is forming and is less highly mineralized. Field width — 1.8 mm. *Fig. 54.* S.e.m. of worn tritural surface etched to show difference between petrodentine and c.p.d. around pulp canals. Many small tubules throughout petrodentine. Field width — 60 μm. *Fig. 55.* S.e.m. of field from Fig. 53, interwoven matrix between pulp canals, many small tubules between crystal-fibre bundles. Field width — 180 μm. *Fig. 56.* S.e.m. at higher magnification of petrodentine to show separate crystals in random arrangement, although some lie in parallel groups. Field width — 25 μm.



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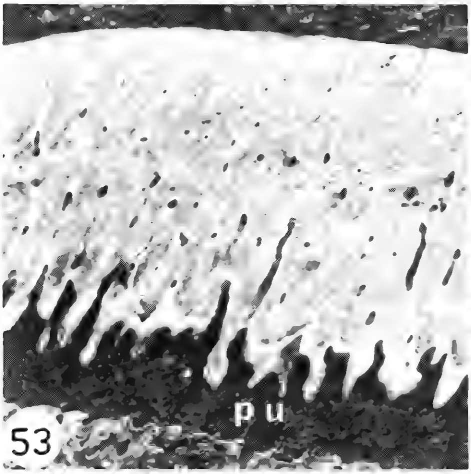

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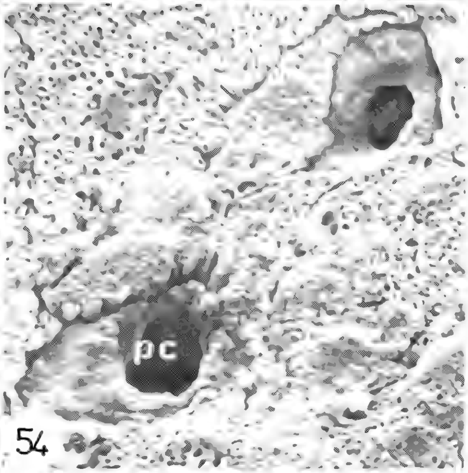

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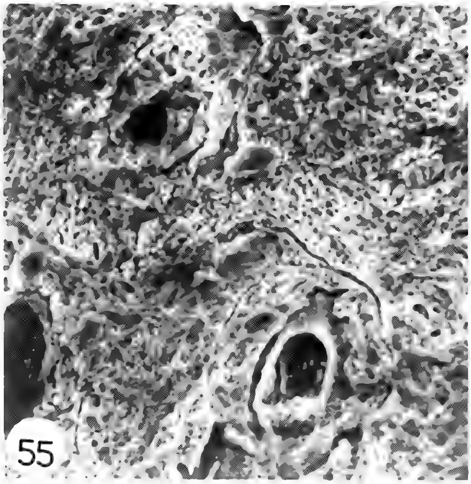

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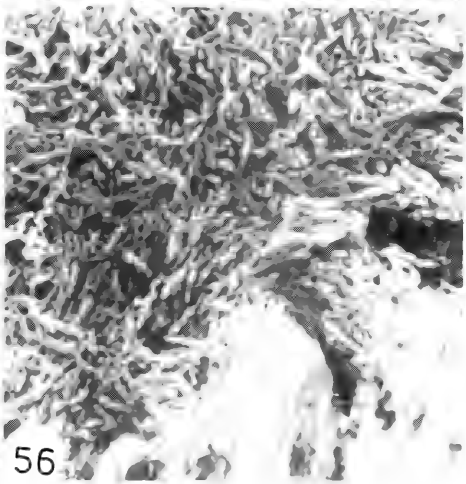

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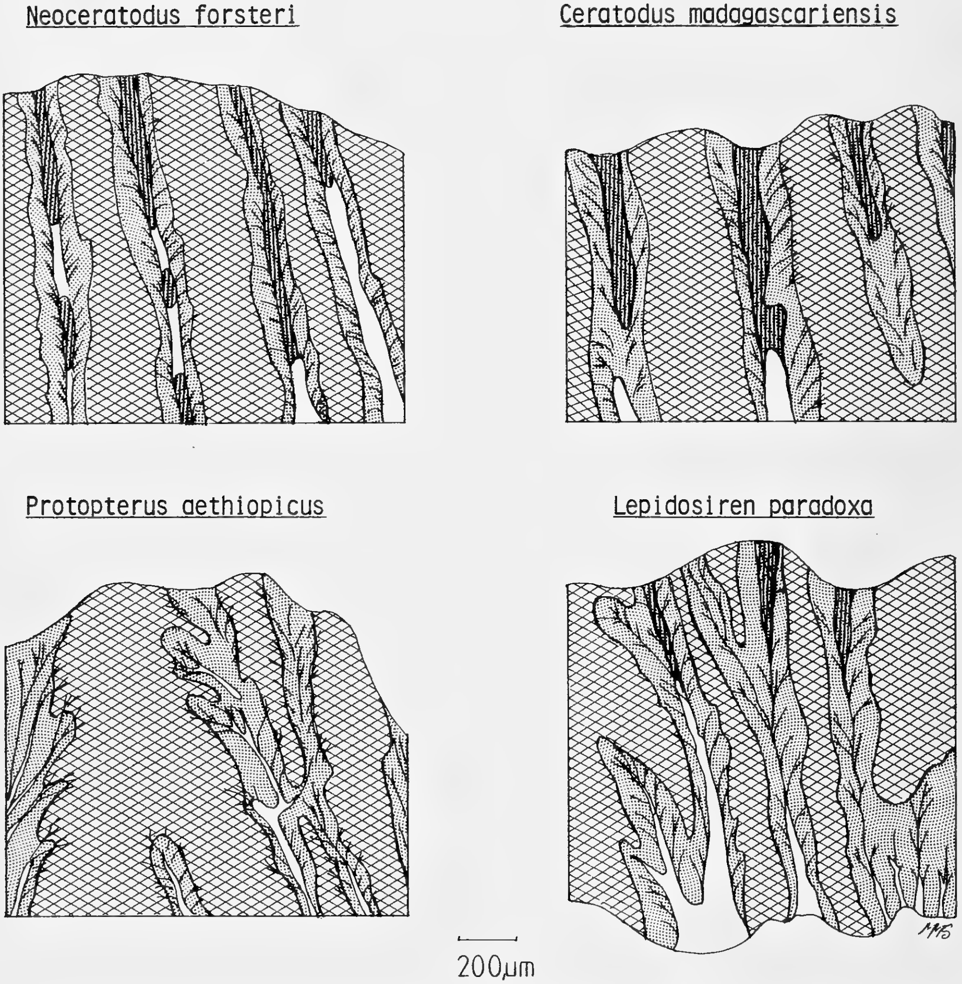

Fig. 57. Each area represents the arrangement of tissues immediately beneath a worn region of the tritural surface. Only in *Lepidosiren* is the formative surface also included (same section as Figs 16, 17). In this region the pulp canals are almost parallel as in the two ceratodontids. The section of *Protopterus* is through the main part of ridge two and is typical of what is called a 'column of petrodentine', as shown in Fig. 6. *Neoceratodus* is from a decalcified section and that of *Ceratodus* from a ground section. The key is the same as Fig. 1 with the addition of vertical-line hatching for infilling dentine in each pulp canal.

type has not been determined. The tooth plates of *Monongahela,* also with petrodentine, are most interesting and together with those of *Gnathorhiza* merit further study.

The term 'columns of petrodentine' has been used to describe the peculiar arrangement of petrodentine in lepidosirenids but it could equally well be applied to the structure in *Sagenodus* or *Dipterus,* except that more vascular canals are found within their petrodentine. It is difficult, therefore, to decide if this is an advanced character, particularly as in some regions of the tooth plate of *Lepidosiren* petrodentine is not arranged as columns but as an extensive region with parallel, vertical pulp canals. A comparison of the proportion of petrodentine to dentine around the pulp canals is made in Fig. 57 where four examples taken close to the tritural surfaces are illustrated.

Growth lines have been identified in many of the fossil forms and these are a guide to both the areas of growth and to the direction of growth. These topics will be pursued in subsequent publications together with the pattern of growth that is established in larval tooth plates and continued into the adult stages (Smith, 1984).

Petrodentine is a feature of tooth plates in genera as old as Middle Devonian but it has not been shown to be present in genera without tooth plates. This question should be investigated using the criteria developed in this paper. If triturating dentitions define a line of evolution as proposed by Campbell and Barwick (1983), then it is important to know if petrodentine is found exclusively in these forms. We also need to know if petrodentine is present in the most primitive representatives of dipnoans such as *Dipnorhynchus sussmilchi* (Etheridge) and *Speonesydrion iani* Campbell and Barwick. Preliminary observations by Smith and Campbell suggest that it is not.

Whether petrodentine occurs in other gnathostomes has not been considered herein. Ørvig (1976, 1983 MS) has described this growth of pleromin in holocephalan tooth plates, producing tritural columns within the plate. There appear to be many similarities with dipnoan tissues; but whether this is indicative of a close relationship between the groups is not possible to decide at present. This may be an example of a convergent specialization but without proper analysis of all the characters of holocephalan dentitions the question must remain open. Kemp (1984) has published some new material to compare the histological structure and growth pattern of tooth plates of *Neoceratodus forsteri* and *Callorhynchus milii.* From this she has concluded that they share a similar growth pattern.

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KEY TO ABBREVIATIONS

b	— bone
d	— dentine
cp.d	— circumpulpal dentine
e	— enamel
g.l.	— growth line
f.s.	— forming surface
M	— medial
od	— odontoblast
p	— petrodentine
1°	— primary
p.c.	— pulp canal
pe	— petroblast
pu	— pulp cavity
r	— resorption surface
t	— tubules
t.s	— tritural surface
Ph	— phase contrast
P.L.	— polarized light
O.L.	— ordinary light

Specimen location — BM (NH) British Museum (Natural History); IMGP — Institute and Museum of Geology and Palaeontology, Tübingen; BMR — Bureau of Mineral Resources, Canberra; FM — Field Museum of Natural History, Chicago. WJ — Warwick James collection, Royal Dental Hospital, London.

Some procedural Problems in the Study of Tetrapod Origins

E. I. VOROB'EVA
(Communicated by A. RITCHIE)

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The historical method of phylogenetic analysis is discussed. It is illustrated by palaeontological, embryological, comparative anatomical, and morphofunctional investigations of rhipidistians and amphibians. Rhipidistians and amphibians (both urodeles and anurans) have some common morphogenetic features that suggest a close phylogenetic relationship.

E. I. Vorob'eva, Institute of Evolutionary Animal Morphology and Ecology, Academy of Sciences of the USSR, Leninsky Prospect 33, Moscow, USSR 117071. *A paper read at the Symposium on the* Evolution and Biogeography of Early Vertebrates, *Sydney and Canberra, February 1983; accepted for publication 18 April 1984, after critical review and revision.*

For several years now, the methods of 'phylogenetic systematics' have been applied extensively to the study of early vertebrates, often with results different from those produced by 'evolutionary' systematists. Nowhere has this been more marked than in the works of Rosen *et al.* (1981) who attempted to reestablish a closer link between tetrapods and dipnoans than between tetrapods and rhipidistians. In their proposed phylogeny, the Tetrapoda and Dipnoi are regarded as sister groups and together form the Choanata.

These sweeping changes have not had support from many specialists. For instance, Schultze (1981) showed that several of the features on which the argument was based would not carry the weight placed upon them. In particular he questioned the homology of the openings referred to as choanae in the two groups. However, the very fact that such a scheme could be proposed points to the incompleteness of our knowledge of the evolution of early tetrapods and the absence of reliable criteria for phylogenetic reconstruction.

The establishment of homologies must logically precede the discussion of phylogeny (Remane, 1964), but the twin difficulties of avoiding circularity in our arguments and distinguishing between homologous and homoplasious structures (Simpson, 1961; Bock, 1973; Vorob'eva, 1980a) continue to bedevil work in real situations. The phylogenetic weight to be attached to various features remains a problem, especially as structural, functional and ontogenetic aspects of such features all have to be considered. In resolving such problems, the essential first step after deciding on homologues is to establish polarized morphoclines (Hecht and Edwards, 1977) and then to trace lines of evolutionary development.

This programme implies extensive morpho-functional and morpho-ecological study of recent groups. Granted the importance of such studies, it is difficult to accept the cladistic conceptions of Patterson (1977) that all problems of phylogeny should be solved exclusively by study of recent groups, and that palaeontological material cannot be used to falsify these solutions. Palaeontology provides historical documents for the study of evolution and thus exerts a control on neontological speculation as well as providing unique data for phylogenetic reconstruction. These leading roles for palaeontology have been repeatedly demonstrated in the works of the founders of vertebrate evolutionary morphology and palaeontology in the USSR (see Schmalhausen, 1964). The 'historical method' continues to be applied by the whole of the

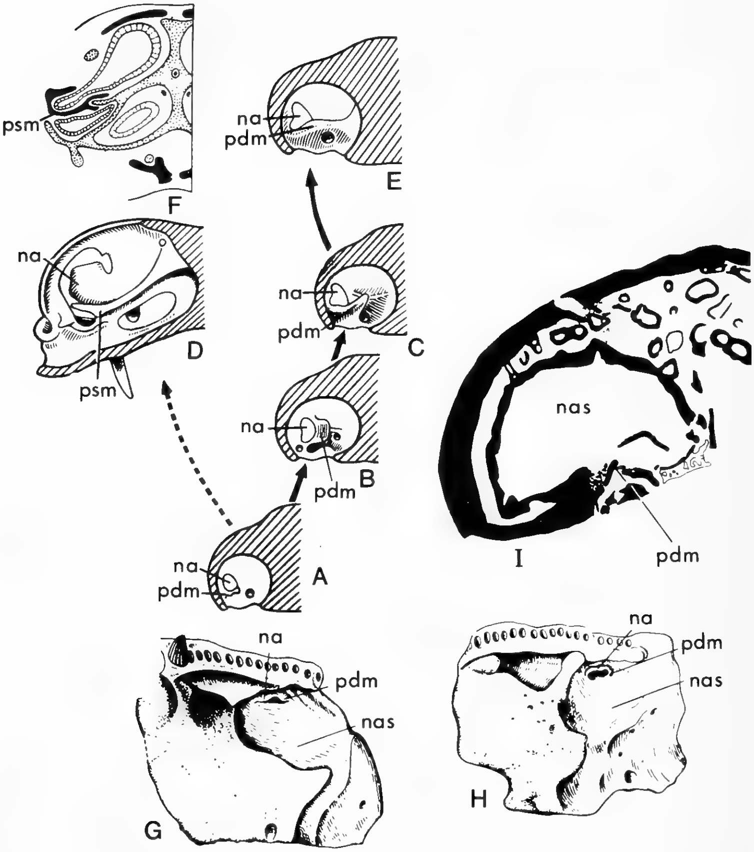

Fig. 1. The different state of the dermintermedial process *(pdm)* in rhipidistians and the septomaxillar process *(psm)* in amphibians. Rhipidistians are **A**, *Thursius;* **B**, *Eusthenopteron obruchevi;* **C**, *E. foordi;* **E**, *Platycephalichthys bischoffi*; **G**, *Gyroptychius elgae*; **H**, *Porolepis polonica*; and **I**, *Youngolepis praecursor.* Amphibians are **D**, *Rana,* and **F**, *Hypopachus cuneus. na,* narina anterior; *nas,* nasal capsule (**A**,**B**,**E**,**G**, from Vorob'eva, 1977; **C**,**D**, from Jarvik, 1942; **H**, from Kulczycki, 1960; **F**, from Jurgens, 1971; **I**, from Chang Mee-Mann, 1982).

Soviet palaeontological and morphological school, as is exemplified by the work of Obruchëv and Schmalhausen and their students.

Fish-tetrapod relationships are at present under examination in the USSR, particularly through study of the historical morphogenesis of the skeleton-muscle systems and receptor organs. Such a study focuses attention on the theoretical problem of the significance of morphogenetic processes for phylogenetic study in general, as well as the functional and ecological meaning of these processes and their significance for the understanding of evolutionary mechanisms. Contributions are being made from the comparative anatomy, comparative and experimental embryology, physiology and morphoecology of fishes, amphibians and reptiles, as well as palaeontological study of crossopterygians and fossil lower tetrapods.

As a result of these studies, several new proposals have emerged. The narrow specialization of some crossopterygians to an amphibian environment may possibly be an 'aromorphic' (Severtsov, 1939) step to a terrestrial way of life (Vorob'eva, 1971,

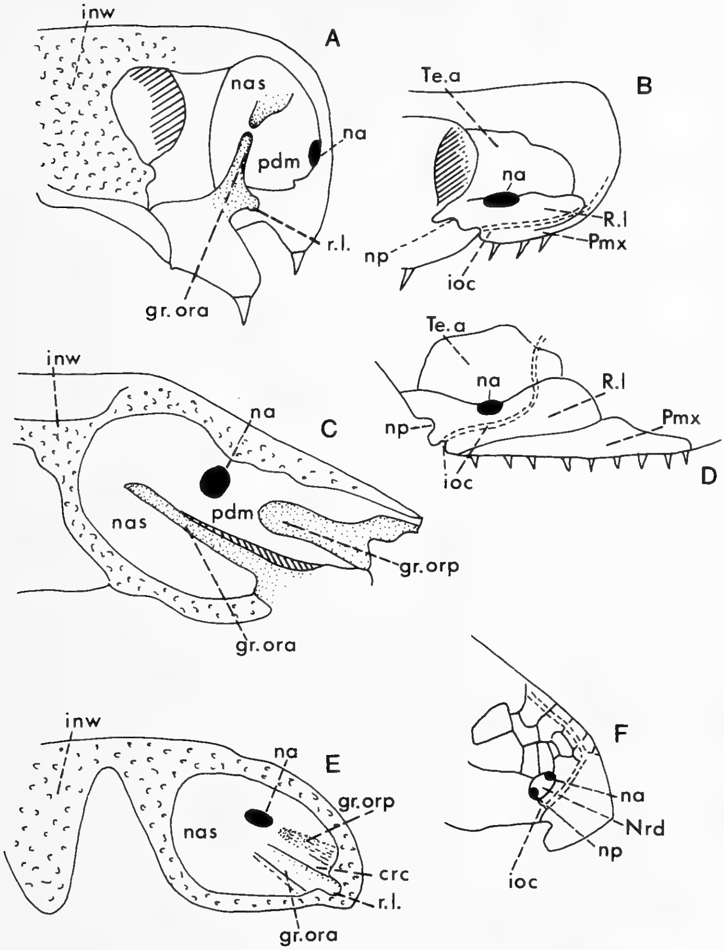

Fig. 2. Similarity and differentiation of the nasal capsule in some rhipidistians. **A,B,** *Panderichthys stolbovi* (from Vorob'eva, 1973), **C,D,** *Powichthys* sp. (from Vorob'eva and Schultze, 1984; **E,F,** *Holoptychius* (from Jarvik, 1980). *gr. ora, gr. orp,* oro-rostral anterior and posterior grooves; *inw,* internasal wall; *ioc,* infraorbital canal; *na, np,* narina anterior, posterior; *nas,* nasal capsule; *Nrd,* nariodal; *pdm,* dermintermedial process; *Pmx,* premaxillary; *R.l.* lateral rostra; *r.l.* lateral recess; *Te.a,* anterior tectal.

1977). The parallelism that often occurs between osteolepid crossopterygians and lower tetrapods may be explained by canalization of morphogenetic mechanisms, and this may be interpreted as an argument favouring the taxonomic propinquity of these groups (Vorob'eva, 1980b). The 'forestall' principle (see below) resulted from the study of crossopterygian material (Vorob'eva, 1980a). The idea of an evolutionary succession of correlated systems in the skulls of crossopterygians, amphibians and reptiles, has been worked out by Lebedkina (1979). The use of functional arguments to identify the homologies of jaw muscles, and the principle of paraconvergent morphological resemblance, have been elaborated (Iordansky, 1982). Smirnov (1984) has proposed extensive heterochrony in the formation of the amphibian middle ear, and the consequences of this idea for the study of changes in crossopterygian skulls have been analysed (Vorob'eva and Smirnov, 1982). Examples of these points follow.

The 'forestall' principle refers to the development of a structure in a taxon more primitive than the one in which it has its characteristic development. It is illustrated by similarity of the dermintermedial process in rhipidistians and the septomaxillary process in anuran and urodele amphibians. A poorly-developed dermintermedial process is found in some Middle Devonian osteolepids (*Gyroptychius pauli, G. elgae, Thursius estonicus* (Vorob'eva, 1977)), and it is also found in some Early Devonian Porolepididae (*Porolepis polonica* Kulczycki, 1960) as well as in *Youngolepis praecursor* (Chang Mee Mann, 1982), which are illustrated in Fig. 1. In the evolution of different lines of osteolepiforms this process becomes stronger until in *Eusthenopteron foordi* it reaches the stage of the septomaxillary process in Anura (*Rana* in particular). In *Platycephalichthys bischoffi* the dermintermedial process fuses with the medial wall of the nasal capsule which is similar to the situation in the microchylid anuran *Hypopachus* (Fig. 1; Jurgens, 1971). In these instances the same degree of structural development is reached independently. Similar examples indicate that this phenomenon is widespread, and results in the well-known mosaic pattern of evolution.

It is important to note that in most osteolepiforms the dermintermedial process develops similarly to the homologous septomaxillary process in Anura, but the majority of porolepiforms differ in that they develop their process in the lateral nasal capsule wall. Jarvik (1980) described a rostro-caudal endocranial crest lying along the lateral wall of the nasal capsule in *Porolepis brevis* and in *Holoptychius,* and this is comparable with the structure in urodeles. Vorob'eva (1973) described a dermintermedial process resembling the above crest in *Panderichthys stolbovi* (Fig. 2), and Vorob'eva and Schultze have been able to show that *Powichthys* has, along the lower edge of the anterior nostril, a well-developed, flat, dermintermedial process which continues caudally into a similar rostro-caudal crest (Fig. 2). This process in *Powichthys* resembles that of *Panderichthys* and probably originated from the lateral rostral, which is present in *Powichthys* but has been lost in porolepids. A dermintermedial process was recorded by Schmalhausen (1958) in the urodele *Onychodactylus fisheri* and by Medvedeva in *Ambystoma.*

A linear sequence in the structural evolution of crossopterygians and tetrapods is also noted by the correlation between the developing exoskeletal and endoskeletal systems in the two groups. A good example is in the morphogenetic similarities of the palatal bones. Jarvik (1954) presented a hypothetical reconstruction of gnathostome palatal and jaw arches (Fig. 3). The arches are isolated and both carry isolated shagreened plates. He assumed that the ancestors of the Rhipidistia showed a similar condition.

Lebedkina (1979: figs 76a, 80) showed that in the larvae of the primitive urodeles *Ranodon* and *Hynobius,* the jaw arch bones (premaxilla), palatal arch (vomer) and parasphenoid, are not linked together. Their force lines which reflect the orientation of collagen fibres and the direction of static forces, do not form an integrated system (Fig. 3**C**). In the upper jaw (premaxilla) and palate (vomer and pterygopalatine) they are oriented parallel with the jaw margins, but in the anterior part of the parasphenoid they are longitudinal. At metamorphosis the vomers are formed with their force lines parallel with those of the parasphenoid. These new vomers lie close to the recently formed process of the premaxillary and later with the parasphenoid (Fig. 3**D**). As a result a new system is formed in which forces are differently transmitted from the jaw arch to the parasphenoid.

In larval dipnoans the force lines of the palatal arch and the parasphenoid are independent (Fig. 3**E**) though the pterygoid lies quite close to the parasphenoid. Lebedkina (1979) thought this primitive condition to be an argument in favour of phylogenetic affinity of dipnoan and crossopterygian ancestors. It has been assumed

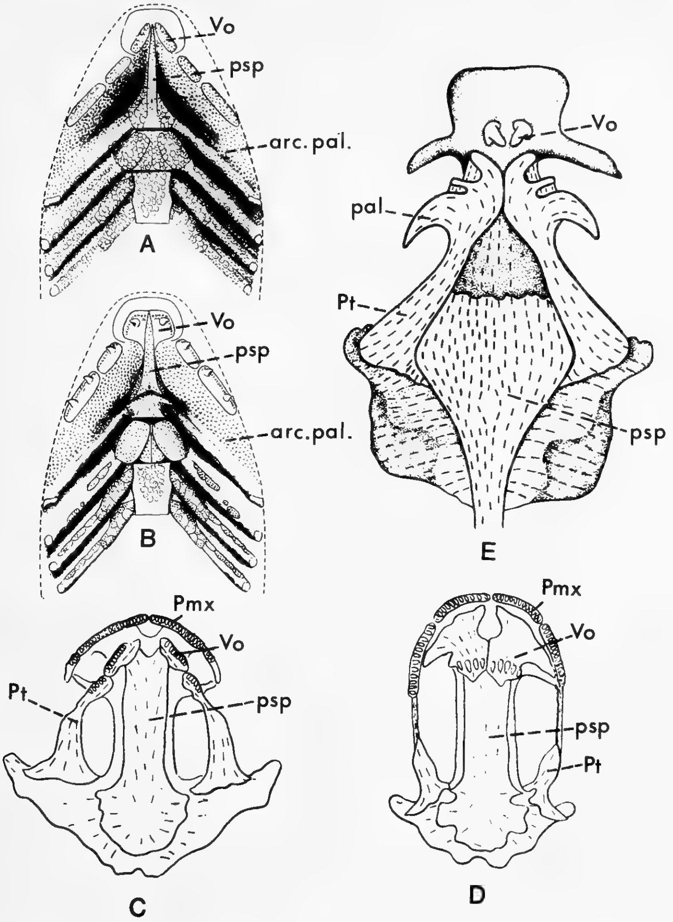

Fig. 3. State and development of the palatal surface in Gnathostomata: **A,** hypothetical primitive condition; **B,** generalized rhipidistian condition; **C,** larval urodele; **D,** adult urodele; **E,** larval dipnoan; *arc. pal,* palatal arc; *Pt,* pterygoid; *pal,* palatinum; *psp,* parasphenoid; *Pmx,* premaxillary; *Vo,* vomer (**A,B,** after Jarvik, 1954; **C-E,** after Lebedkina, 1979).

that the order in which connections between bones were formed during the larval development of the Rhipidistia (premaxilla to vomer: vomer to parasphenoid) can be traced during phylogeny of that group. Thus in ancient Rhipidistia *(Porolepis, Youngolepis, Powichthys, Thursius, Gyroptychius latvicus)* the vomers are short, widely spaced, have no contact with the parasphenoid and are weakly linked with the premaxilla. That is why they are often missing in fossil material (Vorob'eva, 1977, 1981; Jessen, 1980; Chang Mee-Mann, 1982). The parasphenoid is short and does not reach the internasal region, though exceptions such as *Youngolepis* are known.

In osteolepiform phylogeny it is possible to trace progressive development of the dermal palate. This process can be traced as follows. The vomers become elongate, join, and develop processes (Fig. 4**F**). Similar changes can be traced in the Anura, particularly in the Pelobatidae as was shown by Roček (1980). Urodeles and anurans, though similar in morphogenesis, have distinctive features. Thus in the Anura the link

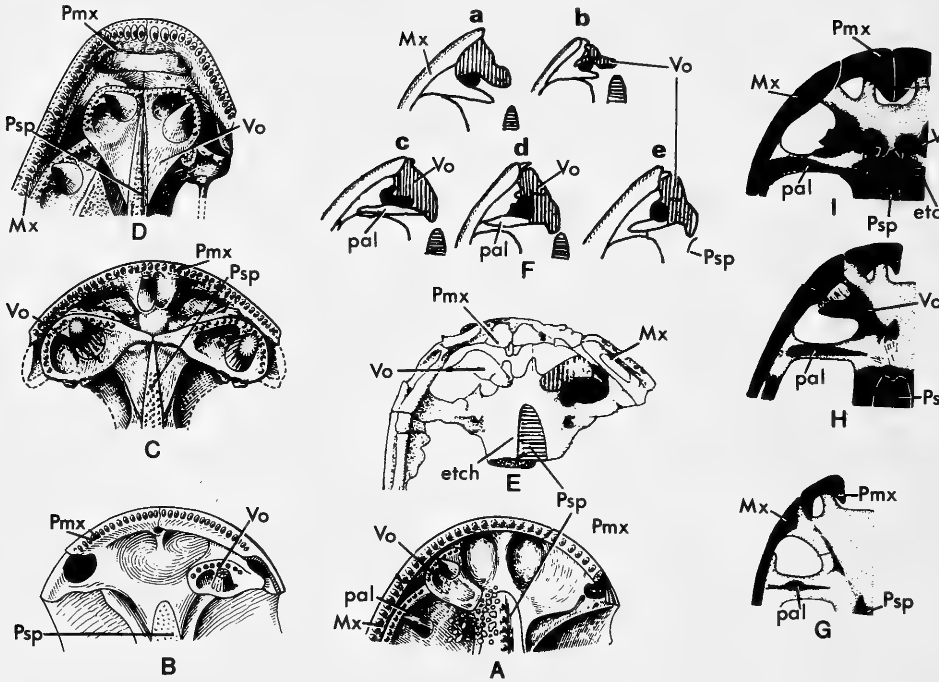

Fig. 4. Comparisons of the palatal surface in Rhipidistia (**A**-**D**) and Anura (**E**-**I**). **A,** Porolepiformes *(Porolepis)*; **B**-**D**, Osteolepiformes (**B**, *Thursius;* **C**, *Megalichthys;* **D**, *Eusthenopteron*); **E**, *Eopelobates;* **F**, various primitive anurans (Pelobatidae); **G**, prometamorphic state in *Rana temporaria;* **H,I,** different ontogenetic states (adult) in *Rana esculenta, etch,* ethmosphenoid; *Mx,* maxillary; *Pmx,* premaxillary; *Psp,* parasphenoid; *pal,* palatinum; *Vo,* vomer. (**C-D,** from Jarvik, 1980; **E-F,** from Roček, 1980; **G-I,** from Lebedkina, 1979).

between the premaxilla and vomer develops at the end of metamorphosis and then reduces (Fig. 4**G**), as is known in a clearly-defined way only in *Xenopus* and *Ascaphus* (Lebedkina, 1979). The tendency to reduce the ethmoidal endoskeleton and exoskeleton, typical of adult anurans, is expressed in the weakening of the vomers, the absence of vomer-parasphenoid links and the displacement of the premaxilla by the maxilla. However, the palate in some Anura suggests recapitulation of a rhipidistian pattern. In this respect *Eopelobates leptocolaptus* from the Upper Carboniferous is interesting (Roček, 1980). In this form, well-developed premaxillaries are preserved. They may contact the vomers (Fig. 4), which in this form are of primitive shape, being short, widely spaced, and well separated from the parasphenoid. *Amphibamus grandiceps* from Mazon Creek, noted above, adds to this picture. It probably represents a juvenile dissorophoid form (Bolt, 1979), and displays the primitive gnathostome condition for the palate — an undivided palatal arch covered by a shagreen of teeth.

In the presence of a shagreen of denticles this form resembles the ancient crossopterygian *Youngolepis.* Palatal tooth arrangement in *Amphibamus grandiceps* 'is also similar to that of lissamphibians, which commonly have a row of bicuspid pedicellate palatal teeth in a short row sub-parallel to the marginal tooth row' (Bolt, 1979: 555). It is for this reason that juvenile dissorophids can be regarded as lissamphibian ancestors. According to Bolt (1979) juvenile features of the ancestors appear in the adult stage of the descendants as a result of paedomorphic evolution (Gould, 1977), and lissamphibians can be viewed as paedomorphic dissorophoids.

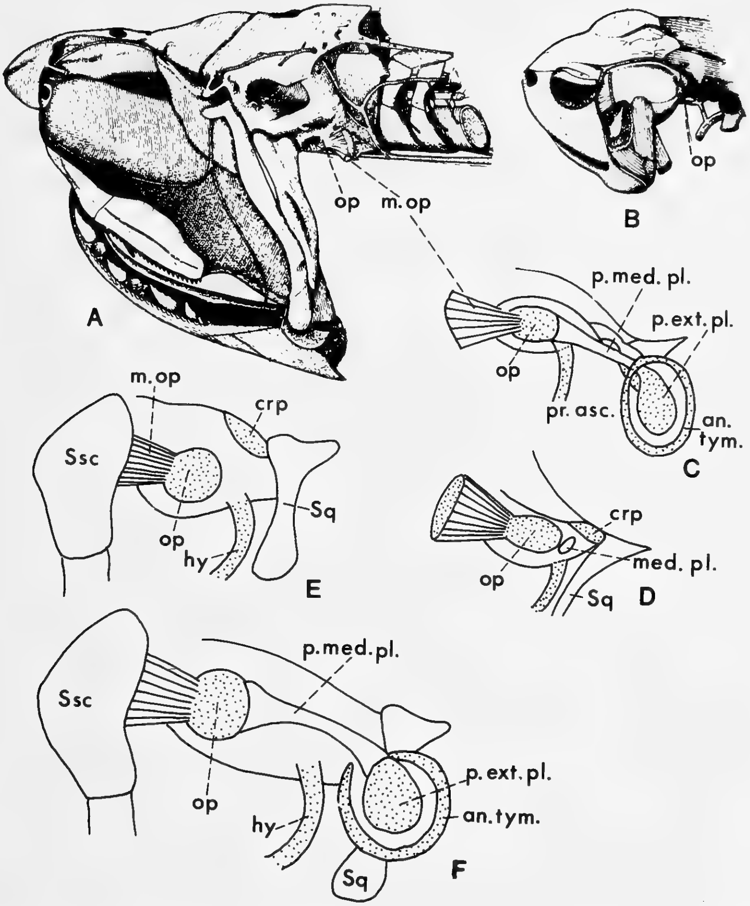

Fig. 5. Structure of the otic region in rhipidistians and anurans. **A**, *Eusthenopteron foordi;* **B**, *Pelobates fuscus;* **C-F**, middle ear structure (**C**, *Rana ricketti;* **D**, reduced state in *Bombina orientalis;* **E**, reduced state in *Microhyla heymonsi;* **F**, *M. berdmorei. an. tym,* annulus tympanicus; *crp,* crista parotica; *hy,* hyoideum; *m. op,* opercular muscle; *op,* opercula; *p.ext.pl,* pars externa plectri; *p.med.pl,* pars media plectri; *Sq*, squamosal; *Ssc*, suprascapula. (**A,B**, from Jarvik, 1975; **C-F**, from Smirnov, 1983).

This example shows that various different comparisons must be made when homologies are looked for between urodeles or anurans and ancient amphibians (labyrinthodonts) or fishes, depending upon the evolutionary stability of the structures concerned. Thus we may compare adult recent forms with their larvae, adult recent with fossil forms, or recent larvae with adult fossil forms (rhipidistians in particular). The principles and advantages of such wide-ranging comparisons were discussed by Roček (1980).

The wide occurrence of heterochrony and parallelism in the fish-tetrapod transition shows that caution must be exercised in reaching any phylogenetic conclusions based on comparison of separate structures or in making direct extrapolations of recent particularities to structures observed in fossil forms. A good example to illustrate this point is the otic region of the skull. The form of the stapes and the condition of otic notch are widely used as phylogenetically significant features of early tetrapods. But the study of the middle ear in modern amphibians and lizards (by the methods of comparative anatomy, embryology, physiology and morphometry) has demonstrated considerable variability in its morpho-functional condition. Thus the operculum in the foramen ovalis is weakly developed in arboreal amphibians (Hylidae and Rhacophoridae), and a marked reduction in the middle ear may be traced in the transition from terrestrial to aquatic and burrowing amphibians (Fig. 5**C-F**).

The first stage in this transition appears to be the enlargement of the *pars externa plectri* (Smirnov, 1983). As a result the surface of the tympanic membrane becomes smaller, and its mass and rigidity increase. This leads to a reduction in frequency range acceptability. In the next stage the tympanic membrane is overlain by depressor mandibulae muscle, and the pars externa plectri increases further in size, with a reduction of the ascending process. The annulus tympanicus disappears, and the plectrum degenerates. In extreme cases (*Pelobates, Bombina, Ascaphus,* etc.) all traces of the middle ear (with exception of opercula) may disappear.

Thus, in families at different stages of phylogenetic development (Leiopelmidae, Pelobatidae, Microhylidae), different degrees of middle ear reduction are noted as a result of adaptation to a burrowing way of life *(Microhyla butleri, M. heymonsi, Pelobates fuscus)* or to the torrent-dwelling mode *(Ascaphus truei).*

It has been shown also that in a number of Anura (Hylidae, Bufonidae Microhylidae, Ranidae) the middle ear is non-functional, and completely reduced in the adult. A definitive condition of middle ear development is observed only in the mature stage. These observations on modern forms show that past evolutionary changes in middle ear structure may have been much more complex than indicated by the application of traditional principles of comparative anatomy to the study of fossils known only from adults. Morphological change at early ontogenetic (larval) stages of development, perhaps involving secondary reduction of previously evolved structures, may have significantly altered the course of evolution in the labyrinthodont middle ear. The possibility of the latter mode was demonstrated on brachiopoid labyrinthodonts (Shishkin, 1975), and the many modifications in the state of the acoustic system in recent Amphibia indicates the possibility of such modifications having occurred in fossil forms as well. As already noted, the morphofunctional analysis applied to the acoustic system of recent forms shows that caution should be exercised in applying structural principles based on recent forms to an interpretation of their possible ancestors.

Thus the otic opercula and opercular muscle have been reconstructed in *Eusthenopteron foordi* by Jarvik (1975). This is a typical representative of the Osteolepiformes which is assumed by Jarvik to be an anuran ancestor (Fig. 5**A**). However, the opercula was obviously developed as a terrestrial adaptation (Noble, 1931), probably to transmit substratum oscillations from the extremities via the shoulder girdle to the inner ear. However, *Eusthenopteron* is clearly an aquatic form, with no need for such a sound-transmitting mechanism, nor for a tympanic membrane, since the acoustic resistance of body tissues and water are practically the same (Vorob'eva and Smirnov, 1982).

It is possible that sound oscillations of lower frequencies could have been transformed into mechanical oscillations of the fish operculum, and transmitted through the hyomandibula to the inner ear liquid. However, such a mechanism would have been useful only for certain rhipidistians (e.g. *Sauripterus,* Thomson, 1966) which may be assumed to have taken occasional terrestrial excursions, but in such cases there was already a direct way of sound transmission from the limbs and through the shoulder girdle to the occipital region of the skull. The necessity for tetrapod opercula arose only when the contact between the skull and the shoulder girdle had been lost, and this happened for the first time in amphibians.

The above examples show that the fish-tetrapod transition may have been complex, and interpretations based only on the principles of classical morphology may be inadequate. These should be supplemented by morpho-functional analyses of structures, and a consideration of the ecological aspects of adaptive radiation in recent groups. Only by such a multi-faceted approach can we expect to understand the biological and functional significance of structural change, and at the same time come closer to comprehending the nature of evolutionary mechanisms. By such a complex historical approach, which traces morpho-functional and structural changes in ontogenetic and phylogenetic series of both fossil and recent forms, might we expect to develop an objective view of the phylogeny of various forms.

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Thelodont, Acanthodian, and Chondrichthyan Fossils from the Lower Devonian of southwest China

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(Communicated by A. RITCHIE)

WANG NIANZHONG. Thelodont, acanthodian, and chondrichthyan fossils from the Lower Devonian of southwest China. *Proc. Linn. Soc. N.S.W.* 107 (3), (1983) 1984: 419-441.

Thelodont, acanthodian, and chondrichthyan remains have been extracted from bone beds in the Xitun Member of the Cuifengshan Formation (Lower Devonian) in south China by treatment with acetic acid. The thelodontid *Turinia asiatica* sp. nov., and the chondrichthyans *Gualepis elegans* gen. et sp. nov., *Changolepis tricuspidus* gen. et sp. nov., *Peilepis solida* gen. et sp. nov., and *Ohiolepis ? xitunensis* sp. nov., are the first records of these groups in the Devonian of China. The acanthodians *Youngacanthus gracilis* gen. et sp. nov., Ischnacanthidae gen. indet., and *Nostolepis* sp. indet. are the first reliable reports of Devonian acanthodians from Yunnan. It is concluded that the South China block may have been closer to Baltica and North America in the Early Devonian than to the other main tectonic blocks. There may have been some primitive thelodontids before the mid-Silurian in China, from which *Hanyangaspis* Pan *et al.* (Agnatha) and some advanced thelodontids developed. The mode of development of the cephalic shield in *Hanyangaspis* may be very similar to that of heterostracans, judging from the ornamentation of the cephalic shield in *Hanyangaspis* compared to the scale crowns of *Thelodus sculptilis* Gross and *T. admirabilis* Marss, and the ornamentation of the cephalic shield in *Porophoraspis* Ritchie and Tomlinson. There are two horizons containing acanthodians in south China — in the Lower Devonian deposits of southwest China, and in the Silurian deposits of the middle and lower reaches of the Yangtze River. Climatiid and ischnacanthid remains occur in both, but there are no genera in common. The presence of chondrichthyans suggests that the Xitun Member was marginal marine.

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INTRODUCTION

Thelodont, acanthodian and elasmobranch vertebrate microfossils have not previously been recorded from the Early Devonian of China, and their apparent absence has attracted some comment (e.g. Blieck and Goujet, 1978; Young, 1981, 1982). It is of some interest therefore to be able to report here an abundant and diverse microvertebrate assemblage in the Xitun Member of the Cuifengshan Formation (Qujing district, Yunnan Province). At my disposal are numerous thelodont, acanthodian, and chondrichthyan scales of varying size and shape, a few fragments of acanthodian dentigerous jaw bones, and several isolated chondrichthyan teeth. All were extracted by treatment with dilute acetic acid from samples of greenish-grey argillaceous limestone or greenish-yellow siltstone from the Xitun Member. As well as thelodonts, acanthodians, and chondrichthyans, there are, in the same member, other microvertebrate fossils (Actinopterygii, Crossopterygii, Dipnoi, Placodermi, etc.). These will be dealt with elsewhere. Material described below is housed in the Institute of Vertebrate Palaeontology and Palaeoanthropology (IVPP), Beijing, China.

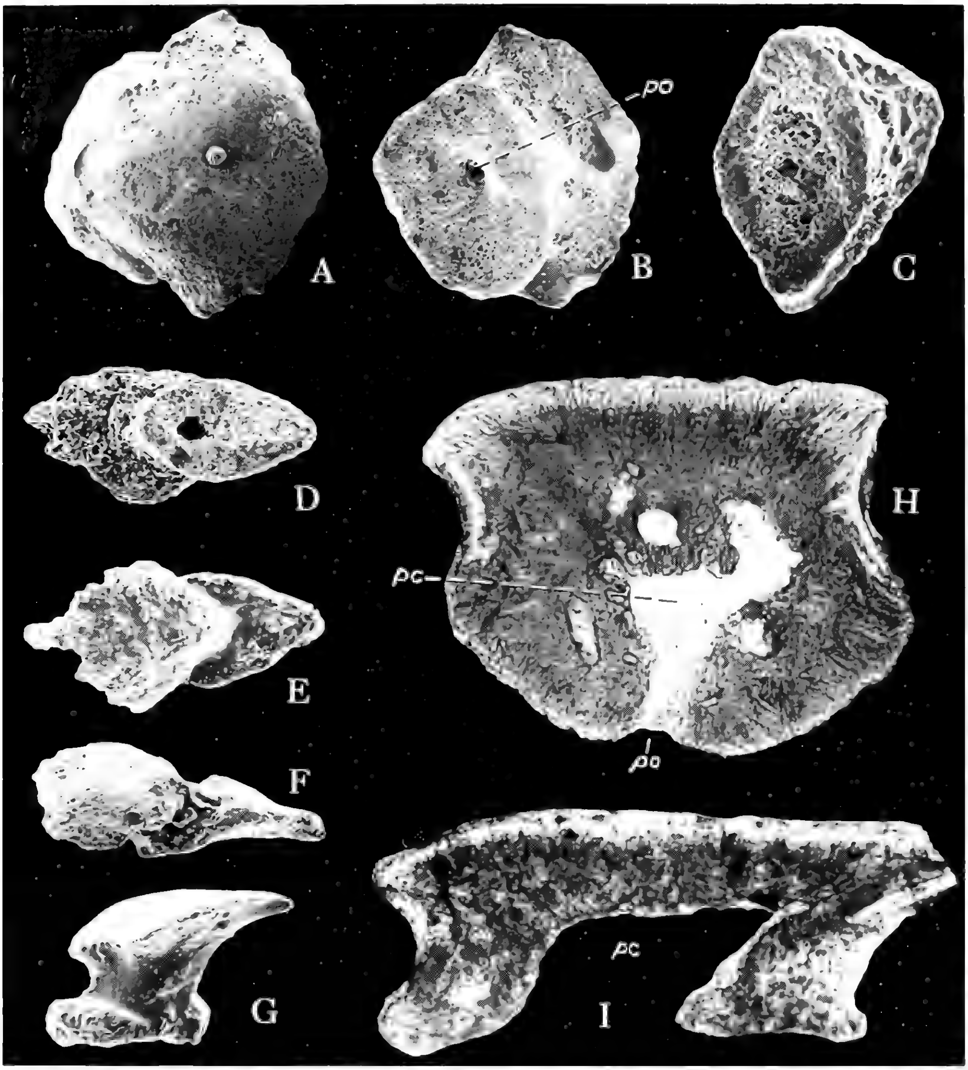


Fig. 1. Turinia asiatica sp. nov. V7215. **A** and **B**, No. 7 (× 75), head scale. **A**, crown view; **B**, basal view. **C**, No. 9 (× 105), basal view of a body scale. **D**, No. 2 (× 71), basal view of a body scale. **E**, No. 3 (× 71), crown view of a body scale. **F**, No. 4 (× 71), crown view of a body scale. **G**, No. 5 (× 71), lateral view of a transitional scale. **H**, No. 1 (× 113), vertical longitudinal section of a body scale. **I**, No. 8 (× 113), vertical longitudinal section of a body scale. *pc,* pulp cavity; *po,* pulp opening.

SYSTEMATIC DESCRIPTION

Subclass THELODONTI
Order THELODONTIDA
Family TURINIIDAE Obruchev 1964
Genus *TURINIA* Traquair 1896
Turinia asiatica sp. nov.
Figs 1, 2

Diagnosis: Small head, transitional, and body scale types. Crowns rounded, elliptical,

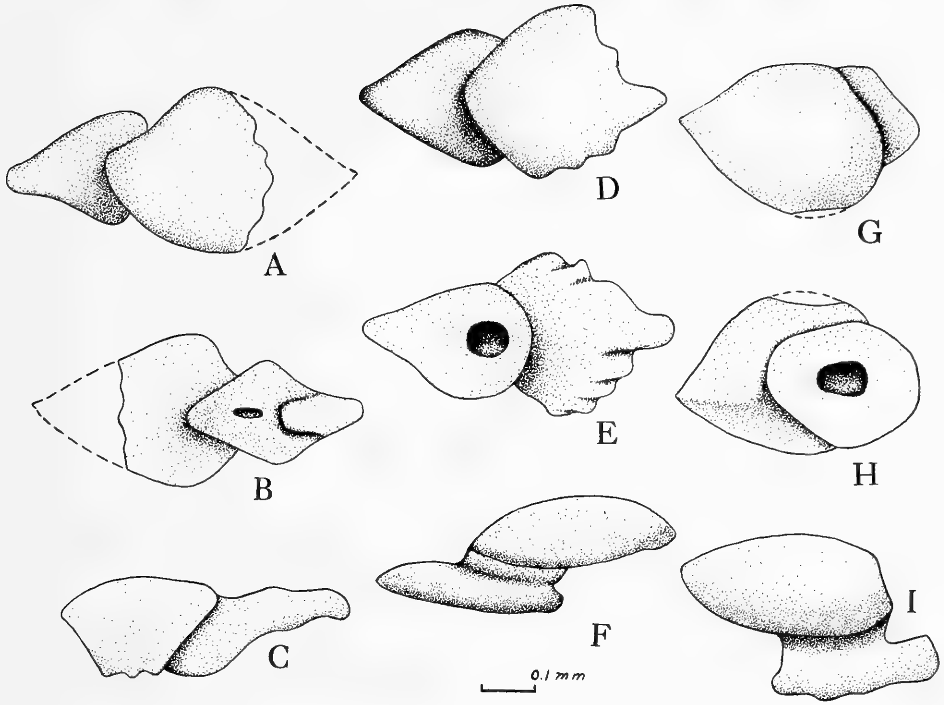


Fig. 2. Turinia asiatica sp. nov. V7215. **A-C**, crown, basal, and lateral views of No. 4: **D-F**, crown, basal, and lateral views of a body scale, No. 3; **G-I**, crown, basal and lateral views of a transitional scale, No. 5 (all × 70).

or rhombic, with a smooth unornamented surface and smooth or dentate posterolateral margins; wall of scale neck smooth; scale base rounded, elliptical, or irregular in shape, with a prominent anterior process; *Thelodus*-type histology (*sensu* Gross, 1967), with a large pulp cavity and a small central pulp opening; dentine tubules long and densely distributed.

Holotype: V7215.3, a body scale.

Other material. V7215.7, a head scale; V7215.5, a transitional scale, and V7215.2,4,9, three body scales; V7215.1, a longitudinal section of a head scale, and V7215.8, a longitudinal section of a body scale.

Locality and Horizon. Xitun member of the Cuifengshan Formation (Lower Devonian), Qujing district, East Yunnan, China.

Description: The small scales range in maximum rostrocaudal length from 0.30 to 0.60 mm (Table 1). They may be separated into head, transitional, and body scale types. The head scales have a rounded crown, with a simple smooth and unornamented crown surface. The wall of the scale neck is smooth and the base is rounded with a large pulp cavity of *Thelodus*-type (Gross, 1967; Moy-Thomas and Miles, 1971), and a small pulp opening. The transitional scales have an elliptical and slightly convex crown, with a small posterior cusp, and a shallow base with a middle-sized pulp opening. The body scales possess an elliptical or rhombic crown, with a smooth but slightly convex surface, a smooth anterolateral margin, and a smooth or dentate posterolateral edge. The wall of the neck is smooth, and the shallow base is the same depth in both anterior and posterior parts (e.g. specimens V7215.2 and 3). Commonly the base is elongated to

TABLE 1

Turinia asiatica *sp. nov. Dimensions of scales (in mm)*

V.7215	Length of crown	Breadth of crown	Length of base	Breadth of base	Depth of scale	Length of scale
2	0.04	0.28	0.35	0.18	0.20	0.53
3	0.37	0.30	0.32	0.20	0.20	0.60
4	0.35	0.30	0.30	0.20	0.20	0.60
5	0.37	0.30	0.28	0.20	0.30	0.50
7	0.50	0.50	0.30	0.35	0.35	0.55
9	0.27	0.32	0.17	0.30	0.15	0.30

form a prominent anterior process (e.g. specimen V7215.4). The base has a pulp opening of small or medium size in a posterior or central position. The dentine tubules are long and densely distributed.

Remarks: These scales resemble in some respects those of *Turinia polita* Kar.-Tal. from the Lower Devonian of Lithuania, Volynia, and Podolia, USSR (Karatajute-Talimaa, 1978), but they differ in their smaller size, in having fewer denticles at the posterolateral margin of the crown in the body scales, and in possessing more dentine tubules in the crown. There is also a resemblance, particularly in the more elongate scales, to those described by Hoppe (1931) as *Thelodus trilobatus*. This form ranges from the lower Ludlow to lower Downtonian in Europe (Turner, 1976), and may be close to the ancestry of the turiniids according to Karatajute-Talimaa (1978). With the new species described here generic assignment is uncertain, and for the present it is described as a new species of the genus *Turinia*.

Subclass ACANTHODII Owen 1846
Order CLIMATIIDA Berg 1940
Family CLIMATIIDAE Berg 1940
Genus *NOSTOLEPIS* Pander 1856
Nostolepis sp. indet.
Fig. 3

Material: V7216.1,4,5,7, and a section V7216.2, all body scales.

Locality and Horizon: As for V7215.

Description: Among the acanthodian scales of the Xitun member, one type, represented by V7216.1,4,5 and 7, comes mainly from the argillaceous limestone. These scales have more or less rhomboidal-shaped crowns which may be flat (e.g. 7) or elevated (e.g. 4). The ornamentation of the crown is of two types: a few long ridges extend from the anterior part of the crown to the posterior margin, converging posteriorly (Fig. 3**D-F**), or more and shorter ridges are restricted to the anterior part of the scale crown (Fig. 3**A-C**). The scale base is rhombic in shape, and clearly tumid. Its anterior margin may be more advanced than that of the crown (Fig. 3**D**), or it may extend forward as far as the anterior margin of the crown (Fig. 3**C**). The scale has a clear constricted neck between the crown and base. Scale dimensions are given in Table 2.

The structure of these scales is of the *Nostolepis*-type (Denison, 1979; Gross, 1940, 1947, 1957, 1971). There is a crown of mesodentine tissue which is penetrated by vascular canals, and a base of cellular bone (Fig. 3**G**).

Remarks: The material dealt with here is referable to the genus *Nostolepis* according to scale shape and structure, but it is not clear from the available material whether or not it represents a new species.

Fig. 3. Nostolepis sp. indet. V7216. **A-C**, isolated scale, No. 7. **A**, crown view; **B**, basal view, and **C**, slightly oblique lateral view (× 72). **D-F**, isolated scale, No. 4. **D**, crown view (× 96); **E**, basal view, (× 72), and **F**, lateral view (× 96). **G**, vertical longitudinal section of scale No. 2 (× 176).

Order ISCHNACANTHIDA Berg 1940
Family ISCHNACANTHIDAE Berg 1940
Genus *YOUNGACANTHUS* nov.

Diagnosis: Teeth anchylosed to the jaw bone; main tooth cusps of the dentigerous jaw bone stout, triangular in parabasal section, and with three dentine ridges at anterior, posterior, and medial margins of the main tooth cusp; each main tooth cusp having two small anterior side cusps and two small posterior side cusps, but medial side cusps are absent.

Youngacanthus gracilis sp. nov.
Figs 4,5

TABLE 2

Nostolepis *sp. indet. Dimensions of scales (in mm)*

V.7216	Length of crown	Breadth of crown	Length of base	Breadth of base	Depth of scale
7	0.65	0.60	0.60	0.60	0.30
4	0.50	0.30	0.45	0.40	0.20
1	0.60	0.50	0.50	0.60	0.30
5	0.80	0.60	0.70	0.70	0.70

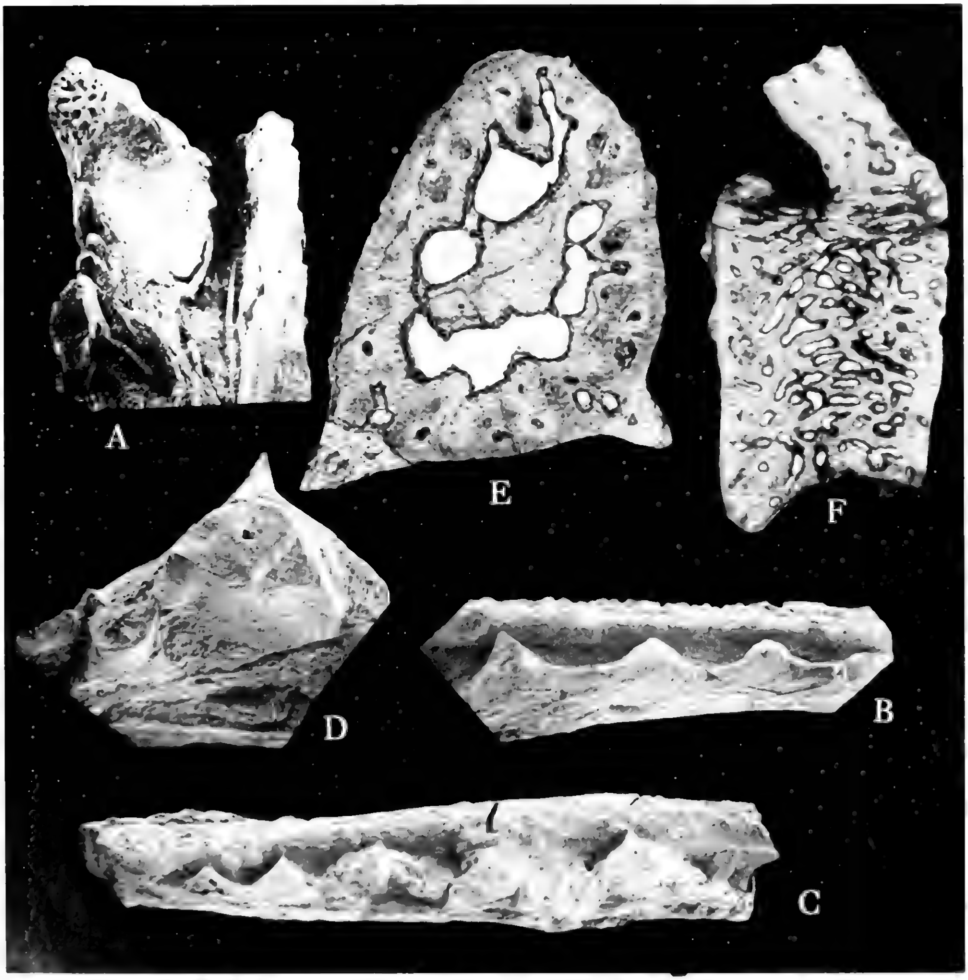


Fig. 4. Youngacanthus gracilis gen. et sp. nov. V7217. **A**, holotype, crown-medial view of part of a dentigerous e (× 14.4); **B**, crown-exterior view of part of a dentigerous jaw bone, No. 2 (× 17); **C**, crown view dentigerous jaw bone, No. 3, oriented with its anterior part to the right (× 16); **D**, detail of p in C (× 58); **E**, parabasal section of a main cusp, No. 4 (× 136); **F**, vertical transverse gerous jaw bone, No. 5 (× 32).

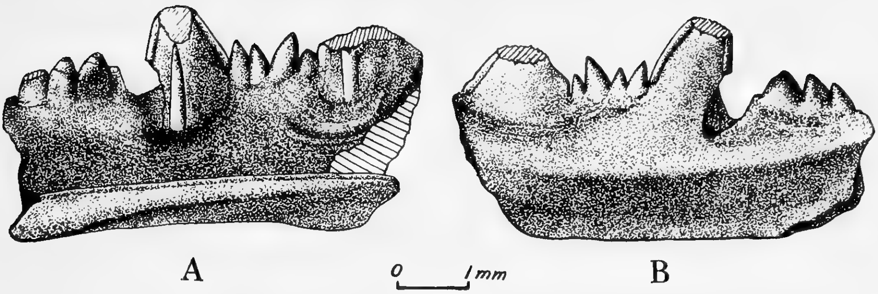


Fig. 5. Youngacanthus gracilis gen. et sp. nov. Holotype, V7217, in medial (**A**) and exterior views (**B**).

Derivation of name: After the late Professor C. C. Young, *akantha* (Gr.), a thorn, and *gracilis* (L.), slender.
Holotype: V7217.1, a fragment of dentigerous lower jaw bone.
Other material: V7217.2 and 3, two other fragments of dentigerous jaw bones; V7217.4, a parabasal section of an isolated tooth, and V7217.5, a vertical transverse section through the dentigerous jaw bone.
Locality and Horizon: As for V7215.
Diagnosis: As for genus (the only species).
Description: The dentigerous jaw bones are slender and h-shaped in transverse section. The dentigerous side is much higher than the medial side at the face of the crown. There are many tubercles on the surface of the medial side. The basal part of the jaw bone is concave upwards, perhaps a cavity for the meckelian cartilage. Numerous vascular spaces are observed in the transverse sections (Fig. 4**F**).

The teeth anchylosed to the jaw bone consist of large main tooth cusps and small anterior and posterior side-cusps. The jaw bone carries two main tooth cusps and six side tooth cusps in the holotype, five main cusps and twelve side cusps in specimen V7217.2, and four main cusps only in V7217.3. The main tooth cusps and side cusps vary in size and shape: they become smaller and show more wear towards the posterior end, so the characteristics of the main and side tooth cusps are clearer in the anterior part of the jaw bone than posteriorly.

Each cone-shaped main tooth cusp is triangular in parabasal section, and shows a pulp cavity divided into several small parts (V7217.4). It carries three triangular dentine ridges at its anterior, posterior, and medial sides. Only the ridges on the anterior and posterior sides extend upwards to the tip of the tooth. Each main tooth cusp has two smaller side cusps anteriorly, and two posteriorly, which have less developed anterior and posterior ridges, and lack the medial ridge (in the holotype and V7217.2).
Remarks: The new dentigerous jaw bones are in general shape similar to those of *Xylacanthus grandis* Ørvig from the Lower Devonian of Spitsbergen (Ørvig, 1967), but can be distinguished by the shape of the main tooth cusps in transverse section, and the presence of three stout dentine ridges on the main tooth cusps, and of two small tooth cusps attached posteriorly. They also differ slightly from *Persacanthus* (Janvier, 1977), but are clearly referable to the Ischnacanthida, the only acanthodians possessing such dentigerous jaw bones (Moy-Thomas and Miles, 1971; Denison, 1976, 1978).

genus indet.
Figs 6-8

Material: V7218.1,3,6 and 8, four isolated scales, and V7218.4 and 7, two longitudinal sections.

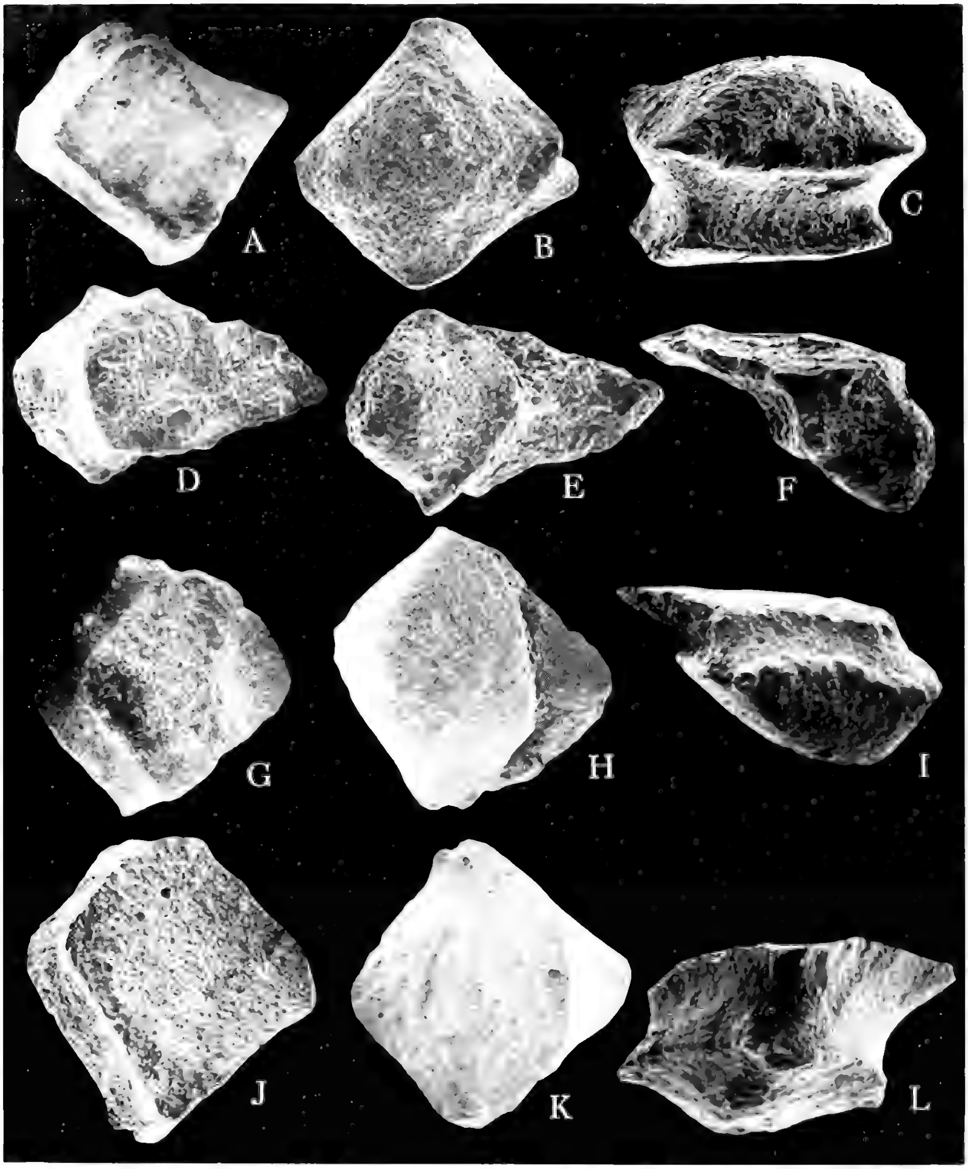


Fig. 6. Ischnacanthidae gen. indet. V7218, body scales. **A-C**, No. 6 (**A**, × 36; **B**, × 38; **C**, × 48). **D-F**, No 3 (× 67). **G-I**, No. 1 (× 34). **J-L**, No. 8 (× 42). **A, D, G,** and **J,** crown views: **B, E, H,** and **K,** basal views; **C, F, I,** and **L**, lateral views.

Locality and Horizon: As for V7215.
Description: Of the many isolated scales at my disposal from the Xitun member, most are acanthodian scales of which the type exemplified by V7218 is the most common.

These scales have a more or less rhomboidal-shaped crown which is flat and smooth. The length of the crown may equal its breadth or be somewhat longer. The tumid scale base is longer than broad. The scale neck is clearly constricted. The an-

TABLE 3

Ischnacanthid indet. Dimensions of scales (in mm)

V 7218	Length of crown	Breadth of crown	Length of base	Breadth of base	Depth of scale
1	1.20	1.20	1.00	1.80	0.50
3	0.60	0.30	0.30	0.40	0.30
6	0.90	0.80	0.95	0.95	0.60
8	1.10	1.10	0.80	1.00	0.50

terior edge of the base is more advanced than that of the crown, but the posterior edge of the crown extends backwards past the edge of the base. Scale dimensions are given in Table 3.

The scales are made up of concentric layers of dentinous tissue in the crown, and of concentric layers of bone tissue in the scale base. The thick base of acellular bone lacks a pulp cavity. This structure is clearly of the acanthodian type.

Remarks. The scales described here are similar to *Ischnacanthus* in their flat and smooth scale crowns, and also resemble scales of *Acanthodes*. However, they are possibly not congeneric with either form, and may be referable to *Youngacanthus* gen. nov.

Subclass CHONDRICHTHYES

Genus *GUALEPIS* nov.

Diagnosis: Scales of varying size, with crowns more or less triangular in shape, and ornamented either with anterior stout ridges and corresponding deep furrows, or with a series of concentric minor ribs and carrying a dentate posterior margin; constricted neck with a few pulp openings behind the neck; rhomboidal scale base funnel-shaped, flat, or convex in ventral view, and having a small pulp cavity.

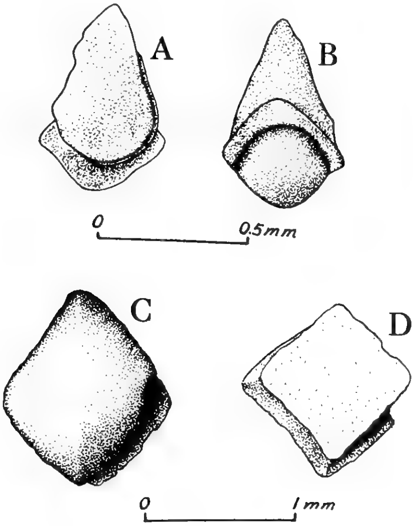


Fig. 7. Ischnacanthidae gen. indet. V7218, body scales. **A**, **B**, No. 3, crown view (**A**) and basal view (**B**), oriented with its posterior part upwards; **C**, **D**, No. 2, crown view (**D**) and basal view (**C**), oriented with its posterior part to the right.

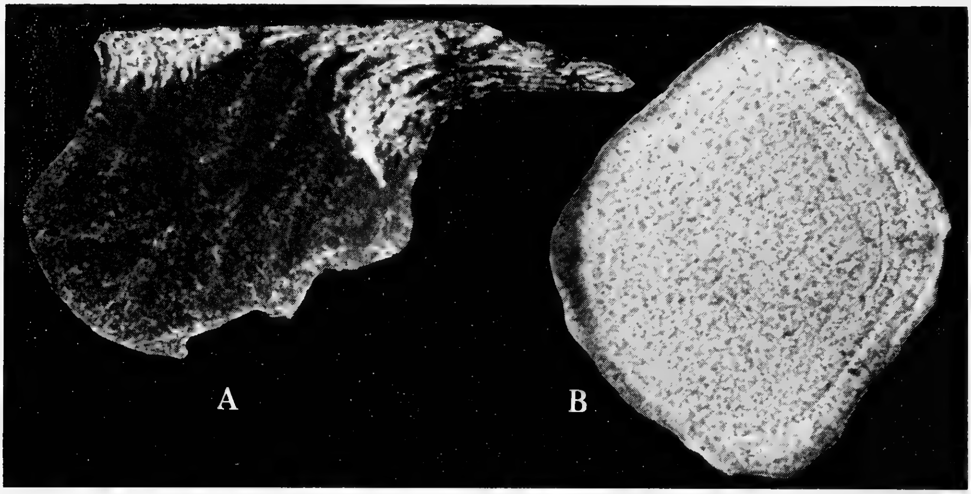


Fig. 8. Ischnacanthidae gen. indet. V7218. **A**, vertical longitudinal section of a body scale, No. 4 (× 134); **B**, crown horizontal section of a body scale, No. 7 (× 58.5).

Gualepis elegans sp. nov.

Figs 9-11

Derivation of name: After the late Professor M. R. Guo, previously Head of Academia Sinica; *lepis* (Gr.), a scale, and *elegans* (L.), fine.

Holotype: V7219.8, an old scale.

Paratype: V7219.3, a juvenile scale.

Other material: Many isolated scales of juvenile, adult, and old stages of growth.

Locality and Horizon: As for V7215.

Description: According to their stage of development and derivation from different areas of the body, the scales vary in size and shape. The juvenile scale has a thin crown and base, and a very clear neck. The crown is more or less triangular in shape. The length and width of the smallest scales are about the same, but with larger scales the width of the crown increases (Table 4). When the crown is broader than long it ranges in maximum rostrocaudal length from about 0.30 to 0.55 mm, and in maximum transverse breadth from about 0.40 to 0.80 mm. The crown has several anterior ridges and corresponding deep furrows which extend back to the middle of the crown surface. The number of ridges and furrows increases with the development of the scale. For example, there is only one furrow in specimen V7219.7, four ridges and three furrows in V7219.5, and six ridges and five furrows in the paratype. The crown carries a dentate posterior margin, in which the number of posterior denticles increases with scale growth. The paratype has about 19 denticles, but other scales may have a smooth posterior margin (e.g. V7219.5). The interior surface of the crown is smooth in all juvenile scales.

The juvenile scale has a clearly constricted neck, to which the ridges and furrows of the crown may extend (e.g. V7219.5). Visible posteriorly is a variable number of vascular canal openings between the crown and base (Ørvig, 1966). Specimen V7219.6, for example, shows 7 neck openings (*no,* Fig. 9**H, I**).

The rhomboidal base of the juvenile scale is more or less funnel-shaped in ventral view. The bases are broader than long and range in maximum rostrocaudal length from 0.20 to 0.30 mm, and in maximum transverse breadth from 0.30 to 0.60 mm.

TABLE 4

Gualepis elegans *gen. et sp. nov. Dimensions of scales (in mm)*

V 7219	Length of crown	Breadth of crown	Length of base	Breadth of base	Depth of scale
3	0.55	0.80	0.30	0.60	0.25
5	0.40	0.70	0.30	0.60	0.30
2	0.30	0.40	0.20	0.30	0.25
6	0.50	0.70	0.30	0.45	0.20
4	0.40	0.60	0.25	0.40	0.25
7	0.30	0.40	0.30	0.40	0.30
1	0.60	0.85	0.50	0.70	0.40
8	0.70	1.10	0.30	0.80	0.40
10	0.70	0.90	0.45	0.90	0.20
9	0.50	0.60	0.30	0.50	0.20
11	1.10	1.40	0.60	1.10	0.30
12	0.80	1.00	0.40	0.80	0.40
13	0.50	0.90	0.40	0.60	0.15

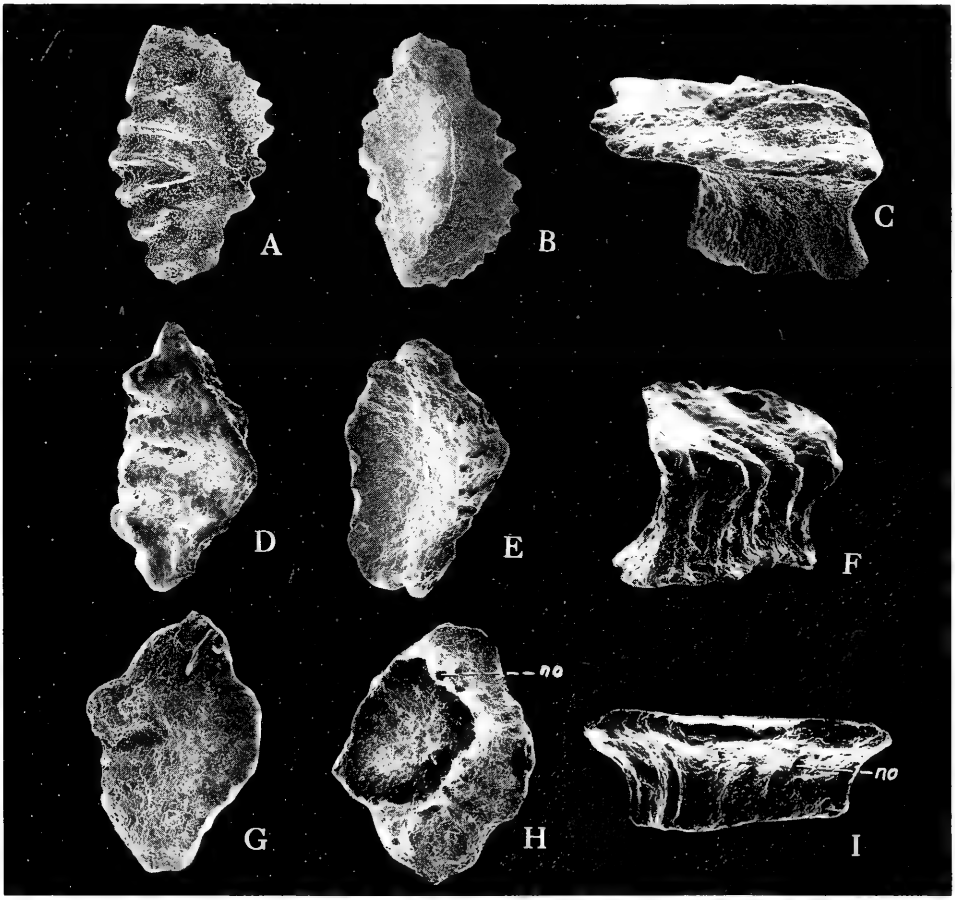
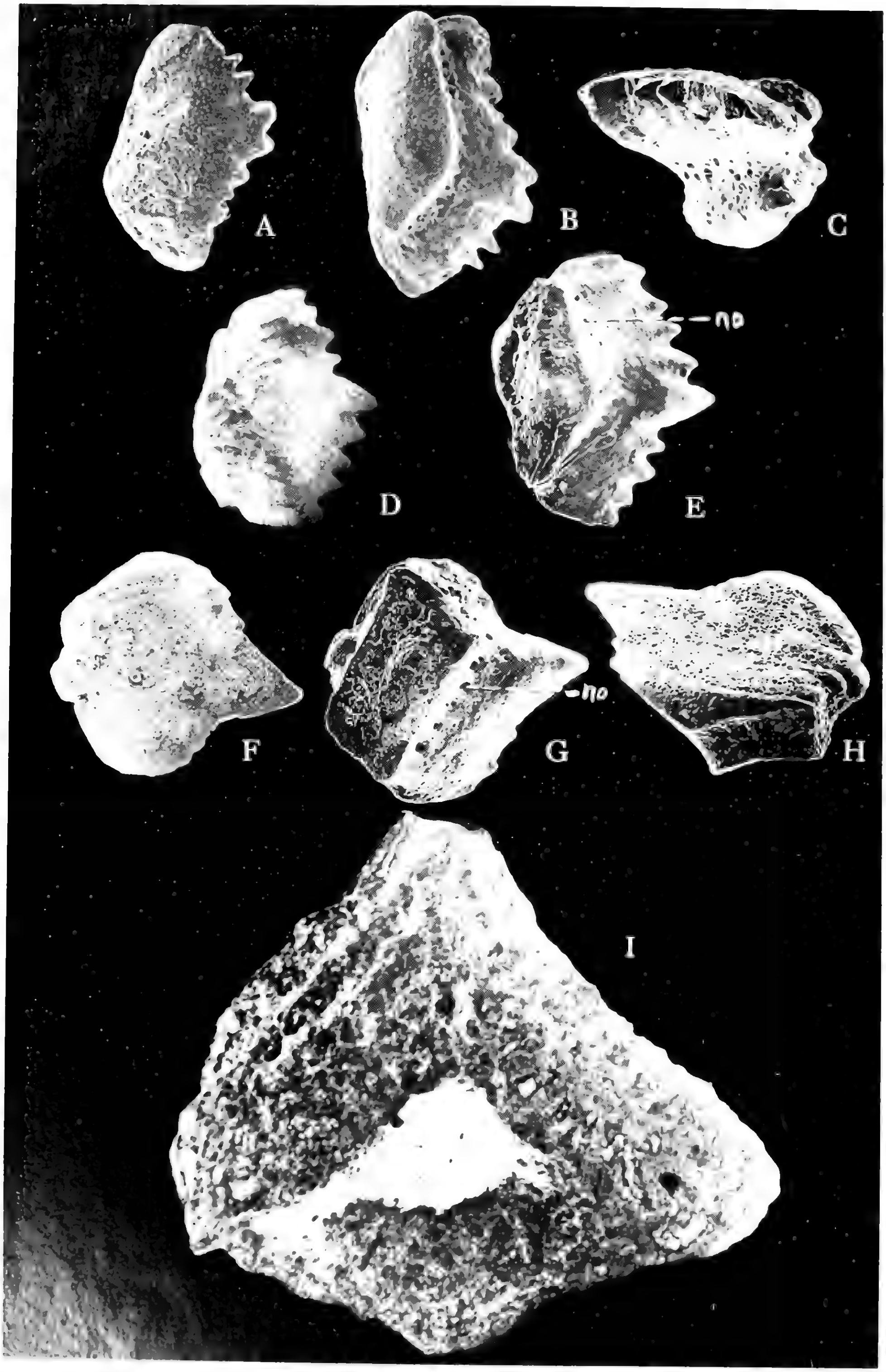


Fig. 9. Gualepis elegans gen. et sp. nov. V7219, juvenile scales. **A-C,** paratype (**A, B** × 51; **C,** × 80). **D-F,** No. 5 (× 55). **G-I,** No. 6 (× 68). **A, D,** and **G,** crown views; **B, E,** and **H,** basal views; **C,** oblique lateral view; **F,** oblique anterior view; **I,** posterior view. *no,* neck opening.


A
B
C
no
D
E
F
no
G
H
I

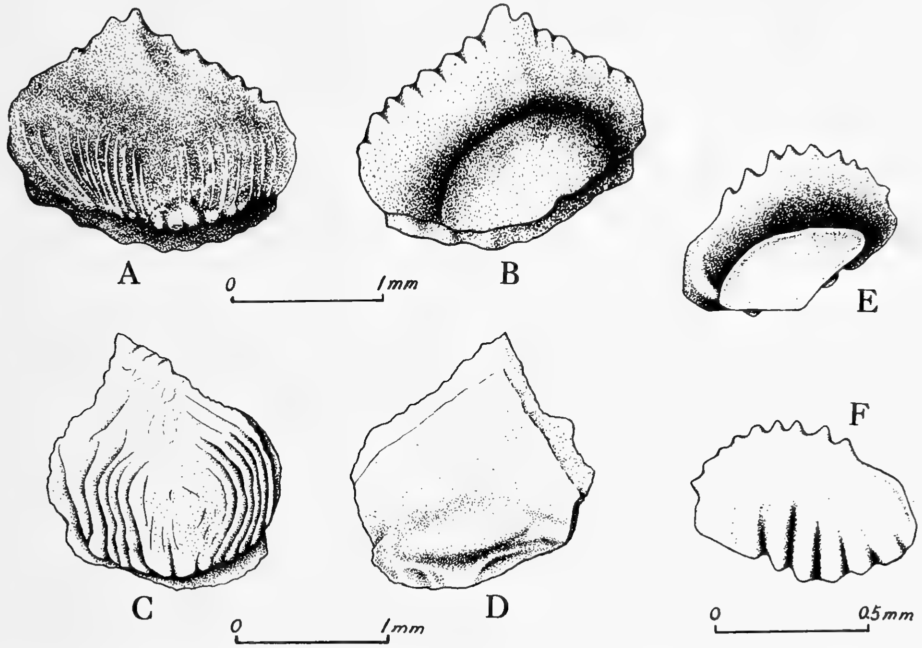


Fig. 11. Gualepis elegans gen. et sp. nov. V7219. **A, B**, an old scale, No. 1; **C, D**, an old scale, No. 4; **E, F**, paratype, a juvenile scale. **A, C,** and **F**, crown views; **B, D**, and **E**, basal views.

In length and breadth the scale crown equals the base in the smallest juvenile scales, but the scale crown is proportionately larger than the base in larger juvenile scales. The depth of juvenile scales is fairly constant (0.20 to 0.30 mm deep).

In mature and old scales the crown and base are thicker, and the crown is bigger than the base. The stout ridges of the juvenile stage decrease in number in adult and old scales (e.g. the holotype), or fuse to form a large anterior point as in specimen V7219.12. Some concentric minor ribs may develop on the exterior surface of the crown (e.g. V7219.12 has 7 ribs on each side). Posteriorly the crown can carry a few stout denticles. The maximum rostrocaudal length of the crown varies from 0.50 to 1.10 mm, and the maximum transverse breadth from 0.60 to 1.40 mm.

The rhomboidal scale base is again broader than long, with a maximum rostrocaudal length between 0.30 and 0.60 mm, and maximum transverse breadth between 0.50 and 1.10 mm. The base is flat or convex in basal view.

Remarks: These new scales recall in their general shape *Elegestolepis grossi* Kar.-Tal. from the Upper Silurian of Tuva (Karatajute-Talimaa, 1973), but they differ in having a more or less triangular crown, and carrying the characteristic ornamentation on the exterior surface of the crown with a few denticles along its posterior margin, and in possessing more neck openings. For these reasons a new genus and species has been erected. The affinities of such scales within the Chondrichthyes are at present uncertain.

Fig. 10. Gualepis elegans gen. et sp. nov. V7219. **A-C**, holotype, an old scale. **A**, crown view (× 38); **B**, basal view (× 41); **C**, lateral view (× 57.5). **D, E**, an old scale, No. 9 (**D**, × 38; **E**, × 43). **F-H**, an adult scale, No. 7 (**F**, × 62; **G**, × 67; **H**, × 80). **I**, crown horizontal section of an old scale, No. 2 (× 80).

TABLE 5

Changolepis tricuspidus *gen. et sp. nov. Dimensions of scales (in mm)*

V 7220	Length of crown	Breadth of crown	Length of base	Breadth of base	Depth of scale
1	0.70	0.80	0.50	0.70	0.45
2	0.70	0.80	0.60	0.70	0.30
3	0.80	0.90	0.80	0.85	0.50
4	0.50	0.60	0.35	0.50	0.30
5	0.70	0.80	0.50	0.70	0.20

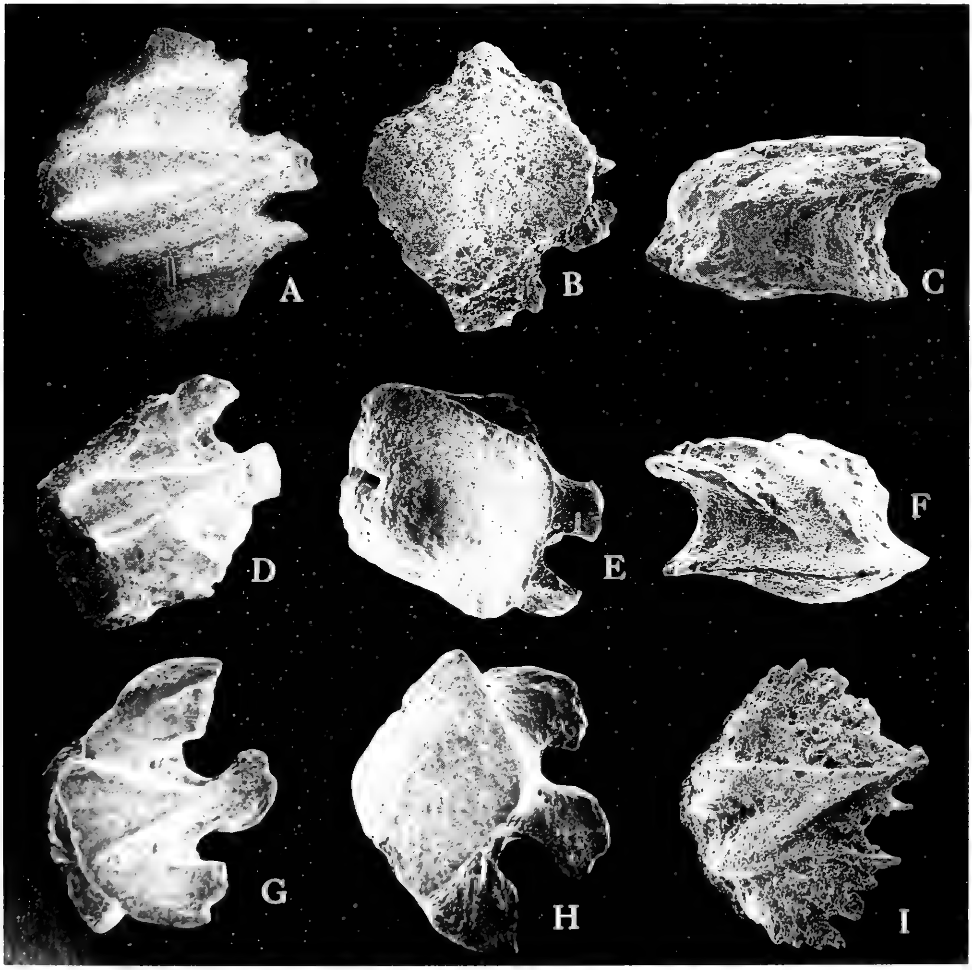


Fig. 12. Changolepis tricuspidus gen. et sp. nov. V7220. **A-C**, paratype (× 52); **D-F**, No. 8 (× 40); **G, H**, holotype (× 40); **I**, No. 9 (× 48). **A, D, G**, and **I**, crown views; **B, E**, and **H**, basal views; **C** and **F**, lateral view.

Genus *CHANGOLEPIS* nov.

Diagnosis: Scale having a more or less rhomboidal crown, with ornamentation on the exterior surface divided into three parts: a strongly convex central rib which forms a long main cusp posteriorly, and lower lateral ribs which have shorter posterior cusps; neck region well defined, with a few neck openings; rhomboidal scale base funnel-shaped, flat, or convex in basal view.

Changolepis tricuspidus sp. nov.

Fig. 12

Derivation of name: After the late Professor C. L. Chang, who first systematically studied fish fossils in China, and *tricuspidis* (L.), three pointed.
Holotype: V7220.1, an old scale.
Paratype: V7220.2, a juvenile scale.
Other material: Eight isolated scales at juvenile, adult, and old stages of growth.
Locality and Horizon: As for V7215.
Description: The specimens included here are isolated scales. They have a more or less rhomboidal crown which is slightly broader than long, and ranges in maximum rostrocaudal length from 0.50 to 0.80 mm, and in maximum transverse breadth from 0.60 to 0.90 mm (Table 5). The ornamentation on the exterior surface of the crown is divided into three parts: a strongly convex central rib forms a long main cusp posteriorly, and two lower lateral ribs have shorter posterior cusps. The neck is constricted, and posteriorly has a clear neck opening between the crown and base (e.g. specimen V7220.3). The rhomboidal base is broader than long, and varies in maximum rostrocaudal length from 0.35 to 0.80 mm, and in maximum transverse breadth from 0.50 to 0.85 mm. The shape of the base in basal view is variable in different scales; it is funnel-shaped in V7220.5, flat in V7220.4, convex anteriorly and flat posteriorly in V7220.2 and 3, and slightly convex in V7220.1.
Remarks: These scales are similar to the placoid scales described from the Middle Permian of Japan (Reif and Goto, 1979), but they differ greatly from the latter in many characters, in particular in the shape of the scale neck and base. They are therefore proposed as a new scale form, *Changolepis tricuspidus* gen. et sp. nov.

Genus indet.

Fig. 13

Material: Four isolated teeth, two complete (V7221.1 and 2), and two incomplete (V7221.3 and 4).

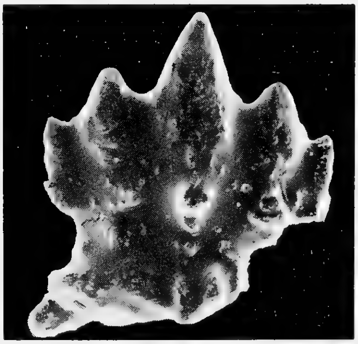


Fig. 13. Chondrichthyan? indet. V7221, an isolated tooth (× 60).

TABLE 6

Chondrichthyan? indet. Dimensions of teeth (in mm)

V 7221	Maximum breadth of tooth	Depth of main cusp	Breadth of base in main cusp	Depth of interior side cusps	Depth of exterior side cusps
1	0.60	0.50	0.22	0.30	0.20
2	0.68	0.65	0.35	0.40	0.14

Locality and Horizon: As for V7215.

Description: These four teeth vary in size (Table 6), but have the same shape, with a relatively small base and smooth, conical cusps. There is a high central cusp, and two pairs of low side-cusps of which the outer cusps are the smaller. The tooth consists of a dentine crown covered by a shiny, very hard, enamel-like substance. The base is usually broken, but a few openings of vascular canals can be observed. A few tubercles between the cusps and the base are arranged in two rows: smaller ones near the cusps, and larger near the base. Perhaps the connective tissue was attached to these tubercles.

Remarks: These specimens show some resemblance to teeth or denticles of elasmobranchs, for example the Carboniferous form *Symmorium* Cope. On the other hand they are not dissimilar to some figured teeth of climatiid acanthodians (e.g. Denison, 1979: fig. 13A). If the chondrichthyan affinities of these teeth are confirmed, they may prove to belong either to *Gualepis,* or to *Changolepis.*

Genus *PEILEPIS* nov.

Diagnosis: Scales with an elliptical crown, bifurcated posteriorly; surface of crown with three flutings and some minor ribbings; scale base flat and rhombic-shaped; scale neck well defined, with three small posterior neck openings; pulp cavity large and wide.

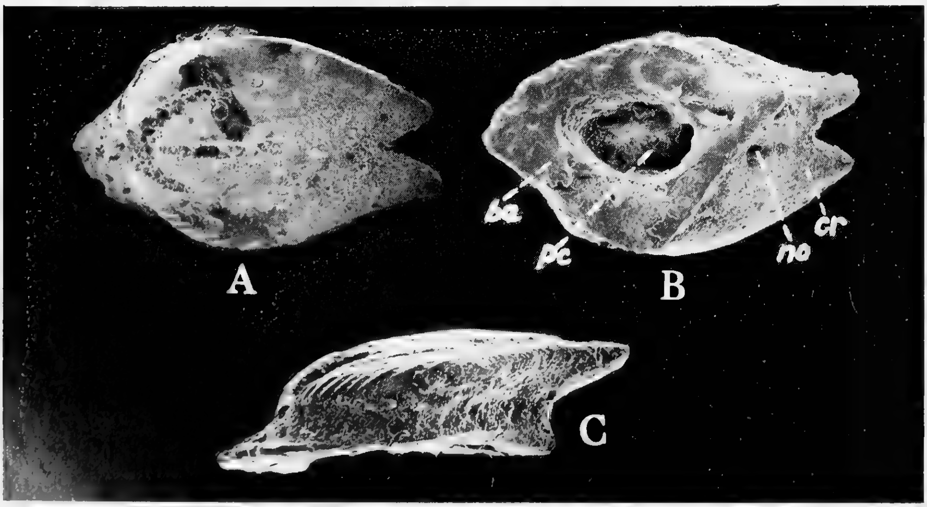


Fig. 14. Peilepis solida gen. et sp. nov. V7222, a body scale. **A**, crown view, **B**, basal view, and **C**, latero-crown view (× 15). *ba,* base; *cr,* crown; *no,* neck opening; *pc,* pulp cavity.

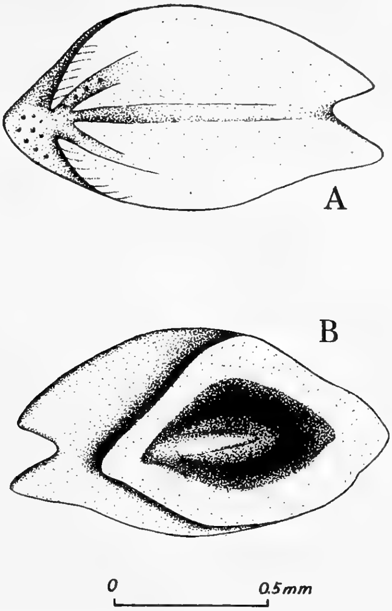


Fig. 15. Peilepis solida gen. et sp. nov. V7222. **A**, crown view; **B**, basal view.

Peilepis solida sp. nov.
Figs 14, 15

Derivation of name: After the late Professor Pei, and *solidum* (L.), dense.
Diagnosis: As for genus (only species).
Holotype: V7222, a body scale.
Locality and Horizon: As for V7215.
Description: This complete isolated scale is composed of a scale crown, base, and neck region. The crown is elliptical and flat, with a maximum rostrocaudal length of 1.1 mm, and maximum transverse breadth of 0.75 mm. There are three flutings on the anterior part of the crown surface. The middle one is longer than the two V-shaped lateral ones. There are also 14 fine parallel ribbings on the anterolateral margins. The posterior part of the crown is bifurcated and extends back over the base. The base is flat, and approximately rhombic in shape. Its maximum rostrocaudal length is 1.0 mm, and its maximum transverse breadth is 0.65 mm. The anterior part of the base extends in front of the crown. The base possesses a large, wide, elliptical pulp opening, 0.5 mm long and 0.3 mm wide. The scale neck is distinct, and carries posteriorly three small rounded foramina (*no,* Fig. 14**B**).
Remarks: Is is clear that this scale belongs to a chondrichthyan, but there is no previously described material resembling this scale. It differs from *Gualepis elegans* gen. et sp. nov. and the other kinds of chondrichthyan scales produced from the same layer in having an elliptical crown, bifurcated posteriorly, with a special ornamentation, and a large wide pulp cavity. A new scale genus and species has therefore been erected.

Genus *OHIOLEPIS* ? Wells 1944
Ohiolepis? xitunensis sp. nov.
Figs 16, 17

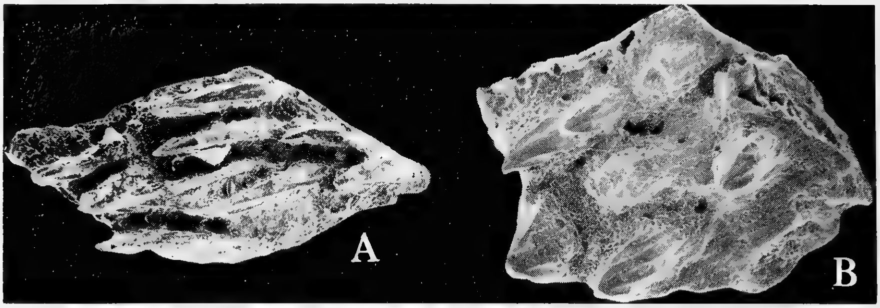


Fig. 16. Ohiolepis? xitunensis sp. nov. V7223. **A**, complete scale, crown view, No. 1 (× 30); **B**, incomplete scale, crown view (× 50).

Diagnosis: A complex scale of rhomboidal shape and consisting of denticles arranged in four rows, which slope backwards, with spaces between rows and between adjacent denticles; each cone-shaped denticle covered by a thin layer of dentinous tissue and carrying a few ribs; base of the scale flat, with a clear, central part in ventral view.
Holotype: V7233.1, a complete scale.
Other material: V7223.2, an incomplete scale.
Locality and Horizon: As for V7215.
Description: The holotype is a complete, highly specialized complex scale. It has a rhomboidal base, giving the scale its rhomboidal shape. Its maximum rostrocaudal length is 2 mm, and its maximum transverse breadth is 0.9 mm. The scale crown consists of nine denticles arranged in four rostrocaudal rows which slope backwards. The tips of the most posterior denticles project over the posterior margin of the scale. There are spaces between adjacent rows and adjacent denticles. Each cone-shaped denticle is covered by a thin dentinous layer which carries three to five longitudinal ribs at its surface. The base of the scale is flat, and possesses in ventral view a clear central part which perhaps contains all pulp openings of the denticles.
Remarks: These scales show some resemblance to those of *Ohiolepis* (e.g. Gross, 1973: pl. 31), to which this new species is provisionally referred for the purposes of description. It is certainly not conspecific with *Ohiolepis newberryi* Wells from the Middle Devonian of Ohio, USA, which differs in the shape of the denticles, and the shape and structure of the base. On the other hand the rhomboidal shape, and the pores opening to the surface between the denticles, are somewhat reminiscent of early teleostome scales (e.g. Gross, 1969). More material is required to permit a histological examination of this scale type, so that its proper affinity can be established. For the present it is tentatively included with the other chondrichthyan scales from the Xitun member.

DISCUSSION

Many areas of the world were apparently not part of the main tectonic blocks of Laurentia, Angaraland, and Gondwanaland, yet these may have played a critical role in providing terrestrial connections between the major tectonic blocks (Turner and Tarling, 1982). Such an example is the South Chinese block. The new thelodont, acanthodian and chondrichthyan remains from the Lower Devonian of southwest China should provide some evidence of this.

Turinia asiatica sp. nov. has been compared with *Turinia polita,* Kar.-Tal. from the Lower Devonian of Lithuania, Volynia, and Podolia, USSR, and *Thelodus trilobata*

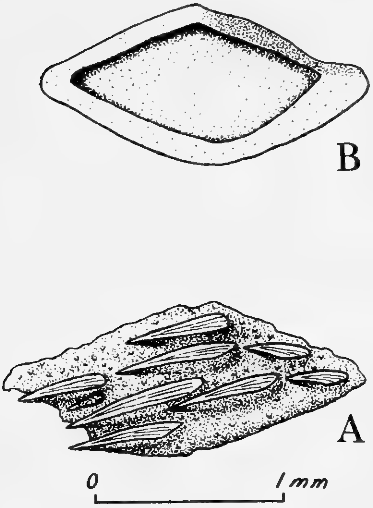


Fig. 17. Ohiolepis? xitunensis sp. nov. V7223, No. 1. **A**, crown view; **B**, basal view.

from the Ludlow and lower Downtonian of Europe. *Youngacanthus gracilis* gen. et sp. nov. resembles *Xylacanthus grandis* Ørvig from the Lower Devonian of Spitsbergen, and *Gualepis elegans* gen. et sp. nov. is similar to *Elegestolepis grossi* Kar.-Tal. from the Upper Silurian of Tuva, USSR.

In addition, the crossopterygian *Youngolepis praecursor* Zhang and Yu (1981) resembles *Powichthys* Jessen from the Lower Devonian of the Canadian Arctic, and *Szelepis yunnanensis* Liu (1979) is similar to *Kujdanowiaspis* from the Lower Devonian of Podolia.

In such circumstances there is reason to believe that the vertebrate fauna in the Xitun Member shows affinity to that of Baltica and North America in the Early Devonian. Thus, the relation between the South China block and Baltica and North America may have been closer in the Early Devonian than that between it and the other main tectonic blocks. However, it is difficult to ascribe the dispersal of thelodonts across the South China and Baltica blocks during the Early Devonian to direct land connections, or to the result of temporary land-bridge connections.

During the study of thelodont scales, the author has noted the similarity between some European Silurian thelodont scales and the ornamentation of the cephalic shield in the eugaleaspid agnathan *Hanyangaspis* Pan and Wang (1978) from the Middle Silurian of Hubei Province, China (see Pan, 1984). Each ornament tubercle of the cephalic shield in *Hanyangaspis* looks like a snowflake. It is subdivided by deep furrows forming numerous fine ridges, which converge towards the centre of the tubercle and tend to bifurcate at its outer margin (Fig. 18). The ornament surface is slightly convex or flat.

It is of interest that each of these tubercles is closely comparable to the crown of an individual scale in *Thelodus sculptilis* Gross (1967) or *T. admirabilis* Marss (1982) from the late Ludlovian to Early Devonian in Baltica and Western Russia, and to the ornament of *Porophoraspis crenulata* Ritchie and Tomlinson (1977) from the Middle Ordovician of Australia. This could indicate that the cephalic shield of forms like *Hanyangaspis* or *Latirostraspis* Wang *et al.* (1980) from the Middle Silurian of Anhui Province, China, was derived from the coalescence of many thelodont scale-like

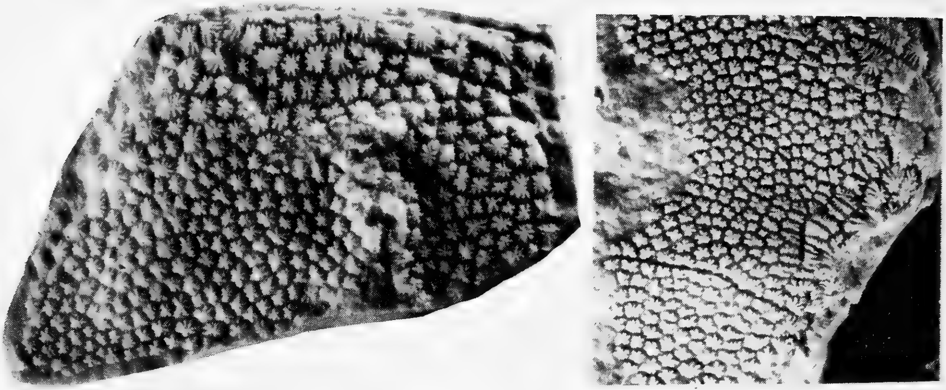


Fig. 18. Two moulds of the ornament of the cephalic shield in *Hanyangaspis* Pan and Wang (× 2).

tesserae. This might be supposed to have occurred with the crowns of the tesserae remaining free from each other, while the upper part of each base fused together, but with the limits of the lower part of each base still distinguishable on the inner surface of the shield. The mode of formation of the cephalic shield in *Hanyangaspis* may thus have been similar to that of the heterostracans. If this was the case, it is possible that there may have been some primitive thelodont-like agnathans in China before the Middle Silurian (Ordovician or Cambrian), from which *Hanyangaspis, Latirostraspis,* and the advanced thelodonts could have developed. This would assume that the cephalic shield of eugaleaspids evolved independently of the corresponding structure in other agnathan groups.

Turning now to the occurrence of acanthodian dentigerous jaw bones and scales in the Xitun Member, these are the first certain records of Early Devonian acanthodian remains from Yunnan Province. Previously in the Early Devonian of Yunnan two acanthodian species have been described: *Asiacanthus multituberculatus* T. S. Liu (1948) and *Yunnanacanthus cuifengshanensis* S. F. Liu (1973). However, Denison (1978) suggested that *Asiacanthus* and *Yunnanacanthus* may not be acanthodian remains, but probably spinal plates of Placodermi indet. After restudy and judging by new material, S. F. Liu (1982) has referred *Asiacanthus multituberculatus* and *Yunnanacanthus cuifengshanensis* to the arthrodires.

It is interesting that in South China there is another acanthodian assemblage consisting of more or less complete fin spines, from the Silurian in the region of the middle and lower reaches of the Yangtze River. The systematic position of these acanthodian genera is not clear, but it seems that they probably also belong to the Climatiida and Ischnacanthida (but are not congeneric or conspecific with those from the Xitun Member). This is based on my new finds of ischnacanthid tooth whorls and some typical acanthodian fin spines from the same horizon in this region. These new tooth whorls and fin spines will be described in another paper.

Regarding the discovery in the Xitun microvertebrate assemblage of many chondrichthyan scales of varying size and shape, it is noteworthy that these are much more abundant in the argillaceous limestones of the Xitun Member than in the siltstones. This is the first record of chondrichthyan fossils from the Devonian deposits of China. They not only enlarge the Lower Devonian vertebrate assemblage known from the Xitun Member, but give some new evidence for determining the depositional environment of the Xitun Member.

Previously, some authors (e.g. Liu and Wang, 1973) considered that the Xitun Member was predominantly a continental deposit, on the basis of its supposed freshwater fishes (e.g. *Polybranchiaspis, Yunnanolepis,* etc.). But other authors (e.g. Li and Cai, 1978) regard the Xitun Member as a marginal marine or brackish deposit (perhaps near a river mouth), on the evidence of fossil algae *(Uncatoella verticillata, Discinella cuifengshanensis),* pelecypods, and brachiopods (*Lingula* sp.).

Most Palaeozoic chondrichthyans occur in marine or paralic deposits, and may be assumed to have been marine. Only two elasmobranch groups make an exception to this; members of the ctenacanth and xenacanth sharks were either freshwater or euryhaline (Zangerl, 1981). However, these are typically Late Devonian or younger forms, and there is no clear indication that the scales described here belong to either of these groups. The new scales support the view that the Xitun Member, which is the richest layer both in diversity and abundance of Agnatha and fish fossils from the Cuifengshan Formation, was probably a marginal marine deposit, as indicated by its chondrichthyan, invertebrate, and algal fossils.

To conclude, the vertebrate assemblage from the Xitun Member of the Cuifengshan Formation (Qujing district of Yunnan), including the new forms described above, may be listed as follows:

eugaleaspids:	*Polybranchiaspis liaojiaoshanensis* Liu, 1965
	Eugaleaspis (Galeaspis) changi Liu, 1965
	Nanpanaspis microculus Liu, 1965
	Laxaspis qujingensis Liu, 1965
thelodontids:	*Turinia asiatica* sp. nov.
acanthodians:	*Youngacanthus gracilis* gen. et sp. nov.
	Ischnacanthidae gen. indet.
	Nostolepis sp. indet.
crossopterygians:	*Youngolepis praecursor* Zhang and Yu, 1981
dipnoans:	*Diabolichthys* Zhang and Yu, 1984
arthrodires:	*Szelepis yunnanensis* Liu, 1979
antiarchs:	*Yunnanolepis chii* Liu, 1963
	Y. parvus Zhang Guorui, 1978
	Phymolepis cuifengshanensis Zhang Guorui, 1978
	Qujinolepis gracilis Zhang Guorui, 1978
	Zhanjilepis aspratilis Zhang Guorui, 1978
chondrichthyans:	*Gualepis elegans* gen. et sp. nov.
	Changolepis tricuspidus gen. et sp. nov.
	Peilepis solida gen. et sp. nov.
	Ohiolepis ? xitunensis sp. nov.

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Comments on the Phylogeny and Biogeography of Antiarchs (Devonian Placoderm Fishes), and the Use of Fossils in Biogeography

G. C. YOUNG

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A new cladogram for 24 antiarch genera based on 40 synapomorphies unites the bothriolepidoids and sinolepids as sister groups. Together with asterolepidoids these form a major group of advanced antiarchs (the Euantiarcha), characterized by an armoured pectoral fin with complex proximal and distal joints. The yunnanolepids from south China are a plesiomorph sister group of euantiarchs, and the most primitive known representatives. The known distribution of these 24 genera suggests that a few (e.g. *Bothriolepis*) had different dispersal capabilities from the majority of antiarchs. An attempted designation of areas of origin for the major subgroups gives the following: asterolepidoids, an area excluding south China; bothriolepidoids plus sinolepids, south China, or south China plus Australia; yunnanolepids, south China; euantiarchs and antiarchs, cosmopolitan. In considering the types of evidence used in developing biogeographic hypotheses involving Palaeozoic fossils, it is suggested that biostratigraphic data may indicate changing barriers with time, and palaeogeography based on current geological theory is essential to relate modern fossil occurrences to past geography. Biogeographic problems concerned with taxon and area relationships should be delineated such that one of three sets of initial conditions can be specified: either there was a common ancestral biota in the areas under consideration, or one or more of the areas lacked any biota, or differences in fauna and flora between areas was at such high taxonomic levels as to be irrelevant to the problem being investigated. Assumptions about appropriate initial conditions may be influenced by geological theory. Arguments that the progression rule of Hennig is unfalsifiable, and assumes a complete fossil record, are rejected. In certain cases either a vicariance or a dispersal explanation may be indicated, using the distribution pattern of a single group, and geological theory of the areas concerned, but neither possibility can be conclusively refuted. Since this is also the case when whole biotas are investigated, it is suggested that the method of analysis outlined by Platnick and Nelson (1978) is more appropriately termed 'pattern' biogeography. The notion that vicariance is a preferred explanation, because dispersal explanations are unfalsifiable, results from the influence of geological theory (super-continent breakup) in the appraisal of modern distribution patterns. This would not necessarily apply in Palaeozoic times, where dispersal may have been a predominant cause of disjunct distributions. In such cases the same method of analysis is applicable, but an assumption that there was a common ancestral biota can be replaced by an assumption that there was a centre of origin for the taxa in question.

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INTRODUCTION

The antiarchs are an early order of jawed fishes belonging to the Placodermi, which attained a wide distribution during Middle and Late Devonian time. One genus, *Bothriolepis* Eichwald, is known from the Late Devonian of Britain, Belgium, Greenland, the Baltic area and the Russian platform, Siberia, Kazakhstan, China, Ellesmere Island, Canada, and the eastern and western United States in the northern hemisphere, and Australia and Antarctica in the southern hemisphere. Only from Africa and South America are Devonian antiarchs not yet known, although one un-

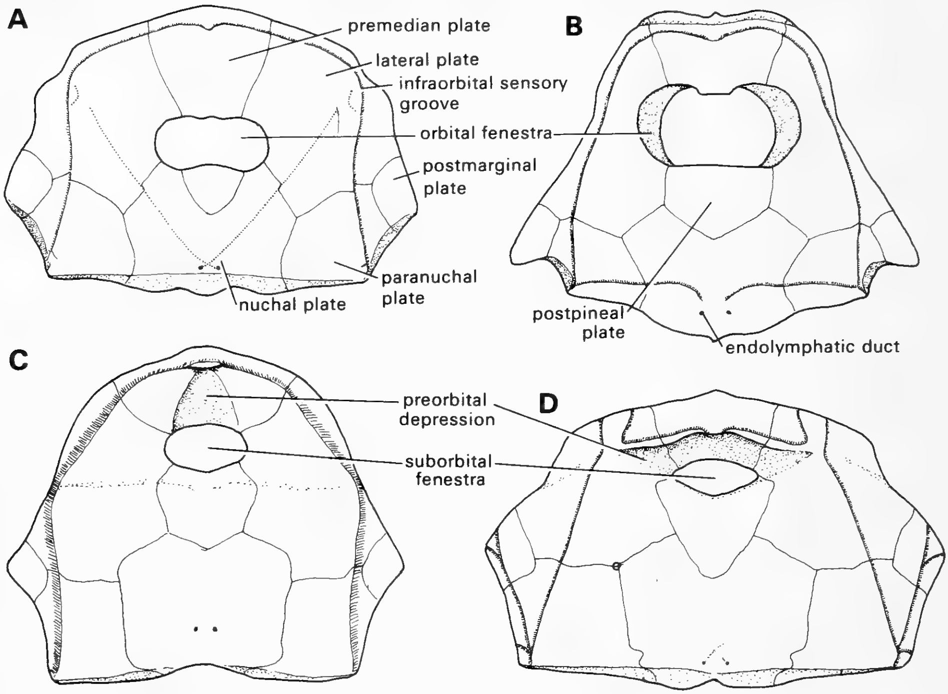

Fig. 1. Skull roof patterns for representatives of the four major antiarch subgroups. **A,** *Bothriolepis* (after Stensiö, 1948); **B,** *Asterolepis* (after Karatajute-Talimaa, 1963); **C,** *Sinolepis* (after Liu and Pan, 1958; and Long, 1983); **D,** *Yunnanolepis* (after Zhang, 1978). Not to scale.

confirmed report from Argentina (Frenguelli, 1951:86) awaits further investigation. The genus *Bothriolepis* (Fig. 1**A**) is the most widespread known placoderm, being represented by over fifty named species (e.g. Denison, 1978). By way of contrast the earliest known antiarchs, which belong to the primitive suborder Yunnanolepidoidei (Fig. 1**D**), apparently occur only in Siluro-Devonian strata in south China, where they form a major component of a highly endemic fauna of early gnathostomes defining the so-called 'south China Province'.

Their cosmopolitan distribution in the Late Devonian and restriction to the south China region in the earliest Devonian, and their predominant occurrence in apparently non-marine sediments, has made the antiarchs a group of some interest in biogeographic studies. In a previous discussion of the biogeography of Devonian vertebrates (Young, 1981), I proposed a cladogram of the major subgroups of antiarchs as a basis for preliminary biogeographic analysis. Since then new forms have been described from Iran (Janvier and Pan, 1982) and Australia (Young, 1983, 1984), and the former authors (also Long, 1983) have presented more detailed assessments of antiarch interrelationships. The purpose of the present paper is to present in detail my own view of antiarch interrelationships, and to consider further some aspects of their distribution in the light of more recent discoveries. This leads to a more general discussion of some methodological problems regarding the use of fossils in palaeobiogeography which have attracted comment in recent papers on vicariance biogeography (e.g. Nelson and Rosen, 1981).

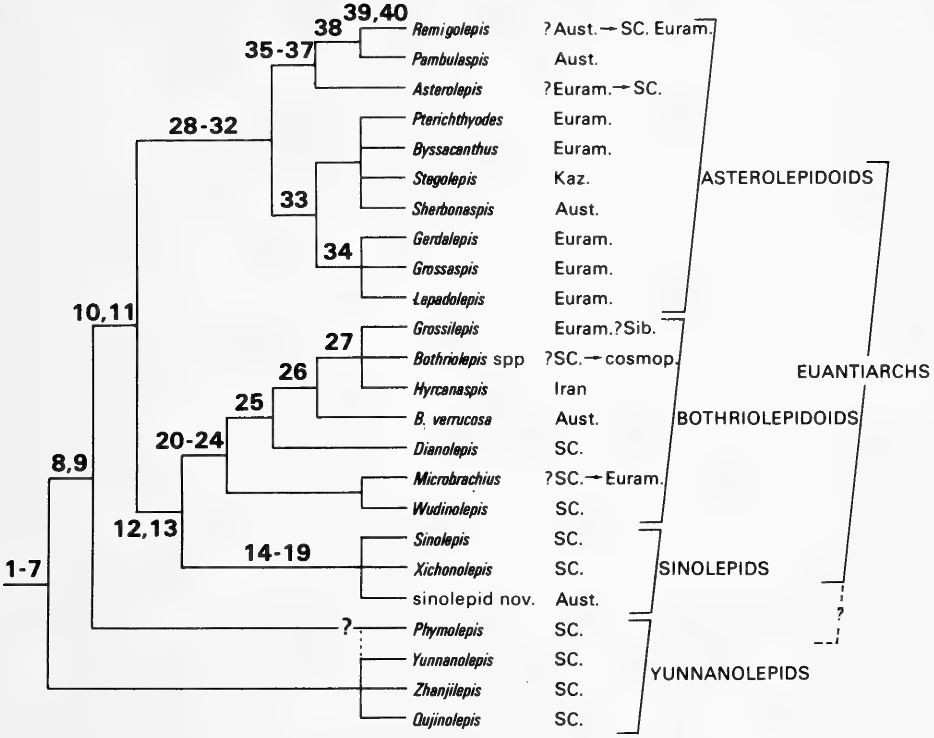

Fig. 2. Scheme of interrelationships for antiarchs, based on 40 shared derived characters (synapomorphies), with known distribution for each genus summarized on the right (arrows indicate presumed dispersal). For discussion of synapomorphies see text.

ANTIARCH INTERRELATIONSHIPS

There are several current opinions regarding the relationships of antiarchs as a group to other groups of placoderms. One viewpoint (Denison, 1975, 1978; Miles and Young, 1977; Young, 1979, 1980) is that their closest placoderm relatives are the euarthrodires, with which they share an elongate box-like body armour which completely enclosed the pectoral fin base in dermal bone. An alternative hypothesis (Goujet, 1984) assumes that this resemblance was the result of parallel evolution, and that antiarchs are instead immediately related to some palaeacanthaspids (a grade group), with which they share nasal openings in a dorsal position near the midline, with a large premedian plate forming a dermal rostrum to the skull.

For present purposes, I have assumed the first hypothesis to be correct. In the following analysis this assumption affects certain decisions of character polarity using the technique of outgroup comparison. In particular, under Goujet's alternative hypothesis a different set of antiarch synapomorphies would apply instead of those listed below (characters 1-7), and some other characters would be subject to alternative interpretation.

My view of the interrelationships of various antiarch taxa is expressed in a cladogram for all genera for which there is reasonable knowledge of morphology (Fig. 2). The 40 shared derived characters (synapomorphies) on which it is based are listed below in groups of characters defining the antiarchs and their major subgroups.

antiarch synapomorphies

1) incorporation of an extra (probably posterior) median dorsal element in the trunk-shield.

2) loss or fusion of the anterior lateral plate, so that the pectoral fenestra is bounded only by the spinal (if present) anteriorly and laterally, and elsewhere by the anterior ventrolateral (see Zhang, 1980).

3) development of a lateral plate in the head-shield, bounding the orbits laterally.

4) concomitant with 3), and associated with dorsal migration of the orbits toward the midline, the reduction and loss (and/or fusion with surrounding bones) of the preorbital and postorbital plates.

5) reduction of sclerotic plates to three in number (see Hemmings, 1978: 18).

6) associated with posterior migration of the nares to a dorsal midline position, the reduction and loss (and/or fusion with other plates) of the postnasal element (in *Yunnanolepis* the anterior portion of the lateral plate bounds the naris laterally, as does the postnasal in some primitive euarthrodires).

7) concomitant with (6), the enlargement of an internasal element (or appearance of a new unpaired dermal element in the skull), to form the premedian plate.

euantiarch synapomorphies

8) development of small dermal plates covering the pectoral appendage.

9) development of the processus brachialis, foramen axillare and associated structures involved in a complex proximal dermal articulation between the pectoral fin and shoulder girdle.

10) development of a distal joint in the pectoral fin.

11) loss of interolateral and spinal plates, assuming these are present in *Yunnanolepis* (Zhang, 1980: pl. 5, fig. 3) in addition to paired semilunars (Zhang, 1978: fig. 1B). Alternatively, the semilunar may be a modified interolateral.

synapomorphies of sinolepids and bothriolepidoids

12) elongation of the proximal part of the pectoral fin, with reduction of dorsal central plate 2 (poorly known in *Sinolepis*).

13) posterior ventrolateral and posterior lateral fused to form (or replaced by) a single plate (*sensu* Janvier and Pan, 1982; status in sinolepids uncertain, alternatively a bothriolepidoid synapomorphy).

sinolepid characters

14) posterior ventral pit and process lie behind the crista transversalis interna posterior (status uncertain, as this condition may be primitive for placoderms generally).

15) anterior and posterior ventrolateral plates much reduced both laterally and ventrally: median ventral plate, if present, very large and subrectangular in shape (A. Ritchie, *pers. comm.*).

16) parallel-sided posterior median dorsal plate.

17) anterior median dorsal overlaps posterior dorsolateral or mixilateral plate over the length of their common suture.

18) loss of lateral corners and development of wide anterior margin on anterior median dorsal plate (the condition in *Xichonolepis* compared to *Sinolepis* shows that these features developed within the group).
19) occipital commissure on nuchal and main lateral line of trunk armour reduced or absent.

bothriolepidoid synapomorphies

20) posterior ventrolateral and posterior lateral fused to form (or replaced by) a single plate (assuming absence or separate development in sinolepids; cf. character 13 above).
21) posterior dorsolateral overlaps anterior median dorsal over most of their common suture.
22) anterior median dorsal with broad anterior margin.
23) unpaired semilunar plate.
24) posterior oblique cephalic pitline developed.

bothriolepid characters

25) preorbital depression replaced by preorbital recess.
26) nuchal with orbital facets, and postpineal excluded from contact with the lateral plate.
27) enlarged foramen axillaris.

asterolepidoid synapomorphies

28) short obstantic margin facing posteriorly.
29) posterolaterally extended postmarginal plates.
30) enlargement of suborbital and orbital fenestrae to incorporate the preorbital depression.
31) loss of anterior ventral pit and process on anterior median dorsal plate.
32) mental plates meet in the midline.

asterolepid characters

33) high, short trunk-shield.
34) similar dorsal spongiose layer in dermal bone of trunk-shield (see Gross, 1965).
35) nasal openings on anterior margin of broad rostral plate.
36) unornamented shelf, premedian notch, and rostrocaudal groove on premedian plate.
37) reduced endocranial postorbital processes.
38) pronounced postpineal thickening.
39) loss of posterior ventral pit and process on posterior median dorsal plate.
40) loss of distal joint, and ventral central series of plates, in pectoral fin.

Regarding the interrelationships of the four major antiarch subgroups this new scheme differs from previous arrangements (Young, 1981; Janvier and Pan, 1982; Long, 1983) in that sinolepids and bothriolepidoids are placed as sister groups. Otherwise the major groupings are strengthened with additional synapomorphies, although there are some minor changes. *Microbrachius* and *Wudinolepis* are included as stem bothriolepidoids, following Janvier and Pan (1982; also Hemmings, 1978; cf. Young and Gorter, 1981; Long, 1983). The idea of Janvier and Pan (1982: fig. 11) that there are two differently derived types of mixilateral plate in antiarchs is incorporated, and the arrangement of plates in the proximal segment of the pectoral fin in asterolepidoids is assumed to be primitive, and that in bothriolepids and sinolepids advanced (Young, 1984: 74). It is for this reason that the latter two groups are united as sister groups. Long (1983) has suggested that the pectoral fin of bothriolepids is more advanced in several characters, but he gave no evidence to justify interpreting reduction of the second dorsal central plate in these two groups as a parallelism. Several new synapomorphies are proposed to support the sister group relationship of *Xichonolepis* and *Sinolepis,* as previously suggested (Janvier and Pan, 1982; Long, 1983). However, Long's characterization of the group by the relatively long post-orbital division of the skull and the ventral pits beneath the dorsal trunk-shield plates is invalidated by the presence of these features in yunnanolepids. Some unpublished evidence on the morphology of sinolepids (A. Ritchie, *pers. comm.*) is incorporated, but this will be dealt with more comprehensively elsewhere, and is included here only as a basis for the biogeographic discussion. A previously proposed asterolepidoid synapomorphy (loss of the prelateral plate; see Young and Gorter, 1981: 100) has been deleted since this bone is now known to occur in *Asterolepis* (Lyarskaya, 1981).

Broad agreement on the interrelationships of the major antiarch subgroups, as now known, suggests that some meaningful biogeographic conclusions might be produced by appropriate analysis. Known distributions of the various genera are summarized in Fig. 2, but before discussing details some general questions regarding method need to be considered.

COMMENTS ON THE USE OF FOSSILS IN BIOGEOGRAPHY

Three recent publications have stimulated the discussion presented here. Patterson (1981) in particular has provided a comprehensive review of method in palaeobiogeography, and raised several important issues requiring further comment. Nelson and Rosen (1981) and Nelson and Platnick (1981) have extended the vicariance concept beyond the first detailed exposition by Platnick and Nelson (1978), which formed the basis for my previous discussion of Devonian vertebrate biogeography (Young, 1981). That discussion is now reconsidered in the light of these more recent contributions, particularly those issues relating to the distribution of fossil groups.

The evidence of biostratigraphy. In my previous discussion I suggested an origin in the Australian region for the Late Devonian placoderm *Phyllolepis,* and I argued that the early biostratigraphic appearance of this form in Australia supported this view (Young, 1981: 237). Patterson (1981: 403) has pointed out, however, that this type of argument is unreliable since any new discovery of the group in older rocks and in a different region would imply a different centre of origin. He concluded (1981: 461) that the so-called 'Matthew's rule of thumb that the site of the oldest fossils is the centre of origin' did not work for certain groups of fossil mammals, and furthermore that the general assumption on which it was based — that the fossil record is complete — is wrong. These conclusions were reached in relation to groups with living representatives, as a refutation of Keast's (1977) claim that centres of origin and dispersal cannot be reliably estimated from contemporary distributions, but only when a good fossil record is available. In this context Patterson's criticism is accepted; fossils, properly analysed within a phylogenetic framework, provide no special distributional data over and above that available from Recent forms. The fallacy of a complete fossil record on which Matthew's rule depends may be put another way — it is the fallacy that distributional (like phylogenetic) history may be read from the fossil record like pages in a book.

However, I do not believe that biostratigraphic evidence can be dismissed out of hand on the grounds that a complete fossil record is thereby assumed. In one sense — that hypotheses must be constructed on the basis of available data, however limited — this assumption is always made. Moreover, fossils can provide minimum ages for related taxa which may be critical to hypotheses postulating correlations between geological and dispersal or vicariance events (e.g. Platnick and Nelson, 1978: 3; Patterson, 1981: 453). For groups like the placoderm fishes, without modern representatives, the particular problem of a time dimension is accentuated; palaeogeography changes with time, and this may be manifested in the biostratigraphic record of any group by approximately contemporaneous presences or absences in particular regions. Rejection of all biostratigraphic data would imply that a sequential biogeographic analysis incorporating a variety of geographies through time is not possible. Patterson (1981) draws an analogy between biogeography and systematics, and in phylogenetic systematics also the use of biostratigraphic data has been rejected (e.g. Nelson, 1970). But there is an important distinction here which shows that Patterson's analogy does not apply in this case. Biostratigraphic data are widely used in traditional stratigraphic palaeontology to recognize ancestor-descendant relationships amongst fossil taxa which appear to show a consistent trend of morphological change. This 'stratophenetic' approach has been validly criticized because a complete fossil record must be assumed. Put another way, to propose one fossil species as the ancestor of another taxon, it must first be postulated that there are no unknown forms which are possible candidates for the ancestor position. The criticism of this procedure is based on the argument that we can never assert complete knowledge of a particular group. In the case of biogeography however, any assumption regarding unknown taxa is much more specific. The postulated absence of a particular taxon refers to a particular area at a particular time. Clearly, such negative evidence can never be definitely established, and some judgement must be made about the reliability of absence data in each case (Young, 1984). But the resultant predictions are precisely specified, and are testable. To return to the example of the placoderm *Phyllolepis* mentioned above, the evidence that it occurs in Devonian fish faunas of a certain age (Frasnian-Famennian) in Australia, but is absent from faunas of Frasnian age in Europe, may alternatively be presented as the hypothesis that there was an effective barrier between these areas for this taxon during the Frasnian, but not during the Famennian. This hypothesis would be refuted only by the demonstration that *Phyllolepis* had been overlooked in European vertebrate faunas of Frasnian age. In this limited sense, therefore, such biostratigraphic evidence may imply biogeographic conclusions, and they are no more dependent on assumptions of complete information than any observation about the modern distribution in space of an extant organism. The further conclusion, that the taxon originated in the area of its earlier occurrence, cannot be reached without additional evidence (see below).

The evidence of palaeogeography. That earth history and the history of the earth's biota are causally related is a basic tenet of vicariance biogeography (e.g. Croizat, 1964; Platnick and Nelson, 1978). However the degree to which geological data might influence the formulation of biogeographic hypotheses has been questioned, although such data have been put forward as potential tests of particular biogeographic models. Platnick and Nelson (1978) suggest that independent evidence of historical geology may be used to decide whether vicariance or biotic dispersal is the likely explanation of a general pattern of distribution of organisms between areas. However Patterson (1981: 455) has noted that apparent concordance between relevant geological theories and a biogeographic explanation is, on the lesson of history, hardly a reliable indicator that the explanation is correct. On the contrary, past experience suggests that biogeography has often been held back by allegiance to geological ideas current at the time.

In my 1981 paper I proposed that five distinct faunal provinces could be identified for Early Devonian vertebrates, and the delineation of these provinces was partly based on geological and geophysical evidence (e.g. palaeomagnetic data, distribution of post-Palaeozoic orogenic belts) suggesting that the areas in question were separate continental regions during the Middle Palaeozoic (Young, 1981: 226). To this extent my analysis was eclectic in applying a particular geological model about Palaeozoic continent configurations (there are others; e.g. Boucot and Gray, 1979) as a preliminary step in identifying areas of endemism based on distributional data. Contrary to the attitudes noted above I suggest that such an approach is necessary when the group concerned is known only as Palaeozoic fossils. As stated elsewhere (Young, 1984), in dealing with such groups there is no recourse to a set of reliable distributional data as is claimed to be available for some living taxa. Patterson (1981: 463) makes reference to the distribution of extant forms which 'may be regarded as completely known in many groups', but the formulation of any statement about the distribution of modern groups is dependent, if not on current geological theories, then at least on the modern result of historical geological processes; that is, on modern geography. As we go farther back in geological time, and certainly in the Palaeozoic, any notion of a particular palaeogeography is inextricably linked with global geological hypotheses, perhaps encompassing tens of millions of years of earth history. Yet, as Janvier and Pan (1982) have noted, a particular set of biogeographic relationships can apply only for a particular time; to attempt even a preliminary biogeographic analysis for Palaeozoic fossils without utilizing geological and geophysical data, and therefore without any meaningful reference to the modern geography of fossil occurrences, would be impossible. For the biogeographic analysis of living forms also, geological hypotheses cannot be excluded. The 'vastly different geological story' (that is, an unchanging geography) referred to by Patterson (1981: 455) was more of an axiom than a theory. Rejection of that axiom, and acceptance of the idea that completely different continental distributions have occurred in the past, has permitted the development in historical geology of competing hypotheses, which must influence our comprehension of, and approach to, the distributional aspects of biological data (see further below).

Biogeographic provinces and the evidence of faunal affinity. Ball (1976) identified an empirical or descriptive phase in biogeographic investigations as one concerned with identifying regions characterized by particular groups of organisms. It was noted however that an elucidation of the history of such regions as reflected by historical analysis of their characteristic faunas or floras is the real aim of historical biogeography. From this viewpoint, the suggestion (Young, 1981) that at least five distinct faunal provinces may be recognized for Early Devonian vertebrates, can be seen as a bringing together of empirical data for meaningful analysis. In general terms, given a pattern of geographic regions, each characterized by particular faunas or floras, two questions of relevance to palaeobiogeographers concerned with geological history and its influence can be asked. These are:

1. What criteria should be used to assess affinity or relationship between characteristic biotas defining particular geographic regions (biogeographic provinces)?
2. Having assessed such relationships, what can be inferred about the history of the areas occupied by those biotas?

The most widely used criterion of overall affinity has been based on taxa in common between areas. There are many palaeontological examples (e.g. Middlemiss, Rawson, and Newall, 1971; Hallam, 1973). Various statistical techniques or special coefficients have been employed to handle these similarity data (e.g. Sneath and McKenzie, 1973; Henderson and Heron, 1977) but as has been noted (Ball, 1976; Patterson, 1981) this is essentially a phenetic approach, an assessment of faunal similarity, but not of relationship. Nevertheless, to show that two areas share more taxa than either does with a third area is a desirable outcome of a comparative analysis of three distinctive faunas. But the inferences which may be drawn therefrom regarding 'affinity' between the areas concerned is a point of dispute. Almost without exception it has been assumed that areas with more taxa in common have had a more recent connection. This has been challenged by Platnick and Nelson (1978; see also Nelson and Platnick, 1979, 1980, 1981). They analyse a hypothetical example in which three areas result from subdivision of one original area containing a single widespread species. Allopatric speciation of the ancestral species during subdivision is assumed, to give taxa endemic to the three areas. Allowing for different dispersal capabilities, and the possibility that the barriers which subdivide the area may be effective for some taxa but not others, it can be shown that the same historical sequence of separations can result in a single species being shared between any two of the three areas (e.g. Nelson and Platnick, 1980: 340). In another graphic example (Nelson and Platnick, 1981: 56, 57), a hypothetical problem is posed involving three areas, each containing 100 species. In area A all 100 species are endemic, but in areas B and C 99 species are shared, and only one species is unique to each. By any of the usual measures or coefficients based on overall similarity, it is clear that areas B and C would be judged to show far greater affinity to each other than either shows to A. However, Nelson and Platnick argue that this analysis does not necessarily reflect the history of area interconnections. What is needed is a phylogenetic analysis of a species group with an endemic representative in each area. For example, if in such a group the species endemic to areas A and B are more closely related than either is to the endemic species of area C, this indicates a more recent interconnection between areas A and B, regardless of the fact that 99 species are shared between B and C, but not with A.

A central issue in this example is the basis on which the three areas are identified. If they are seen as areas of endemism, then areas B and C can be characterized only by the presence of one endemic species in each area. On the other hand, if the areas are initially recognized by geographic or other non-biotic criteria (for example three islands, three patch reefs separated by open water) then the fact that 99 species are distributed across two of the areas (as continuous interbreeding populations) shows that for these species at least the two areas have no separate identity. The essence of Nelson and Platnick's argument is that for these 99 species there are only two areas (A, and B + C), and therefore no problem of recency of area interconnections. They summarize their position by stating (Nelson and Platnick, 1980: 341) that 'shared (widespread) taxa . . . contribute no unambiguous information about area interrelationships'.

It is important to consider if, and how, this proposal can be reconciled with the many examples in palaeobiogeography of faunal provinces defined on overall similarity. What is to be made, for example, of the so-called Appalachian, Malvinokaffric, and Old World provinces for Early Devonian trilobites and brachiopods (e.g. Johnson and Boucot, 1973; Eldredge and Ormiston, 1979), in which widely-separated regions are united on the basis of shared widespread taxa?

For the palaeontologist, it should first be noted that the arguments just discussed are not necessarily valid when extinct species are involved. In the examples from the modern biota used by Nelson and Platnick (1979, 1980), interbreeding continuity of a widespread living species is assumed. The species is widespread with respect to regions

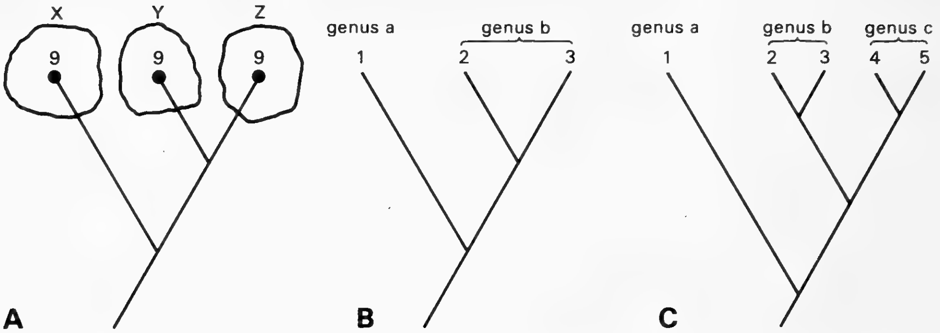

Fig. 3. **A.** Phylogenetic relationships of 27 species distributed as endemics in three areas (X, Y, Z). **B.** Three species from the three areas, related as in **A,** and classified in two genera a and b. **C.** Five species from the three areas, classified in three genera a, b, and c, each endemic to one of the areas (X, Y, Z). For discussion see text.

recognized by their endemic biotas, and it is argued that such species are not relevant to the problem of elucidating the history of those endemics and the regions they occupy. On the other hand, the distribution of an extinct species widespread with respect to modern geography may have been considerably altered by geographic change. Interbreeding continuity between modern geographic localities cannot be assumed, and to the palaeobiogeographer evidence of widespread fossil species may be of central importance in attempting to reconstruct former geographies. I refer here specifically to species, as different arguments are involved with higher taxa (see below).

The palaeobiogeographer might also question the underlying assumptions of Nelson and Platnick's argument. These seem to be 1) that speciation was allopatric; 2) that barriers effective for one species may not be effective for others; and 3) that the three areas and faunas being analysed were originally a single area with a single fauna. I know of no valid grounds for rejecting the first two assumptions, but the third might be challenged as being a special case, and therefore not generally applicable. In the 3-area example used by Nelson and Platnick (Java, Sumatra, and Borneo) it might be reasonable to suggest an originally continuous area, but there are many other examples for which there may be no evidence of original continuity. It is worth reiterating here the distinction between biotic and geographic continuity, as it is the former which is essential to Nelson and Platnick's case. There may be no evidence for geographic continuity, but the evidence for biotic continuity is simply that there are, in the areas concerned, faunas or floras which may be compared. It is the nature of this continuity which is important, and Nelson and Platnick's assumption may alternatively be expressed as the assumption that geographically distinctive biotas were emplaced by range enlargement or dispersion, and specifically not by any migration or dispersal event associated with speciation (for a discussion of the terms dispersal and dispersion, see Platnick, 1976).

This type of biotic continuity is implicit in the assumption that certain areas and their biotas comprise a particular faunal province, but it is not normally assumed by palaeobiogeographers to apply between provinces — that is, between different areas each definable on their possession of endemic taxa. The reason for this is that the faunas are seen to be different, and it is assumed therefore that dispersal across biogeographic barriers must have occurred. But, as pointed out by Platnick and Nelson (1978), there is a mechanism (vicariance) which can account for the occurrence of different taxa in different areas, and does not involve dispersal.

In assessing any scientific hypothesis it is instructive to consider possible alternatives or competing hypotheses. In the present case the specific points of difference between the vicariance approach and a more traditional provincial analysis may be brought into focus by formulating another hypothetical example in which original biotic continuity is not assumed. For supraspecific taxa this inevitably involves 'dispersal' of the type associated with speciation. We can propose three separate areas (X, Y, Z), each containing nine species (Fig. 3). None of the species is shared with the other areas. A common narrative would be that if two of the areas, say X and Y, gradually move closer together, there will be a gradual increase in shared species due to increasing dispersal between X and Y. When faunal interchange is complete, and all species are shared between the two areas, then these two provinces would cease to exist as separate entities. It is in this sense that taxa in common have been regarded as a measure of geographic proximity between areas.

However there are two major criticisms of this model, concerning first the nature of the postulated biotic distinctness of the areas under consideration, and secondly the reliability of results using taxa in common as a means of comparison. Although the three areas may be postulated as initially distinct at species level, this cannot apply for all higher taxa (unless, of course, the difference is due to the complete absence of faunas from some of the areas). The species concerned must be related in some way, and it may be that among the 27 original species specified above there are nine groups of three species, one from each of the areas, and related to each other as shown in Fig. 3**A.** This significant congruence would not come to light if taxa in common were analysed at the species level only. An analysis of genera might bring out the pattern, but this would not necessarily be the case. Consider a group of three species, one from each of the three areas, and grouped in two genera a and b (Fig. 3**B**). If their relationships are the same as in Fig. 3**A,** an analysis of genera in common would indicate closer affinity between Y and Z, the general pattern shown by the species relationships. But if there had been further speciation within areas Y and Z so that three genera (a, b, c) were recognized (Fig. 3**C**), then the absence of genera in common would again cause the relationship between endemic taxa to be overlooked if traditional methods were used. For reasons which are obvious from this example there has been much discussion in the literature (e.g. Campbell and Valentine, 1977) of taxonomic levels to be used in analysis of taxa in common. But one may ask just what special significance is to be placed on endemic taxa of high rank. Middlemiss and Rawson (1971: 201), quoting Ekman, refer to the argument that the higher the rank of an endemic taxon, the longer the isolation of that particular province. If it were true, as this implies, that rates of speciation must remain constant in different areas, then a distribution of five species in three areas as in Fig. 3**C** could not be obtained under any simple model of allopatric differentiation and/or dispersal. But there are in reality many factors which might result in more rapid speciation in one area than another (see also Nelson, 1975: 557), and it is these factors (e.g. a tectonic regime creating many different niches, a more suitable climate for the ancestral species, a lack of competition from other species) which would manifest themselves, but in no clearly-defined way, in any analysis of faunal similarity at different taxonomic levels. It is important also to note that in the example just considered (Fig. 3**B, C**), a further differentiation of endemic species within an area of endemism in no way affects, and is irrelevant to, the historical pattern of connection of that area to other areas, as evidenced by the interrelationships of taxa endemic to those areas. This is another example of confusion between the ecological and historical aspects of biogeography.

It seems, therefore, that as an alternative to hypothesizing that three endemic faunas were derived from a single ancestral fauna, we must propose that these faunas

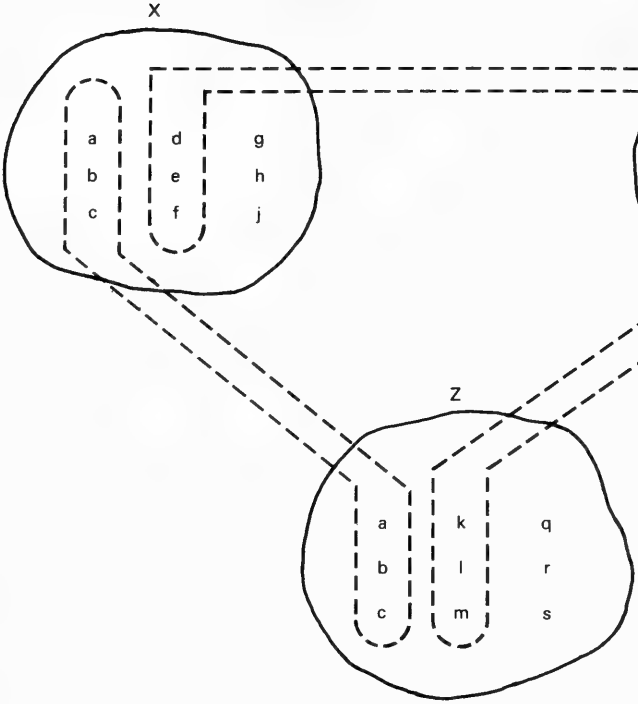

Fig. 4. Three areas (X, Y, Z) each containing nine species (taxa). Each area contains three endemic species (taxa), and each pair of areas shares three species (taxa) as indicated by the broken lines.

were originally different, although the phylogenetic relationships of the faunas, and therefore the nature of these 'differences', are not readily specified. Put another way, it is the delineation of the biogeographic problem at hand which is unclear in such an example. If the initial conditions specified (in the above case three sets of nine species, none shared between areas) are so general as to permit radically different results of analysis, then clearly the limits of investigation must be extended to incorporate those pre-existing conditions (in this example the interrelationships of species and higher taxa between areas). The judgement that assumed initial conditions adequately delimit a particular biogeographic problem may be strongly influenced by non-biological considerations such as the supposed geological history of the areas (see below).

Assuming then that appropriate initial conditions have been specified, we can further consider the reliability of results of comparing taxa in common between areas. Given the same three areas, each with nine species, the analysis of taxa in common in a situation where three species are endemic to each of the areas, and three each are shared between X and Y, Y and Z, and Z and X (Fig. 4), would not resolve any difference in affinity between the three areas. But if species interrelationships for the endemics were as shown in Fig. 5, this would be a strong indication of some special affinity between areas X and Y. Again, as in the previous case, this pattern of interconnection might be indicated by analysis of genera or higher taxa, but the nine taxa in each of the three areas (Figs 4, 5) need not be species, but could be taxa of any rank. If we were dealing with families, then those shared between two areas provide the added complication that their contained genera may be most closely related to other genera in their own area, or may have their sister groups in another area. In any

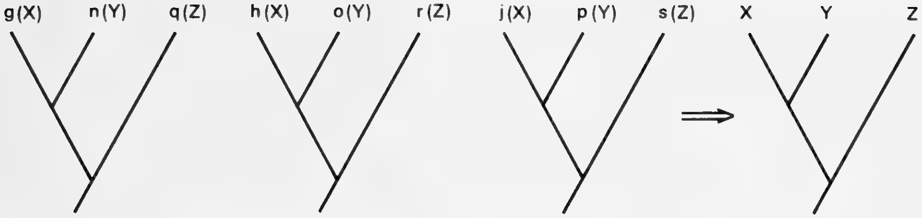

Fig. 5. Hypothetical interrelationships of the nine endemic species (taxa) of Fig. 4, and the implied pattern of interconnection (area cladogram) for the three areas X, Y, Z.

situation it is possible to analyse a set of empirical data to give results expressed either in terms of competing hypotheses, which give direction to future investigations of the problem, or as a blending of different interpretations or influencing factors, for which the future direction of investigation is unclear. In diagram form, an area cladogram might be proposed as an example of the former, and the graphic representations of Savage, Perry, and Boucot (1979: figs 6-10) would seem to be examples of the latter.

In conclusion, I suggest that an alternative to Nelson and Platnick's assumption of a common ancestral biota can only be precisely formulated if there is a complete absence of biota from one or more of the areas, or the faunas and/or floras in the areas considered are completely different at such a high taxonomic level that pre-existing interrelationships are irrelevant to the biogeographic problem being investigated. Both instances would be examples of 'vacuum biogeography', as discussed in more detail below. In other than these special cases, widespread species may be assumed to indicate faunal (reproductive) continuity between areas, and are therefore valid criteria for recognizing faunal provinces (areas of endemism). In the case of fossil species shared between widely separated areas, assumed reproductive continuity in the past may indicate subsequent geographic change, but this does not apply for supraspecific taxa, where continuity between disjunct occurrences is not reproductive (i.e. spatial), but phylogenetic (historical). A consideration of the history of connection between areas of endemism can be based only on the interrelationships of taxa endemic to those areas, and not on other more widespread taxa, which are common to two or more of those areas. These would only be informative at a higher level of analysis (involving more inclusive areas of endemism defined by such taxa). Analysis of taxa in common between areas using various taxonomic ranks may or may not give results reflecting the phylogenetic relationships of endemic taxa (and therefore the history of connection between areas), but may also give results reflecting other factors not relevant to that history. Such results cannot therefore be regarded as reliable, and alternative methods must be sought. One alternative was proposed by Hennig (1966).

Hennig's progression rule. In a short but significant paper, Nelson (1969) attempted to formalize some ideas on biogeography outlined by Hennig (1966: 133-139), and developed by Brundin (1966). Hennig's 'progression rule' provides a method by which the geographic distribution and dispersal history of a group of organisms can be inferred from the distribution of Recent taxa, given a precise hypothesis of phylogenetic (cladistic) relationships for those taxa. As an example, Nelson discussed two hypothetical sister species C and D, occurring in areas x and y, and derived from a hypothetical common ancestral species B. Nelson concluded that, without additional evidence, the most parsimonious hypothesis regarding the distribution of ancestral species B was that it last occurred in both areas x and y (Fig. 6**A**). If, however, a third species E, related to the other species as shown in Fig. 6, also occurred in area y, then

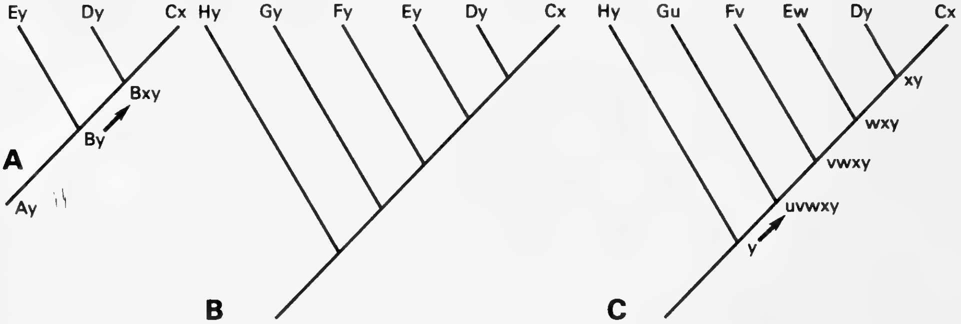

Fig. 6. Formalization of Hennig's progression rule, after Nelson (1969). **A.** Cladogram of relationships of three Recent species C, D, and E, occurring in areas x and y as indicated, with estimated distribution and dispersal (arrow) of hypothetical ancestral species A and B. **B.** Cladogram of six Recent species occurring in areas x and y as indicated. A derivation of species C from area y is indicated. **C.** Cladogram of six Recent species occurring in five areas (u-y), representing a situation where Nelson's formalization is not valid, and demonstrating that Fig. 6**B** is a special case.

the most parsimonious estimation of the distribution of the most recent common ancestor A of these three species was that it occurred only in area y, since this would require only one migration, of species B from y into x. Nelson went on to point out that if further species F, G, and H, related as shown in Fig. 6**B**, were also distributed in area y, there could be little doubt 'that the occurrence of this lineage in area x is a secondary and relatively late one' (Nelson, 1969: 244). The methodological principle employed in this analysis was subsequently paraphrased by Nelson (1973: 314):

> 'A given ancestral distribution is most parsimoniously estimated by combining descendant distributions, when they are completely different, and eliminating the unshared element when the descendant distributions are not completely different.'

In a more general statement the same idea was expressed by Brundin (1975: 70) as 'the fundamental biogeographic principle that a primitive group at least primarily is closer to the area once occupied by the ancestral species than is the comparatively derived sister group'. Regarding the circum-Antarctic distributions of chironomid midges, Brundin (1975: 21) noted that 'the marked primitiveness of the southern representatives is a demonstration of the southern origin of these subfamilies'.

The ideas of Hennig and Brundin were widely discussed and applied to various other groups (e.g. Edmunds, 1972; Cracraft, 1974). I previously expressed the view (Young, 1981: 236) that the 'progression rule' of Hennig was a valid procedure for parsimoniously estimating dispersal history using palaeontological data and phylogenetic analysis. However Hennig's ideas were also criticized on a number of grounds (e.g. Darlington, 1970), and several of these criticisms are still current. Nelson (1975) reconsidered his earlier (1969) formalization of Hennig's methods, and concluded that the procedure previously advocated was defective because it could indicate episodes of dispersal in cases when no dispersal had occurred (Fig. 7**B**). He pointed out that 'eliminating the unshared element' as previously advocated entailed an unnecessary assumption that dispersal must occur with speciation, and he proposed a modified 'rule' that 'for a given group the distribution of ancestral species can be estimated best by adding descendant distributions' (Nelson, 1975: 556). It should be noted that in Nelson's example the erroneous result attributed to defective procedure is due to failure to incorporate the basic empirical data that the problem involves three

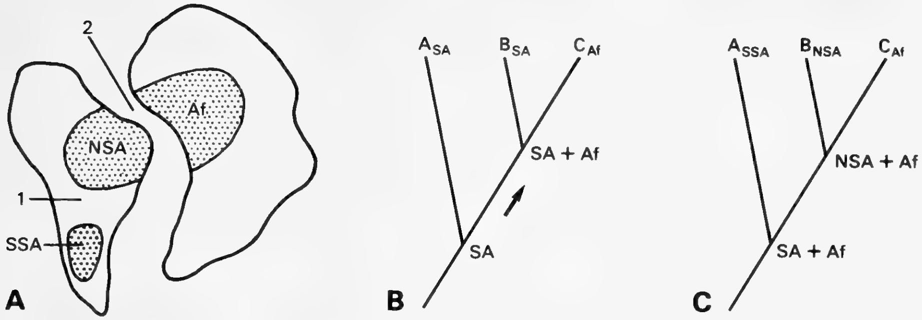

Fig. 7. **A.** Areas of endemism for three species (A, B, C) in southern South America (SSA), northern South America (NSA), and Africa (Af) respectively. The species are hypothesized to have differentiated as a result of two vicariance events, the first (1) within South America, and the second (2) between South America and Africa (modified from Nelson, 1975: fig. 1). **B.** Estimation of ancestral distribution involving dispersal when none occurred (modified after Nelson, 1975: fig. 2). **C.** Estimation of ancestral distribution which does not erroneously resolve dispersal, also using the formalization of Nelson (1969) but with separate areas of endemism for the three species properly specified.

areas, each defined by endemic species, and not two (Fig. 7**C**). Nevertheless, the acknowledgement noted above that dispersal and speciation do not necessarily go together (Croizat *et al.,* 1974; Platnick and Nelson, 1978) is an axiom of cladistic vicariance theory as it has subsequently developed. The issue of dispersal versus vicariance in a Palaeozoic context is further discussed below.

Patterson (1981) has also criticized Hennig's progression rule because of its sensitivity to incomplete fossil data as indicators of centres of origin and dispersal. He suggests (1981: 478; also Parenti, 1981: 490) that this method is reliable only if the fossil record is acknowledged to be complete, and is therefore no better than 'Matthew's rule of thumb'. But here an important difference is overlooked. Under 'Matthew's rule' (see above) the oldest known fossil can indicate a centre of origin only if it is assumed that no older fossils of that group will be found, because none exist. This assumption that the fossil record is complete has been shown repeatedly to be wrong (Patterson, 1981: 463). Under Hennig's progression rule, however, a fossil taxon providing sufficient information for its placement within a synapomorphy scheme (which may or may not include extant taxa) in effect defines a group (characterized by particular synapomorphies that fossil taxon shares with positionally apomorphic taxa within the scheme), and defines a biogeographic problem (the dispersal history of that group). No assumption of a complete fossil record is involved because newly-discovered fossil taxa qualify or not for membership of the group in question based only on their morphological characters. Furthermore, the most primitive known member of the group is in effect assessed as having the earliest separate history, and since this also is based on morphological evidence, the completeness or otherwise of the group's fossil record cannot alter this assessment. For newly-discovered taxa which lack the synapomorphies of the group in question, any resulting biogeographic inferences relate to a different problem, the dispersal history of another group which includes that new fossil. Clearly, new fossil discoveries can show previous schemes of relationship, and estimations of ancestral distribution based on them, to be wrong, but the same possibility exists regarding Recent taxa. The criticism that fossil data, ambiguous because of incompleteness, may inordinately affect conclusions regarding the dispersal history of Recent taxa, is a reasonable one only if it is claimed that all existing taxa and

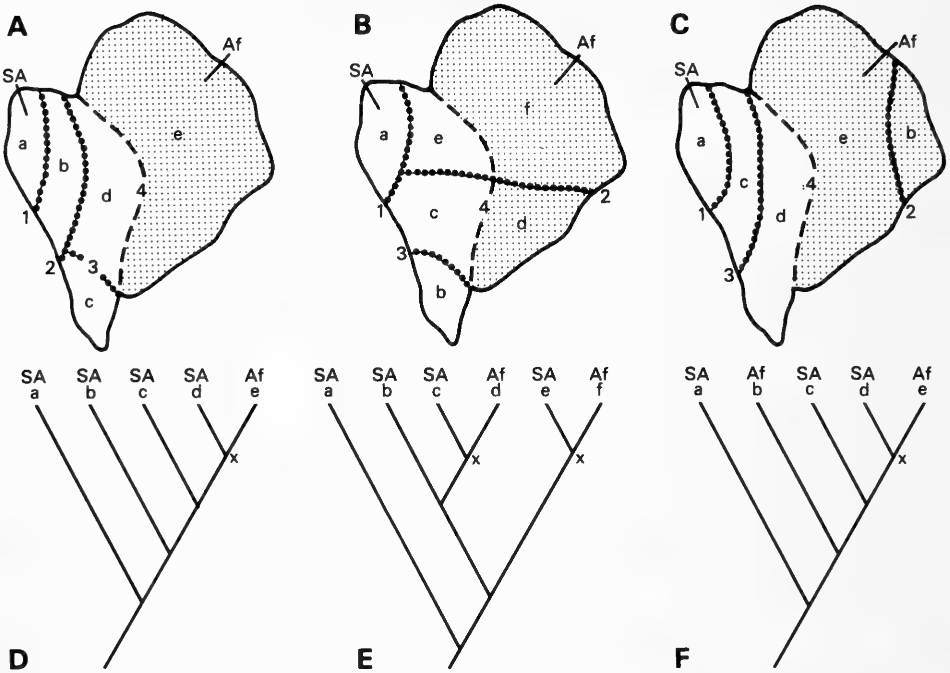

Fig. 8. Three distributions in space of vicariance events (appearance of barriers) in a region which separates into two to give a disjunct distribution for immediately related species a-f. **A** (simplified after Nelson and Platnick, 1981: 44-45). Barriers 1-3 are confined to the South American protoregion (SA), suggesting that those postdated subdivision of the area by barrier 4, and that species e dispersed across this barrier (other cladograms in which one descendant of the most recent speciation event(s) occurs in Africa can be shown to be equivalent by rotation around their nodes). **B.** One of the barriers (2) affected both African (Af) and South American protoregions, suggesting they were not yet distinct, and pointing to a vicariance explanation. **C.** One of the barriers (2) affected the African protoregion. Implications as in **B**, except that a dispersal explanation can only be excluded by adoption of additional methodological assumptions. **D, E, F.** cladograms for the species, and their distributions, resulting from the vicariance patterns of **A, B,** and **C** respectively; x marks the dispersal or vicariance event associated with barrier 4 (the separation of South American and African protoregions).

all Recently extinct taxa, together with their distributions, may be completely known (see above, and Patterson, 1981: 463; also Nelson and Platnick, 1981, on knowledge of Recent distributions). This criticism can hardly apply to groups known only as fossils. Patterson also suggests, in considering the example of giraffoids, that where Matthew's rule and the progression rule give conflicting results, these may reasonably be reconciled by combining the two areas concerned. But few would agree with this, and it is surely a widely-held view amongst palaeontologists that where the earliest known member of a group is not also the most primitive, then an *ad hoc* explanation would be invoked that the biostratigraphic record is incomplete (see also Patterson, 1980: 216). As just noted, the most primitive known taxon must have the earliest separate history, regardless of what is indicated by presence-absence data from the fossil record, and evidence of dispersal origins based on progression rule analysis is thus clearly superior to that based on oldest known fossil data. We assume here, of course, that the morphological evidence has been correctly assessed to recognize the most primitive known taxon.

Other comments on the Hennig-Brundin method have been made by Platnick (1981) in discussing the recent paper by Brundin (1981). Platnick elaborates the distinction between taxic and positional apomorphy, and rightly points out that the concept of taxic apomorphy, implicit in the so-called 'deviation rule' (e.g. Brundin, 1968), is a phenetic rather than a cladistic concept. He also comments on a detailed analysis of an example of amphi-Atlantic distribution presented by Brundin (1981: figs. 3.1-3.5). This is the same type of example (Fig. 6**B**) on which Nelson (1969) based his formalization of the progression rule (see above). Platnick notes that in Brundin's example the progression rule would allow the final speciation (x, Fig. 8**D**) to result either from vicariance caused by, or dispersal across, the proto-Atlantic ocean. On Brundin's argument regarding steady speciation in one area whilst no speciation occurred in the other, Platnick comments (1981:148) that 'it is more likely that the earliest barrier to divide a species widespread over two continents would appear at one end of the total area, not at the middle'. But this does not take full account of Brundin's argument, which would seem to provide a means of distinguishing vicariance from dispersal as a likely explanation in certain cases, based on the distribution pattern of a single group, and some comprehension of the geological history of the areas. Three different examples are illustrated in Fig. 8 of vicariance events in the history of a group distributed across a continental region which divides into two. Where vicariance events have occurred in both protoregions (Fig. 8**B**, **C**; Brundin, 1981: fig. 3.4) a vicariance explanation with a widespread ancestral distribution is indicated. But where (except for the most recent or equally most recent event) the history of allopatric speciation was apparently confined to one protoregion (Fig. 8**A**), it seems more likely that the disjunct distribution involving only one taxon in the other region is due to dispersal. In the sense that these speciation events might be considered attributes of a particular region, it could be concluded from the evidence of Fig. 8**A** that the differentiation of the taxa in question postdated the subdivision of the area into two. Otherwise, the confinement of these speciation events to one protoregion, before it acquired separate identity, could only be attributed to chance.

An example here is the case of the Late Devonian placoderm *Phyllolepis* discussed above. Its apparently earlier biostratigraphic appearance in Australia compared to Europe has already been mentioned. Previously (Young, 1981), the suggestion of Denison (1978) that the Antarctic form *Antarctaspis* might be a primitive phyllolepid, was considered as possible evidence for an origin of the group in east Gondwana. Further evidence is now provided with the description of new phyllolepid taxa from southeastern Australia (Ritchie, 1984; Long, 1984), which (with or without *Antarctaspis*) appear to represent a paraphyletic stem group. That the known occurrence of these primitive representatives is in the Antarctica-eastern Australia region is consistent with the hypothesis that the group evolved and diversified here before it gained access to Euramerica in the latter part of the Late Devonian. The species within the genus *Phyllolepis* can be seen as a crown group for which both regions constitute a single area. In contrast, the paraphyletic stem group is restricted to one of the regions, suggesting a barrier between them.

Thus, given certain data regarding the geographical occurrence of hypothetical barriers affecting the phylogenetic history of a particular group, inferences can be drawn on the likely explanation (vicariance or dispersal) of the distribution of that group in space. But the important point is that those situations where application of the progression rule is convincing (Figs 6**B**, 8**D**; Nelson, 1969: fig. 3) are special cases, and in other cases (Fig. 6**C**) the rule is clearly inappropriate, and obviously represents nothing more than an arbitrary assumption that attainment of a widespread distribution in the ancestral species (y, Fig. 6**C**) was by means of dispersal (associated with speciation), rather than by range enlargement. Another difficulty is that if one is prepared to admit one dispersal episode to explain the differentiation of the most recent sister species (Fig. 8**A**, **D**), then a single dispersal episode earlier in the history of the group should also be accepted. This would provide an alternative to a vicariance explanation in certain situations (e.g. Fig. 8**C**, **F**), unless a methodological rule of minimum dispersal was adopted. But consistently applied this rule would also give a vicariance explanation for the situation of Fig. 8**A.** As pointed out by Platnick and Nelson (1978), in dealing with the history of a single group neither vicariance nor dispersal explanations can be conclusively refuted, and where Hennig's rule might seem appropriate, various additional assumptions or methodological rules must be adopted (e.g. minimum parallel dispersal; minimum number of dispersal plus vicariance events, location and age of barriers as criteria for identifying discrete regions, etc.). Furthermore, in the real situation, it is unlikely that straight-forward distribution patterns of the type discussed above (Figs 6**B**, 8**D**) will be encountered, and it is likely that any appraisal of distributional biological data will be significantly influenced by knowledge of the supposed geological history of the areas (see also below). Despite these difficulties, important results have been obtained from this type of analysis (e.g. Brundin, 1966).

I suggest therefore that certain types of distribution pattern within certain geological contexts may indicate that application of the progression rule is appropriate. Clearly, it is not applicable in all cases. Thus I do not fully agree with Platnick's (1981) conclusion that the progression rule, judged by the criterion of yielding a definitive result, is no different from Darlington's (1957) rule that the centre of origin of a group is marked by the range of its most apomorphic members. Platnick also asserts that under a falsifiability criterion (Popper, 1959) the progression rule fails, since falsification depends on finding certain fossils in certain areas. He implies that any choice between the most primitive (Hennig-Brundin) or advanced (Darlington) members of a group as indicators of a centre of origin would be an arbitrary one, based only on unscientific or aprioristic criteria. But there is an important difference between these two methods, previously discussed in the literature, but worth restating. This is that under Hennig's progression rule a parsimony criterion (minimal dispersal) is employed to estimate ancestral distributions, whereas under Darlington's method an unspecified number of migratory waves are required to displace more primitive members of a group away from the evolutionary centre. Thus the former method is an analytical technique of great heuristic value, but the latter is very much a descriptive explanation of process which provides no direction for future investigations.

Turning now to Platnick's comment on falsifiability, we might also consider on this point Platnick and Nelson's earlier discussion (1978: 3-7), and comments by Patterson (1981:450-453). Because these theoretical discussions are concerned with historical explanation of a distribution of Recent taxa, which is assumed to be known, it is to be expected that the possible discovery of earlier (i.e. fossil) taxa features prominently as a potential falsifier of particular historical explanations. But it is clearly unacceptable then to use this as a ground for criticizing a certain model because of its dependence on an unreliable fossil record for falsification, as Platnick (1981: 147) has done. If the logic (Platnick and Nelson, 1978) on which this claim is based is valid, then it is clear that the falsifying taxa should play the same role in analysis whether extinct or extant, using the earlier argument of Nelson (1969: 245). As such, Platnick's (1981) claim would seem to be no more than an alternative expression of Patterson's assertion (see above) that 'Recent distributions may be regarded as completely known in many groups'. It may well be that studies in palaeontology and geology are 'subject to wide margins of error' (Platnick and Nelson, 1978: 3), and that there are certain groups in

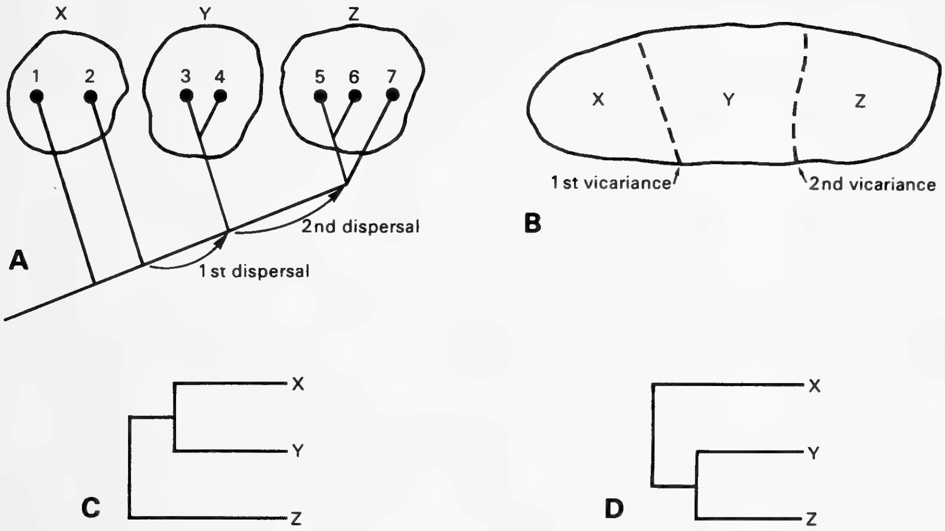

Fig. 9. Seven hypothetical species distributed in three areas (X, Y, Z), and related as shown. **A**, a dispersal explanation involving two dispersal episodes. **B**, a vicariance explanation involving two vicariance events. **C**, a similarity diagram for the areas concerned which might be derived from **A**, on the basis that X and Y are similar in possessing relatively primitive species compared to the more diverse and advanced species in area Z. **D**, an area cladogram based on **B**, consistent with the relative recency of dispersals indicated in **A**.

the modern biota whose geographic distribution may be regarded as completely known. But it surely does not follow that other branches of science are in any general or specific sense subject to less error; nor, that the relationships and distribution of monophyletic taxa amongst an appreciable number of living groups are so well understood that general conclusions can be reached regarding falsifiability of a model seeking to explain such distributions, by pointing to unreliable palaeontological data as the only means of falsification. This is tantamount to a general assumption that Recent groups are completely known. However, as is argued below (Fig. 11), it is the logic of Platnick and Nelson (1978) on which such claims are based which assumes a complete fossil record, and is therefore spurious.

In an actual situation, furthermore, any analysis of phylogenetic relationships and distribution patterns within a reasonably diverse group obviously incorporates numerous assumptions at different levels of generality, for example, empirical statements not definitely established, theoretical considerations of limited applicability, etc. The conclusions of analysis are testable as each of these assumptions is subject to further investigation. In this sense, Brundin's comments (1981: 133) about basing theoretical formulations on the analytical experience of particular cases has some relevance.

On the same issue, Patterson (1981) considers the four classes of potential falsifiers put forward by Ball (1976), and finds them to be inadequate, and to impinge primarily on the cladogram rather than the geography. But if it is assumed that a monophyletic taxon has been correctly identified, its geographic distribution is an immediately derivable empirical statement requiring no analytical procedure, and potential falsifiers concerned with that taxon could only be expected to affect the cladogram (i.e. the analytical procedure to establish monophyly). Falsifiers of the geographic part of the hypothesis would necessarily be concerned with analytical procedures related to our current comprehension of geography. In the present context this would largely involve analysis of historical geology, an aspect which Patterson argues should not be an integral part of hypothesis formulation.

To summarize, I would argue that criticism of Hennig's progression rule on two grounds (falsifiability, and assumption of a complete fossil record) cannot be sustained, and that the method as formalized by Nelson (1969) remains a valid and testable means of estimating dispersal and vicariance history, given a cladogram of interrelationships for the group concerned. If this is so, then one might ask whether the 'cladistic vicariance' method (pattern biogeography) discussed in the next section has any special merit which would justify its use in preference to Hennig's progression rule. It would seem that there is no straightforward answer to this question, because the two methods have different aims. As Platnick (1981) has pointed out, pattern biogeography attempts to discover whether areas of endemism in which many groups co-occur are interrelated to each other according to a particular pattern, which represents a summary of the phylogenetic interrelationships of some or all of the endemic groups occurring in those areas. Progression-rule biogeography, on the other hand, is in any particular example concerned with a parsimonious estimation of dispersal and vicariance history for a single group, which may not be causally related to the history of interconnection between the areas occupied by members of that group. Excluding chance dispersal, however, such analysis can provide information on area connections (Fig. 9). Dispersal events deduced from analysis can be distinguished unambiguously in terms of their chronology, and thus the relative recency of interconnections between the areas concerned can be directly inferred from the relative recency of dispersal events, as has previously been pointed out (Platnick and Nelson, 1978). From this, an area cladogram can be derived, just as can be done when a vicariance explanation is applied to similar data (Fig. 9**B, D**). To the extent that applications of Hennig's progression rule have dealt with dispersal histories of single groups rather than general biogeographic patterns, such applications might be regarded as deficient. But I suggest that attempts to demonstrate that the rule is unfalsifiable derive from misconceptions about the role of fossils in testing procedures, and the distinctness of biological and geological data in hypothesis formulation. These issues are best discussed in a consideration of the method of analysis proposed by Platnick and Nelson (1978).

Pattern biogeography ('cladistic vicariance'). As noted above, the biogeographic method of Platnick and Nelson (1978), here termed pattern biogeography, is concerned with whole biotas, their interrelationships, and the interrelationships of the areas they occupied. Some of the basic assumptions of this method have been mentioned above, and summarized previously (Young, 1981: 232). Under the assumption of allopatric speciation resulting either from subdivision of a continuous ancestral biota (a vicariance event), or by biotic dispersal across pre-existing barriers, it is predicted that a common pattern of interrelationships may result between taxa endemic to the areas in question. Since this pattern, as represented by a cladogram, expresses a relative chronology for the most recent common ancestors of all pairs of endemic taxa (sister groups), it may be directly converted into a cladogram of areas expressing relative recency of connection between those areas. Within the biota however there could be certain groups which were not distributed throughout the original area, did not respond to one or more vicariance events by speciating, have undergone subsequent or chance dispersal, have become extinct, have not had all their relevant species sampled, or have had their interrelationships incorrectly analysed. For such groups a simple conversion of a cladogram expressing their interrelationships into a cladogram of areas may not be valid. (According to Platnick and Nelson's analysis, however, neither extinction nor failure of some groups to respond to dispersal or vicariance events should affect the inferred area pattern). To the extent that such groups form a lesser or greater proportion of all groups investigated in relation to a particular biogeographic problem, then a general pattern will be more or less easy to recognize. A major aspect of this method of analysis is therefore concerned with comparing cladograms to establish whether they are congruent with each other in whole or in part (e.g. Nelson and Platnick, 1981). A significant number of congruent cladograms for different organisms endemic to certain areas would imply a general pattern, a general explanation of that pattern, and therefore that the resulting area cladogram was a valid one. It is possible, of course, that this type of analysis may not produce convincing general patterns because of the predominant influence of the various other factors listed above (Nelson and Platnick, 1981). The usefulness of pattern biogeography therefore awaits future analysis of test cases, since for the majority of areas of endemism, detailed information regarding interrelationships of endemic taxa required to undertake this analysis is not yet available (Nelson and Platnick, 1981).

Possible alternatives to an assumption of original biotic continuity between areas of endemism (biogeographic provinces) were discussed above, and found except in special cases to be incapable of precise formulation. On other grounds the validity of the vicariance approach has also been questioned. Previously (Young, 1981: 235) I suggested that the method may not be generally applicable to palaeobiogeography, since the vicariance analysis of Recent biotas has as its historical geological framework, according to current theory, the Mesozoic and younger fragmentation of a supercontinent (Pangaea). An assumption of primitive (Pangaean) cosmopolitanism for the biogeographic analysis of many Recent animals and plants is therefore not unreasonable. However, as noted by Brundin (1981), extensive prior dispersal must be assumed to achieve that widespread distribution. Although such aspects might be considered unnecessary and irrelevant (Croizat *et al.,* 1974; Platnick, 1981) when analysing modern distributions, they may clearly be very relevant to the palaeobiogeographer concerned with earlier periods of earth history.

It is pertinent here to comment on a point of terminology indicative of a biased approach, which has caused some confusion in the recent literature. The method of analysis outlined by Platnick and Nelson (1978) was not graced with a name, but has subsequently been referred to as 'vicariance' biogeography by Platnick (1981), and as 'cladistic vicariance' by Patterson (1981; also Young, 1981). However neither term is appropriate. Platnick and Nelson (1978: 7) concluded that 'distributional data seem sufficient to resolve a pattern of interconnections among areas that reflects their history, but not to specify the nature of those connections'. Since, according to their analysis, neither dispersal nor vicariance explanations can be unambiguously distinguished using distributional data, then why not 'dispersal' biogeography, or 'cladistic dispersal'? The answer seems to be some perceived difference in the quality of the evidence required to refute an initial assumption of dispersal, or of vicariance, as an explanation of an observed distribution. Thus, Patterson (1981: 465) writes:

> 'The dispersal interpretation is tested only by fossils of that taxon, whereas the vicariance interpretation can be tested by other taxa, fossil or living, that should have been affected by the same barriers and that therefore should show relationships congruent with those of the taxon under study. In other words, dispersal treats each taxon as an individual case, whereas vicariance is a general explanation. . . .'

But Platnick and Nelson's (1978) analysis surely shows that neither explanation of a general pattern can be conclusively falsified; postulating vicariance to explain a congruent pattern is no more general than postulating unidirectional dispersal for the

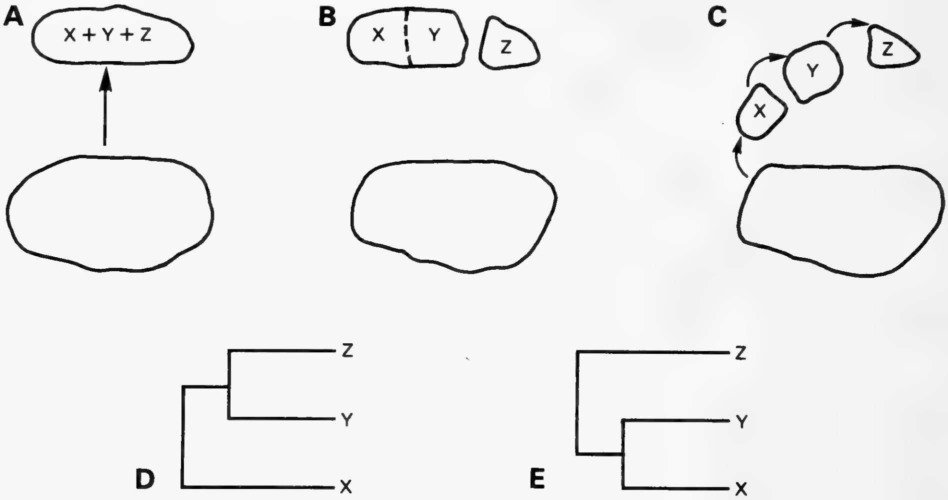

Fig. 10. An example of vicariance giving a unique area cladogram, and of directional biotic dispersal giving a different general pattern of area relationships. **A**, dispersal of founding species onto a newly-formed island (X + Y + Z). **B**, subdivision of this area, causing allopatric speciation. **C**, change in area interdistance, resulting in step-wise dispersal into the three new areas (arrows). **D**, general area cladogram for dispersing species. **E**, unique area cladogram for vicariating species.

same groups showing this pattern. Chance dispersal may be identifiable by a unique pattern, but no purely biological criteria have been proposed for distinguishing biotic vicariance from biotic dispersal as an explanation of a general pattern. And of course a unique incongruent cladogram could be the result of a single case of vicariance within a general pattern resulting from directional biotic dispersal (Fig. 10). It is unclear therefore why it is deemed necessary to demonstrate the non-testability of Brundin's methods, which were after all concerned with congruent patterns amongst three subfamilies of chironomid midges, and a geological area cladogram (e.g. Nelson and Platnick, 1981: 478). As pointed out above, the arguments of Platnick (1981) and Patterson (1981), that dispersal explanations cannot be falsified because a complete fossil record is assumed, can hardly be taken seriously when based on analysis of a theoretical example where interrelationships and distribution of the Recent taxa are taken as given; that is, where complete knowledge of those Recent taxa is assumed. Looking more closely at this theoretical example (Platnick and Nelson, 1978: fig. 1), and applying the methodological rule that fossil taxa should be treated in the same way as living taxa, it would seem that the falsifying widespread fossil taxon must be regarded either as irrelevant to this problem of area relations (Fig. 11**B**), or else as the most recent common ancestral species of the three extant taxa. Thus, it is this particular argument which assumes a complete fossil record (in which actual ancestral species can be recognized), and not the dispersal model itself. Similar arguments could be developed regarding falsification of a vicariance explanation using fossil taxa, and similar difficulties would be encountered. The reason is that the differences between the two models are concerned with the distribution of hypothetical ancestral species, which can only be known through the distribution of their descendants (the same in each case).

If we wish, therefore, to compare the testability of dispersal and vicariance interpretations of a distribution of three related taxa in three areas on its own merits (that

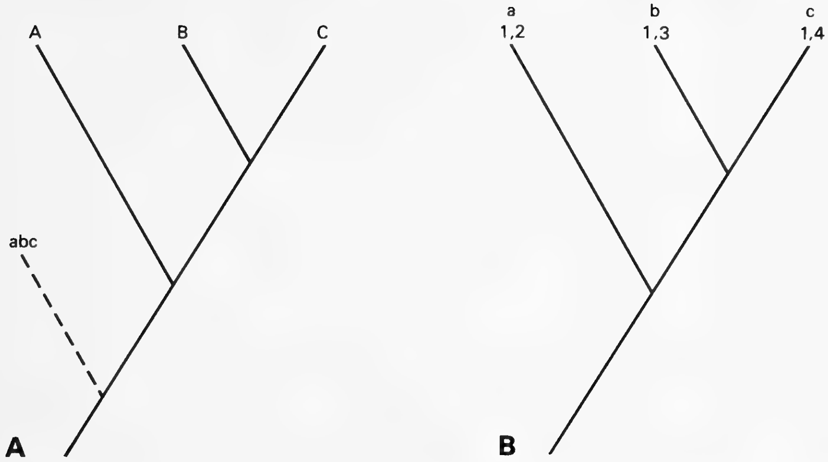

Fig. 11. **A**. Three taxa (A, B, C) distributed in three corresponding areas (a, b, c), and a widespread fossil taxon (dashed line) related as shown (after Platnick and Nelson, 1978: fig. 1.5). **B**. The same example, showing the distribution of the four taxa of A (1-4) in the three areas (a, b, c). The fact that taxon 1 is fossil demonstrates only an extinction event. Whether living or extinct, this taxon is distributed in all three areas, and is therefore irrelevant to the question of the history of interconnection of those areas.

is, not in relation to other groups occurring in the areas), we must assume incomplete knowledge of both Recent and fossil taxa relevant to the problem, and consider predictions regarding the discovery of new related taxa (extant or extinct) in the three areas. One example concerning new taxa within the crown-group (Patterson, 1981: 461) is given in Fig. 12. Another, concerning stem-group taxa, was discussed above (Fig. 8). Compared in this way, I suggest that vicariance and dispersal explanations cannot be differentiated in terms of their falsifiability. Alternatively, if we wish to compare the testability of dispersal and vicariance interpretations of the same distribution in terms of the distribution pattern of other taxa endemic to these areas, we can again consider predictions derivable from each model. Regarding a dispersal explanation, Platnick and Nelson (1978: 4) state that because 'dispersal capabilities of these organisms may or may not be similar to those of other groups, we can make no predictions about what patterns other groups that occupy these areas might show'. Equally however, vicariance events causing differentiation of the taxa in question under a vicariance explanation may or may not affect other species in the same way (e.g. Nelson and Platnick, 1980), so again we can make no predictions about what patterns other groups might show. Compared in this way, I again suggest that vicariance and dispersal explanations cannot be differentiated in terms of their falsifiability.

It is for these reasons that I use the term 'pattern biogeography' for a method of analysis (Platnick and Nelson, 1978) which acknowledges that distributional data are sufficient only to retrieve a biogeographic pattern, but not the cause of that pattern. The belief that vicariance is a preferred explanation, and attempts to justify that belief by claiming that dispersal explanations are unfalsifiable, is perhaps a holdover from earlier discussions in which the vicariance explanation was totally supported (e.g. Croizat, Nelson and Rosen, 1974; Nelson, 1975). In a similar way the notion of a centre of origin has been banished from the literature, yet this concept is still clearly applicable in cases where general patterns are attributable to directional biotic

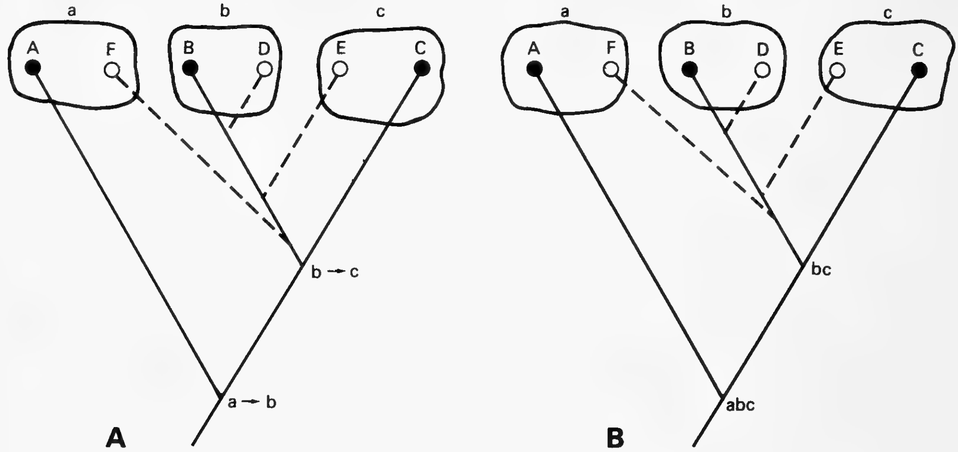

Fig. 12. Alternative hypotheses explaining the distribution of three taxa (A, B, C) in three areas (a, b, c), and tested by the discovery of new taxa (living or extinct) in the three areas (D, E, F). Neither hypothesis can be conclusively refuted. **A**, a dispersal explanation; taxon D is consistent with the dispersal explanation; taxon E can be explained by additional parallel dispersal, but suggests a vicariance explanation; taxon F can be explained by a reverse dispersal, but suggests a vicariance explanation: **B**, a vicariance explanation; taxa D, E, F can be explained by additional vicariance events, within areas b, c, and a respectively.

dispersal. Furthermore, it seems likely that this bias favouring vicariance may be due to the influence of geological theory. Patterson (1981) expresses the view (also Rosen, 1978) that historical geology cannot test biological area cladograms. But Platnick and Nelson (1978) have proposed the evidence of historical geology as a means of resolving causal explanations for a general pattern of area interconnections based on distributional data. In my view it would be false to pretend that current geological theories do not influence the way in which biogeographic problems are approached. As noted above, in the light of the prevailing geological model of breakup of a super-continent (Pangaea) during the Mesozoic-Cainozoic to give the modern distribution of continents, an appraisal of vicariance as a preferable explanation for the biogeography of modern continental (including shelf) biotas seems very reasonable (the 'vicariance paradigm' of Nelson, 1976). Perhaps this results from a general preference for parsimony of hypotheses; that is, the potential of vicariance in this context to explain two or more events (continental breakup, plus dispersal of one or more groups of organisms), by one. However, vicariance is not necessarily an effective explanatory tool in other situations. During the middle Palaeozoic, for example, a plate tectonics interpretation suggests extensive continent collision between regions which had been separated by wide oceans during preceding geological periods. It is possible therefore that we have here completely the reverse, on a global scale, of the historical geological framework applicable to a biogeographic analysis of modern distributions. For modern faunas and floras in open marine situations the model of continental fragmentation during the Mesozoic-Cainozoic is not obviously relevant to an understanding of distribution patterns, and on a more local scale a similar situation has been argued by Holloway (1982) in the case of Melanesia, where emergence of new land areas and convergence of continents are thought to be the predominant features of recent geological evolution of the region.

The question to be asked therefore is what method of analysis is appropriate in those situations where it seems most unlikely that subdivision of an ancestral biota was

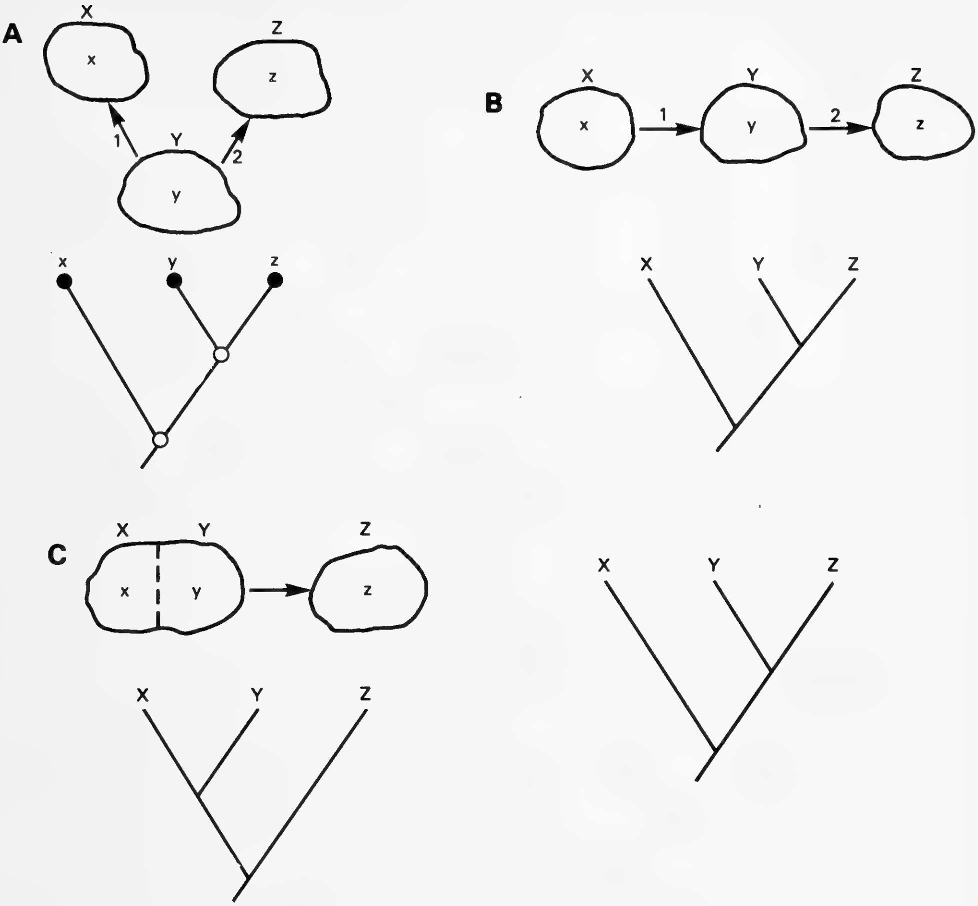

Fig. 13. Three ways in which a species (y), from which a new species (z) is derived by dispersal to colonize a new area or habitat, may be related to a third species (x) outside these areas. **A**, as a result of a previous dispersal to another area; **B**, as a result of a previous dispersal from another area (area cladogram shown); **C**, as a result of a vicariance event, which may have occurred before or after dispersal to area Z (alternative area cladograms shown). For discussion see text.

the predominant means of creating endemic faunas and floras. Holloway (1982) has argued that the biogeography of newly-formed land areas as in Melanesia must be seen in terms of dispersal and colonization from older land areas outside. In attempting to explain the first appearance of diverse early gnathostome faunas in many different regions at about the same time (Late Silurian/Early Devonian), I previously suggested (Young, 1981) that major groups may have evolved from ancestral forms widespread in shallow marine environments, as freshwater habitats were invaded. Both instances would be examples of colonialistic or vacuum biogeography in the sense of Platnick and Nelson (1978: 1). It is relevant to consider what relationships such colonizing forms might be expected to show to taxa of outside areas, and it seems obvious that any newly differentiated endemic species resulting from dispersal into a newly available area or habitat would have its sister group in the area or habitat from which it dispersed. For meaningful comparative analysis at least three taxa and areas must be considered (Fig.

13), and there seem to be only three ways in which outside relationships of the first species may develop:

a) it may have previously given rise to another dispersing species to a different area, which may be expressed in the cladogram of Fig. 13**A.** If there was no change in the area relationships (e.g. distance between areas, nature of barriers, etc.) then conversion to an area-cladogram in this case would seem to be spurious. In other words, it could be predicted that other species endemic to areas Y and Z would show outside relationships conforming to Fig. 13**B** or **C**, and the cladogram of Fig. 13**A** would conflict with a general pattern, and be inferred therefore to result from chance dispersal;

b) the relationship of the first species to a third species may be the result of prior dispersal from another area (giving, for the three areas, a sequential dispersal). As noted above, an area-cladogram in this situation will reflect the relative recency of dispersal events, which, if not due to chance, but to potentially identifiable causal factors (e.g. change in water currents, distance between areas), may form part of a general pattern;

c) the outside relationship of the first species may have resulted from a vicariance event (Fig. 13**C**). Unlike the previous case, there are here two possibilities depending on which event (vicariance or dispersal) occurred first. Either way a taxon cladogram converted to an area cladogram will reflect the relative recency (but not the degree or nature) of interconnections between areas. To the extent that other organisms were involved in both the vicariance and dispersal episodes, then this area cladogram may form part of a general pattern.

In the light of these considerations therefore, I suggest that where geological or other evidence points to directional dispersal across barriers as a predominant cause of disjunct distributions, the appropriate method of analysis is to develop hypotheses of relationship for endemic taxa in the areas concerned, convert the resulting taxon cladogram into an area cladogram, and then repeat the exercise with other groups such that a general pattern might be identified; in other words, the procedure advocated by Platnick and Nelson (1978). In such cases, where dispersal is regarded as the predominant mechanism, an assumption that there was a common ancestral biota (required under a vicariance model), can be replaced by an assumption that there was a centre of origin for those taxa involved in the analysis.

ANTIARCH BIOGEOGRAPHY

We may now consider again the cladogram of Fig. 2, to illustrate some of the points developed above using the distribution pattern of antiarchs as an example. Obviously, the first comment to be made is that by dealing with one group only, no reliable conclusions about general patterns can be drawn, and any inferences regarding area connections must be seen as tentative. Yet, as noted elsewhere (Young, 1984), it is appropriate that such analyses be undertaken, if only to present precise statements of the biogeographic implications of limited available data. In addition, where many sympatric taxa are involved, as appears to be the case within the antiarchs at the present level of analysis, it is possible that congruent patterns amongst antiarch subgroups might be identified. Previously (Young, 1981: 257), I suggested that any clear pattern of allopatric differentiation amongst the antiarchs was probably obscured by extensive dispersal. However, an examination of Fig. 2 suggests that only certain genera *(Bothriolepis, ?Remigolepis, ?Microbrachius)* have a markedly widespread distribution, which might be attributed to different dispersal capabilities of these forms. A detailed analysis, for example, of the distribution of the many species of *Bothriolepis* during the Middle/Late Devonian can thus be seen as a separate biogeographic problem, beyond the scope of this general discussion.

However the primary distribution of the four major antiarch subgroups during the Early Devonian is a matter for consideration. Regarding one of these, the asterolepidoids, it has been pointed out (Janvier and Pan, 1982; Young, 1984) that no representatives are known from south China before the Late Devonian. Considering that diverse fish faunas are known from many localities of Early and Middle Devonian age in the south China region (e.g. Pan, 1981), it seems unlikely that the absence of asterolepidoids is due to lack of preservation or discovery. Since the group is known from various Early and Middle Devonian localities elsewhere, it is reasonable to interpret the two genera known from south China *(Asterolepis, Remigolepis)* as late arrivals in the region. Whether this resulted from dispersal, or from range enlargement and vicariance, would depend on the nature of barriers between south China and other areas during the Late Devonian. Either way, it would seem that there was some change in the nature of these barriers, or with the dispersal capabilities of these late species, relative to the situation in the Early Devonian. The former alternative is perhaps supported by the fact that a marked provincial pattern amongst several groups of marine invertebrates during the Early Devonian was replaced in the Late Devonian by cosmopolitan faunas (e.g. Johnson and Boucot, 1973). This has been attributed to the development of extensive epeiric seas during Frasnian time.

As in the case of the placoderm *Phyllolepis* (Young, 1981), biostratigraphic evidence can be used to cope with a changing situation (palaeogeographic or otherwise) within the history of this group. Regarding the initial distribution ('centre of origin') of the asterolepidoid antiarchs, the earliest form so far recorded probably occurs in central Australia (Young, 1984), but there are good reasons (uncertainty regarding other areas not yet investigated, lack of morphological information permitting an adequate assessment of relationships) for not accepting this occurrence as significant. Considering the ten better-known genera included in Fig. 2, and applying Hennig's progression rule, gives Euramerica as their centre of origin; yet the displayed pattern is clearly not one suggesting that this rule would apply (cf. Fig. 8). The alternative vicariance model implies a widespread ancestral asterolepidoid in all four areas (Euramerica, Australia, Kazakhstan, south China), and in three when the biostratigraphic argument of late dispersal to south China is incorporated. The only reasonable conclusion on available evidence is that a specific area of origin for asterolepidoid antiarchs, if one existed, was in some region other than south China.

Turning to the other major antiarch subgroups (bothriolepidoids, sinolepids, yunnanolepids), south China has been inferred to be an evolutionary centre (Young, 1981), since much of the early differentiation within these groups occurred in this region (Fig. 2). However this general observation requires closer scrutiny. The bothriolepidoids, in contrast to the asterolepidoids, are well represented in the early Middle Devonian of south China (e.g. *Dianolepis, Bothriolepis*), whereas the latter genus only became widespread (Europe, Russia, Greenland, North America, etc.) during the Late Devonian. Again, decreased isolation for the south China region is indicated, and again biostratigraphic evidence suggests a change in the nature of barriers, or in dispersal capabilities, between Middle and Late Devonian time. Before such changes occurred, several more primitive bothriolepidoid taxa differentiated in the south China region, and the same applied for their presumed sister group (the sinolepids). Applying the progression rule gives south China as the centre of origin for this monophyletic group, and if the Australian sinolepid and the Euramerican *Microbrachius* are attributed to later dispersal, then the early vicariance history of the group could be interpreted as confined to the south China region, approximating a pattern of the type in Fig. 8**D**. At least for the Australian sinolepid, which is Late Devonian in age, a case for dispersal might be argued. Alternatively, the involvement of Australia at two positions in the cladogram could indicate that the common ancestor for the group was distributed in both regions, giving a pattern similar to (but more complex than) that illustrated in Fig. 8**E.** This example illustrates the arbitrariness of decisions about vicariance or dispersal mechanisms based on a single group, and also the problems of dealing with fossil data involving incomplete sampling through more than one area pattern (reflecting different palaeogeographies at different times). For resolution it would seem necessary to rely on reciprocal illumination using geological or biostratigraphic data, although neither is yet particularly helpful in this case. Nevertheless, considering together the available distributional data for the asterolepidoids, a vicariance explanation for the differentiation of the two groups is indicated, as argued by Janvier and Pan (1982). Thus the area of origin for the bothriolepidoids (? plus sinolepids) can be specified as including south China, and possibly other areas, of which the most likely is Australia.

The last major subgroup (yunnanolepids) includes remarkably primitive forms which have only been recorded from the Early Devonian (or older) of south China. Janvier and Pan (1982: 388) question whether this means that south China was their centre of origin, but given their known distribution the only reasonable assumption is that the group evolved in place (that is, that their most recent common ancestor also occurred only in south China). The fact that this, the most primitive known group of antiarchs, is restricted to south China, means that application of the progression rule for antiarchs generally also gives their origin as south China. It could again be suggested that there is a biostratigraphic argument supporting this notion (the early antiarchs in south China are considerably older than known elsewhere; Pan, 1981), but in this case the argument is not necessarily valid, and depends on questions of relationship at the base of the antiarch cladogram. Thus, if yunnanolepids are monoplyletic, and the Late Silurian antiarchs from south China (Pan, 1981) can be shown to belong to this group, then this gives a minimum age of Late Silurian for ancestral euantiarchs also (Young, 1984:77), even though they are not recorded until somewhat later (perhaps late Lower Devonian; see Young, 1984). On these theoretical grounds therefore the biostratigraphic argument pointing to a south Chinese origin for all antiarchs would not be valid. On the other hand, if yunnanolepids are paraphyletic, with some members more closely related to euantiarchs (on pectoral fin structure *Phymolepis* is a possible candidate; see Fig. 2), then south Chinese origins for both euantiarchs and antiarchs generally would be indicated, and the biostratigraphic argument would provide supporting evidence. Clearly the morphology and relationships of the Late Silurian antiarchs of south China are of central importance here, as is the position of sinolepids on the cladogram. If sinolepids (in accordance with earlier schemes) were regarded as the sister group of other euantiarchs, then a similar conclusion would be indicated (an implied secondary biostratigraphic argument involving late dispersal of sinolepids into Australia would be subject to independent investigation). However, based on my current appraisal of antiarch interrelationships (Fig. 2), and assuming until there is good evidence to the contrary that yunnanolepids are a monophyletic group, the available evidence indicates a widespread distribution for both ancestral antiarchs and ancestral euantiarchs.

To summarize, the following areas of origin for the major monophyletic groups of antiarchs are suggested: asterolepidoids, an area including part of all of Euramerica, Kazakhstan, and Australia, but excluding south China; bothriolepidoids plus sinolepids, south China, or south China plus Australia; yunnanolepids, south China; euantiarchs and antiarchs, cosmopolitan. On the centre of origin concept generally, Janvier and Pan (1982: 387) have noted aspects in common with the idea of ancestral species or groups, the recognition of which depends on the absence of derived characters, and earlier stratigraphic age. But as stated in the previous section, where dispersal is the cause of general patterns, the centre of origin concept clearly has validity, and, as is clear from the preceding discussion, where the primary distribution of a group has been enlarged by secondary dispersal, one can also develop arguments to specify that primary distribution or area of origin.

Since the issue of completeness of the fossil record appeared in several contexts in the preceding discussion, it is appropriate to conclude by briefly considering the nature of the fossil record of the antiarchs. Regarding future discoveries, it is of course true that 'no one knows what may be found' (Patterson, 1981: 463), and this applies particularly to many areas where there has been little or no search for Devonian vertebrates. But other areas are better known, and some predictions regarding future discoveries might be made. Thus, over the many years that Devonian fishes of Europe have been studied, the antiarch *Bothriolepis* has not been found in strata older than late Middle or early Late Devonian. Similarly, after some two decades during which the Early and Middle Devonian antiarchs of south China have been investigated, no reports of members of the Asterolepidoidei have withstood re-evaluation, the two known representatives *(Asterolepis, Remigolepis)* being Late Devonian in age. Assuming that the presence of these latter forms in south China is due to dispersal (which is demonstrated by sympatry, regardless of differences in age), the known fossil record shows that this dispersal originated outside the areas occupied by the earlier faunas, and gives an indication of the approximate time (late Middle Devonian) when barriers to such dispersal ceased to operate. It would seem that any argument that such biostratigraphic evidence should not be utilized on the grounds that future discoveries (in this case Early Devonian asterolepidoids in south China) might change the pattern, can be rejected as unscientific, because it attributes the observed pattern to chance alone, and such explanations cannot be subjected to further scientific investigation.

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Two new Species of *Glycaspis* (Homoptera: Psylloidea) from tropical Queensland, with Notes on the Genus

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MOORE, K. M. Two new species of *Glycaspis* (Homoptera: Psylloidea) from tropical Queensland, with notes on the genus. *Proc. Linn. Soc. N.S.W.* 107 (4), (1983) 1984: 475-478.

Two new species of the genus *Glycaspis* Taylor from *Eucalyptus raveretiana* and *E. similis* respectively are described. New hosts and localities for other species are recorded. Further indications of the possible occurrence of parthenogenesis within the genus are given. The *Glycaspis* species described from *E. raveretiana* indicates its phyletic affinity with *G. clivosa* from *E. brachyandra.*

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INTRODUCTION

The four tropical *Eucalyptus* species: SBA:A *deglupta* Blume, SBA:C *raveretiana* F. Muell., SBA:D *brachyandra* F. Muell., and SSA:A *howittiana* F. Muell. constitute the subgenus *Telocalyptus* (Johnson, 1976) among some 550 species and subspecies in the genus (Chippendale and Wolf, 1981).

Glycaspis (Glycaspis) clivosa Moore, 1977, was previously described from *E. brachyandra.* As no information was available on possible insect/host relationships of *E. raveretiana* or *E. howittiana,* this project was designed to obtain from them *Glycaspis* specimens and other associated Psylloidea for taxonomic studies.

With the addition of two new species, the subgenus *Glycaspis* now contains 85 of the 135 species in the genus; the subgenera *Synglycaspis* (Moore, 1961, 1970a) and *Boreioglycaspis* (Moore, 1964) contain 38 species and 12 species respectively.

As *Glycaspis* spp. are variable in colour, most species being apparently influenced by temperature and/or seasonal factors, general coloration only is given in the descriptions.

All of the *Glycaspis* species mentioned were collected by the writer, and are lodged in the Australian National Insect Collection, Canberra. Other genera of the Psylloidea collected are being studied by Mr K. L. Taylor, psyllid taxonomist.

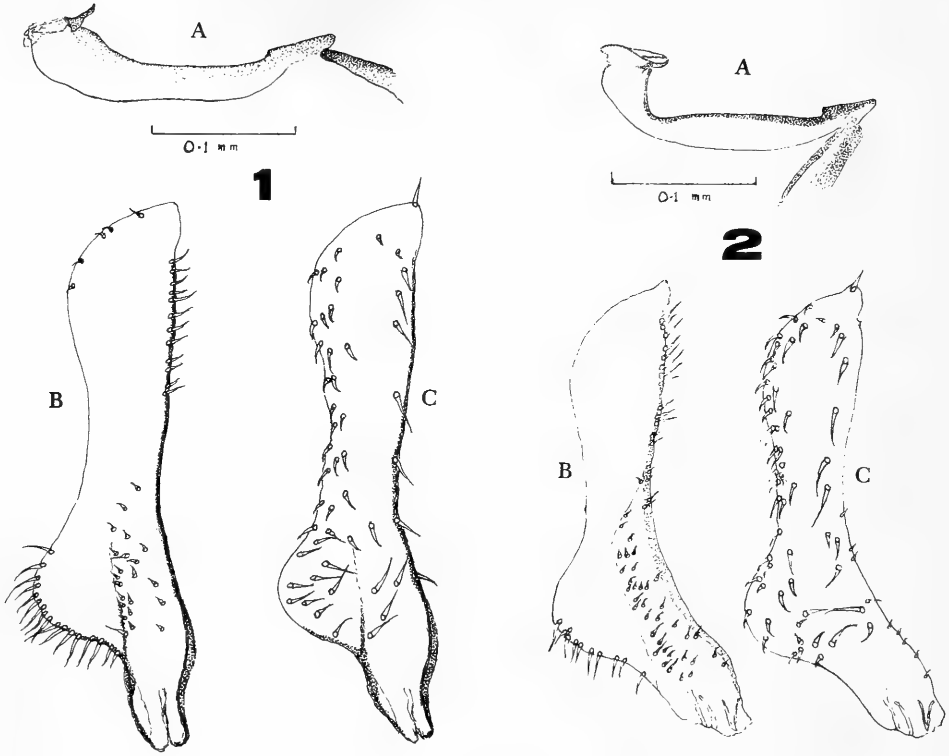
RESULTS

(a) TAXONOMIC

Glycaspis (Glycaspis) operta sp.n.

Fig. 1

Types: — Holotype ♂ on slide labelled 'Boundary Creek, 18 km NE. Nebo, Qld, 6 v 1982, *E. raveretiana*'. Paratypes: 1 slide of a single ♂, with same label data as the holotype; 1 slide of a ♂ labelled 'Denison Creek, 30 km NE Nebo', with same date; 4 slides each of a single ♂ labelled 'Boundary Crk, 18 km NE Nebo, Qld, 14 ix 1982, *E. raveretiana*'. In ethanol: 3 ♀♀, lerps, in tube with same label data as the holotype; 4 lerps in tube with same label data, but dated 29 vii 1981; 1 ♀ in tube with same label data but dated 16 vii 1980; 8 ♂♂ 7 ♀♀ and 8 oval lerps in tube with same label data but dated 14 ix 1982; 5 ♀♀, lerps, in tube labelled 'Denison Crk, 30 km NE Nebo, 7 v 1982, *E. raveretiana'*; 4 ♀♀, lerps, in tube with same data but dated 29 vii 1981; 1 ♀ in tube with same data, dated 16 vii 1980.



Figs 1 and 2. Aedeagi and claspers of *Glycaspis* spp.
1. *G. operta.* (**A**), Aedeagus. (**B**), Claspers: internal face, (**C**), external face.
2. *G. atkinsoni.* (**A**), Aedeagus. (**B**), Claspers: internal face, (**C**), external face.

General colour: Males (live specimens) pale bright green indistinctly marked with black; females as males but lightly marked with black and with red suffusion. The green being fugitive in ethanol, specimens become creamy-yellow.
Claspers and aedeagus: as in Fig. 1.
Length of aedeagus: 0.198-0.208 mm (7 specimens).
Length of hindwing vein Cu_1: as Group (ii) (see Moore, 1970b, 1983).
Lerps: round to oval.
Host: SBA:C *Eucalyptus raveretiana.*

Notes: The phyletic position of *G. operta* appears to be nearest to, and more recent than, *G. clivosa,* and differs in the following characteristics:— aedeagus longer (*G. clivosa* 0.171-0.185 mm, 10 specimens), less upturned and more rounded distally, proximal ridge longer and narrower. Claspers more fragile but with posterior edge more strongly sclerotized, setae more sparse, protrusion toward base less prominent. Lerps are often oval in shape, thus readily distinguishing this species from *G. clivosa* which constructs only round lerps.

The new specific name is the feminine form of the Latin adjective *opertus,* 'hidden, concealed'.

Glycaspis (Glycaspis) atkinsoni sp. n.

Fig. 2

Types: — Holotype ♂ on slide labelled 'c. 15 km NW Basalt River (Gregory Highway), Qld, 18 ix 1982, *E. similis*'. Paratypes: 1 slide of a single ♂ with same label data as the holotype. In ethanol: 1 ♀ with same label data.

General colour: Live males pale bright green indistinctly marked with black; females as the males but lightly marked with black and with red suffusion; in ethanol, orange-yellow.

Claspers and aedeagus: as in Fig. 2.

Length of aedeagus: 0.178 and 0.188 mm (2 specimens).

Length of hindwing vein Cu_1: as Group (ii).

Lerps: only 1 small round lerp was observed, so the shape of late instar nymphal lerps is not known.

Host: EFAAA *Eucalyptus similis* Maiden.

Notes: The phyletic position of *G. atkinsoni* appears to be nearest, and prior to, *G. violae* Moore (1970a: 292), differing from it in the shape of the aedeagus which is distally taller, more curved and with distal outer extremity more rounded, neck narrower, proximal ridge less rounded and more horizontal. Claspers with fewer setae and more peaked distally, distance from anterior protrusion to base, much less than in *G. violae.*

Named for Mr Alan Atkinson, of 'Valley of Lagoons', Qld, who gave assistance with the locating of, and permission to collect from, eucalypts on his property, on 3 occasions.

(b) BIOLOGICAL

Collections from *E. raveretiana* for psyllid specimens during July 1980 and July 1981 yielded only female adults of *Glycaspis,* but the occurrence of round and oval lerps on leaves indicated its role as a host. Male and female specimens were obtained during 1982.

The description of the species *G. operta* indicates the relatively close phyletic affinities of the two known species from *Telocalyptus* hosts. Both of these *Glycaspis* species are included in the tropical *caurina* group of species (Moore, 1983).

E. howittiana was first sampled for psyllid specimens during July 1980, when no evidence that a *Glycaspis* species utilized it as host was obtained. However, female adults, together with round and oval lerps of a *Glycaspis* species, were obtained during August 1981. Specimens of females and lerps were again obtained during September 1982 at 6 km E 'Valley of Lagoons' homestead, c. 170 km W Ingham, but no males were found.

The stand of *E. howittiana* extending over several hectares was intensively sampled on each occasion.

Characters of female specimens by which species of *Glycaspis* may be separated have not yet been determined, so the species utilizing *E. howittiana* as host remains unrecognized.

The absence of male specimens from these intensive and extensive collections necessarily suggests the occurrence of parthenogenesis in the species concerned. Such a possibility for other *Glycaspis* species has previously been reported (Moore, 1970: 345), and to the writer's knowledge, no evidence of parthenogenesis in psyllids has been recorded.

E. similis is included in the subgenus *Eudesmia* of Pryor and Johnson (1971). It was sampled for psyllid specimens during September 1972 at c. 5 km E Alice, Qld, when no evidence of a *Glycaspis* sp. utilizing it as host was obtained (Moore, 1975). The occurrence of *G. atkinsoni* on this host near Basalt River constitutes a new host record for *Glycaspis* species.

Apparently because of drought conditions persisting in that area, foliage of the majority of *E. similis* trees in the large stand was conspicuously yellowish-brown and desiccated, although foliage of other eucalypt species appeared normal.

Glycaspis violae which is known to occur on *E. cambageana* Maiden and possibly *E. melanophloia* F. Muell. shows close affinity with *G. atkinsoni.* It is thus suggested that *E. similis,* the host of *G. atkinsoni,* may have affinity with the 'box' and 'ironbark' groups of eucalypts.

Glycaspis froggatti Moore was collected from an unnamed eucalypt species SUDABB, the eastern arborescent race of *E. normantonensis* Maiden and Cambage at 11 km E of 'Valley of Lagoons' homestead. At the same site, another *Glycaspis* species constructing round lerps (possibly *G. egregia* Moore whose host is known to be *E. moluccana* Roxb.) was collected from SUL:A, the undescribed northern equivalent of *E. moluccana* growing intermingled with the former eucalypt. Distribution of *G. egregia* which was again reared from *E. moluccana,* is now extended to 32 km E of Rockhampton, on the Emu Park Road.

Glycaspis (Boreioglycaspis) melaleucae Moore was collected at Boundary Creek, giving a new locality record for the species. The previous nearest locality was Cape River, 112 km S of Charters Towers, Qld.

ACKNOWLEDGEMENTS

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Thanks are also expressed to Dr L. A. S. Johnson, Director, Royal Botanic Gardens and National Herbarium, Sydney, for the identifications of the two 'box' eucalypts.

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Phyllotaxis and Stem Vascularization of *Dampiera* R.Br. (Goodeniaceae)

M. T. M. RAJPUT and R. C. CAROLIN

RAJPUT, M. T. M., and CAROLIN, R. C. Phyllotaxis and stem vascularization of *Dampiera* R.Br. (Goodeniaceae). *Proc. Linn. Soc. N.S.W.* 107 (4), (1983) 1984: 479-485.

Three types of phyllotaxis are described in the genus *Dampiera*: distichous (1/2), tristichous (1/3) and pentastichous (2/5). The stems of those species having the first two types of phyllotaxis also have cortical bundles while those having pentastichous phyllotaxis do not. The lateral leaf traces are derived from the cortical bundles when the latter are present. The sequence of the derivation of the leaf traces is described for the different types of phyllotaxis. The phyllotaxis and stem vascularization have proved to be significant taxonomic characters.

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INTRODUCTION

Differences in the stem anatomy of *Dampiera* have been recognized by previous workers, particularly in regard to the presence of cortical bundles (Krause, 1912) but neither these nor the phyllotaxis have been emphasized as a taxonomic feature of any importance. Nevertheless, both sets of attributes have proved useful in recognizing infra-generic groupings and the differences are reported here.

MATERIAL AND METHODS

Transverse sections of the young vegetative buds of fresh material of representative species of *Dampiera* were cut after fixation in formalin-acetic-alcohol and embedding in paraffin wax. The apex of the stem is so small that it was necessary to use buds in which the leaves showed fairly significant development to determine the phyllotaxis.

For the study of stem vascularization serial sections were cut individually and drawn with a *camera lucida*. The vascular connections were determined by comparing the individual successive drawings.

This investigation was supplemented by clearing young and old stems of dried material. The stems were bleached with a commercial sodium hypochlorite solution, washed and cleared in aqueous chloralhydrate (50g chloralhydrate, 25g lactic acid, 25g phenol). Sometimes the vascular strands were not well displayed at this stage and instead of mounting them in chloralhydrate they were stained in 10% aqueous safranin and dehydrated in absolute alcohol. The stems were transferred to a mixture of 75% polylite 61-209 resin diluted with 25% acetone. After one to four hours in vacuum the material was passed through two or three changes of pure resin and left to set in moulds with catalyst no 2 (MEKP). Both resin and catalyst were supplied by A. C. Hatrick Pty Ltd, Australia. The blocks could be examined using a stereo-microscope.

Phyllotaxis terms are used as defined by Richards (1948). The terms used to describe the stem anatomy are those proposed by Dormer (1950, 1972). Cortical bundles are those which are present outside the stele as separate bundles in the cortical region of the stem and which supply lateral organs. A trace is a single vascular bundle which, at its upper end, passes out from the stele into some lateral organ without further considerable addition or subtraction of the vascular material.

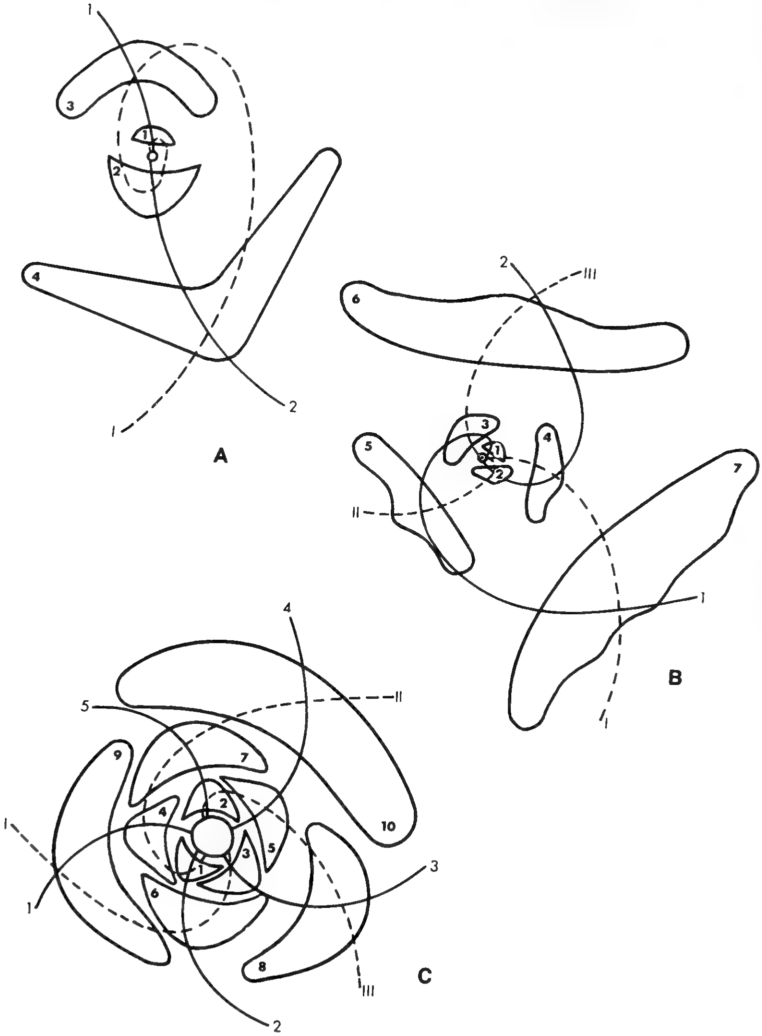

Fig. 1. Sections of leaves and stems near the tips of stems showing phyllotaxis ground plans: **A.** *D. alata,* sect. *Camptospora;* **B.** *D. stricta,* sect. *Dicoelia;* **C.** *D. cinerea,* sect. *Linschotenia.*

RESULTS

LEAF PHYLLOTAXIS

As the leaves are always spirally arranged it is always possible to draw a spiral through the median lines of successive leaves. The angle between the median lines of successive leaves is the angle of divergence and, according to Richards (1948) is constant for any one plant. The phyllotaxis ratio is a fraction of the circumference of the stem. The numerator of the fraction is the number of revolutions of the stem that are necessary to reach the next leaf of the same orthostichy, the denominator the number of plastochrones passed over until this leaf is reached. Three different types of phyllotaxis can be recognized in *Dampiera.*

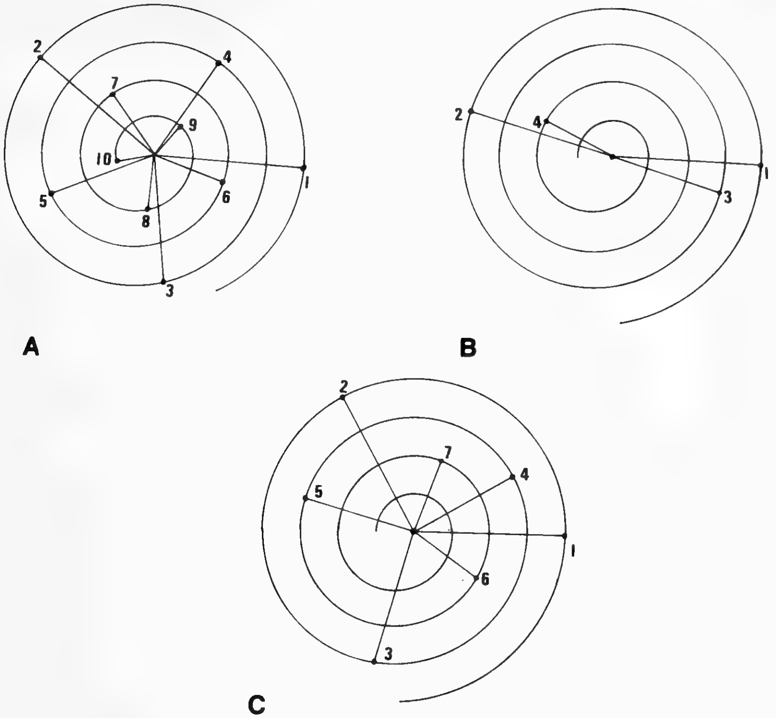

Fig. 2. Diagrammatic representation of phyllotaxis: **A.** *D. alata;* **B.** *D. stricta;* **C.** *D. cinerea.*

1. 1/2 or distichous phyllotaxis. e.g. *D. alata.* only two orthostichies are recognized. The mean angular divergence is 171° and there are (1 + 2) parastichies (Figs 1**A,** 2**A**) (see Church, 1904).

This type of phyllotaxis occurs in those species with a flattened stem and two cortical bundles.

2. 1/3 or tristichous phyllotaxis, e.g., *D. stricta.*

Three orthostichies can be recognized, the mean angular divergence is 131° 2′ and there are (2 + 3) contact parastichies (Figs 1**B,** 2**B**). This type of phyllotaxis is found in those species with triangular stems and three cortical bundles.

3. 2/5 or pentastichous phyllotaxis. e.g., *D. cinerea.*

Five orthostichies can be recognized with a mean angular divergence of 135° 2′ and there are (3 + 5) contact parastichies (Figs 1**C,** 2**C**). This type of phyllotaxis is found in the species with ribbed or unribbed stems without cortical bundles.

Fresh material of the section *Cephalantha* was not available and the rosette arrangement of the leaves made it impossible to determine the phyllotaxis of any species of this section.

STEM VASCULARIZATION

In almost all the leaves of *Dampiera* species there are three traces, one median although it may not be strictly median in position, and two lateral. The departure of the cortical bundles and the bundles of the stele to the leaves of representative species of *Dampiera* are shown in Fig. 3. The single line surrounding the bundles of the stele

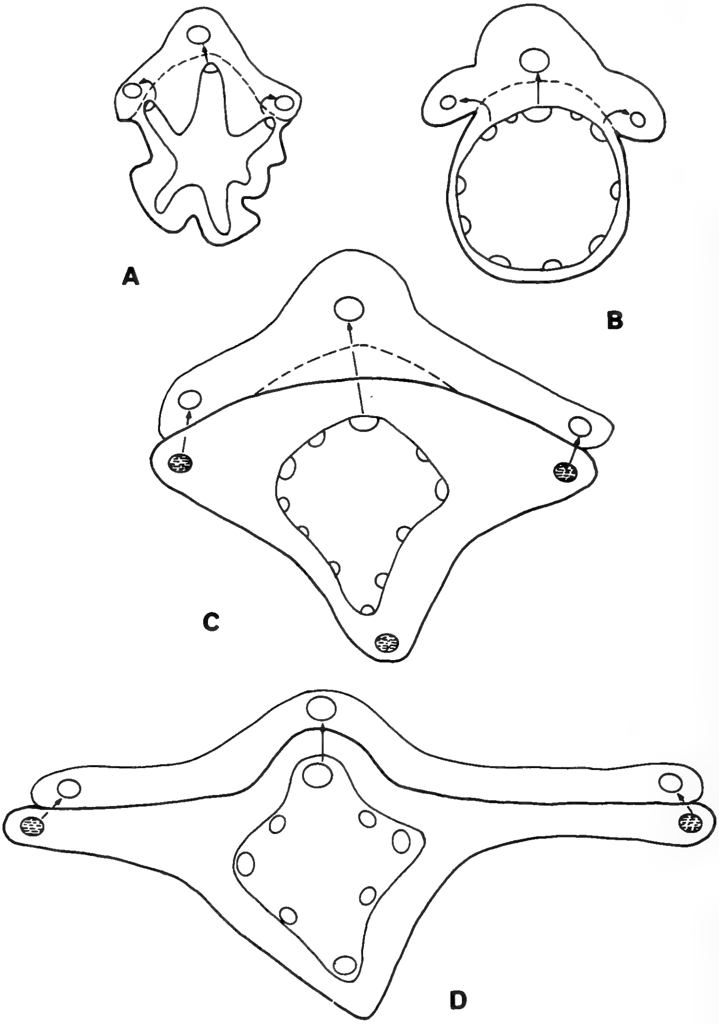

Fig. 3. Schematic transverse section showing origin of vascular traces of leaves from bundles of stems: **A.** *D. alata;* **B.** *D. stricta;* **C.** *D. oligophylla,* sect. *Dampiera;* **D.** *D. cinerea.*

represents a well-defined boundary between sclerenchyma (of the stele) and parenchyma (of the cortex) of small regular cells which are assumed to be the starch sheath.

In order to describe the stem vascularization it was necessary to develop some simple diagrammatic representation of the stem as shown in Fig. 4. The cortical vascular system of the stem is represented as though it has been cut open on one side and then laid out flat. The small circles represent lateral foliar traces and the large circles represent median foliar traces which latter are derived from the stele directly as shown in Fig. 3. Since both lateral and median traces are derived from the stele in *D. oligophylla,* the stelar traces are shown for this species only.

Cortical vascular bundles are absent in all members of sect. *Dampiera,* sec. *Cephalantha,* and sect. *Linschotenia* that have been examined to date, and the foliar traces are supplied directly from the stele at each node.

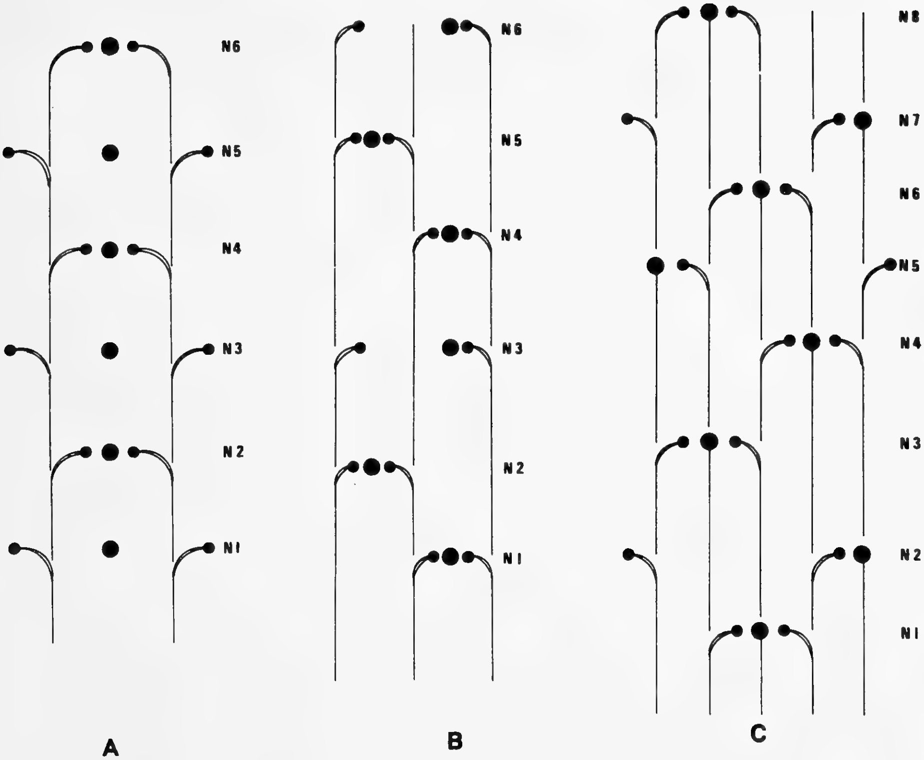

Fig. 4. Diagrams showing the successive origins of vascular strands of leaves from those of the stem: **A.** *D. alata;* **B.** *D. stricta;* **C.** *D. oligophylla.* For explanation see text.

Except for *D. angulata,* the members of sect. *Camptospora* which have been examined here, e.g., *D. lindleyi* have two cortical bundles (Fig. 3**A**), and each passes into the leaf at each node and forms a lateral trace. A median trace is supplied directly from the stele at each node. At the same time two new cortical bundles develop from the stele and then supply the leaf on the next node with the lateral traces, thus each cortical bundle in the stem passes through only one internode. The position in the stele from which the cortical bundles are supplied is the same on nodes two and four (Fig. 4**A**). The leaf vascular supply from the stele of the stem at each node is consistent with the phyllotaxis.

In the members of sect. *Dicoelia* the stem has three cortical bundles and the number of the stelar bundles varies from six to nine in the internode. The case of a stem having three cortical and six well-developed vascular bundles has been examined, e.g., *D. stricta* (Figs 3**B**, 4**B**). Only two of the three cortical bundles take part in the vascular supply of the leaf at each node. One passes through two internodes and the other through only one internode whilst the median trace is supplied directly from the stele at each node (Fig. 4**B**). Two of the six vascular bundles which are present in the stele supply the median trace of the leaf at each node and these two stelar bundles always pass through two internodes (Fig. 4**B**).

The new cortical bundle which passes through two internodes is succeeded by a newly developed cortical bundle which passes through only one internode whilst the cortical bundle which passes through one internode is succeeded by a bundle which passes through two internodes. The position in the stele from which the cortical bundles are supplied is the same at nodes 1, 4 and 7 (Fig. 4**B**). The position of the vascular supply at each node of the stem is consistent with the 1/3 phyllotaxis.

In ribbed stems the cortical bundles are absent but the stele is convoluted and the individual bundles correspond to the ribs, e.g., *D. oligophylla* ssp. *oligophylla* (Fig. 3**C**). In the unribbed stems the cortical bundles are also absent and the vascular bundles of the stele do not usually protrude into the cortex, e.g., *D. cinerea* (Fig. 3**D**).

In sect. *Dampiera* the number of the vascular bundles of the stele which protrude into the cortex varies from five to nine. The case of a stem having five well-developed vascular bundles has been examined. Three of the five vascular bundles which protrude into the cortex take part in the supply of the leaf at each node, one to the median trace and two to the laterals. The vascular bundle which forms the median trace subsequently always passes through two internodes and then forms a lateral trace, subsequently the same bundle passes through one internode to form another lateral trace and after that through two internodes to form a median trace (Fig. 4**C**).

The position in the stele from which the vascular bundles are supplied is the same on nodes 1, 6 and 11. This is consistent with the 2/5 phyllotaxis. This type of vascular supply is also found in members of sect. *Linschotenia.* The stems of members of this section, however, are unribbed and have a narrow cortex with an unconvoluted stele (Fig. 3**D**). Since the members of sect. *Dampiera* have ribbed stems with a wide cortex and stelar bundles protruding into the cortex, this constitutes the main difference in the anatomy of the two sections.

DISCUSSION

A number of elegant ways of describing phyllotaxis have been devised (see Williams, 1975), but virtually the only effective way for taxonomic work remains the well-established phyllotaxis ratio since most apices are so small that it is usually impossible to determine angles of divergence and plastochrone ratios or a generative angle (Thomas and Connell, 1980) at the primordial level. Such is the case with *Dampiera* and leaf initials further away from the apex have to be used for these determinations. There is thus some risk of displacement of these leaves during embedding and cutting.

Several apices each of *D. stricta* and *D. purpurea* were examined. The mean angle of divergence remained constant indicating that displacement in the horizontal plane was insignificant. However, the plastochrone ratio did vary and was considered to be unreliable.

The types of phyllotaxis and stem vascularization clearly have some taxonomic significance. We will deal elsewhere in detail with the taxonomy (Rajput and Carolin, in prep.) and the phylogeny of the genus but some conclusions can be drawn on the information presented here.

Sect. *Dicoelia* in fact consists entirely of species with cortical bundles and 1/3 phyllotaxis. Sect. *Camptospora* consists of species with both triangular and flattened stems also all with cortical bundles and 1/2 or 1/3 phyllotaxis. The implication is that these two sections are more closely related to each other than either is to the other three sections, none of which has cortical bundles. There is thus a clear dichotomy in the genus since even in species such as *D. oligophylla* where the young stems are triangular, they do not possess cortical bundles.

There is also clearly a very close connection between the vascularization and phyllotaxis, which indeed one would expect.

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Variability in the Opercular Structures of the Serpulid Polychaete *Hydroides elegans* (Haswell)

P. J. MORAN

(Communicated by P. A. HUTCHINGS)

MORAN, P. J. Variability in the opercular structures of the serpulid polychaete *Hydroides elegans* (Haswell). *Proc. Linn. Soc. N.S.W.* 107 (4), (1983) 1984: 487-492.

Variations in the structure of both the functional and rudimentary opercula of the serpulid worm, *Hydroides elegans* are described. The possible causes for these observed differences in opercular structure are discussed. Such variability may lead to confusion in the identification of this species.

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INTRODUCTION

The serpulid polychaete *Hydroides elegans* (Haswell, 1883), occurs commonly in fouling communities throughout Australia and in other parts of the world. For many years this polychaete has been referred to in Australia as *Hydroides norvegica* Gunnerus 1768 (Allen, 1953; Dew and Wood, 1955; Wood, 1955; Dew, 1958; Wisely, 1958; Wood and Allen, 1958; Dew, 1959; Wisely, 1959; Blick and Wisely, 1964; Straughan, 1967; Russ and Wake, 1975; Russ, 1977; Dakin *et al.,* 1980; Moran, 1980). However, ten Hove (1974) has pointed out that *H. norvegica* is restricted in its distribution to Mediterranean and North Atlantic waters. Consequently species recorded as *Hydroides norvegica* in Australia should be referred to as *H. elegans* (ten Hove, pers. comm.). A description of the differences between these two species will not be given here since they have been discussed elsewhere in the literature (Zibrowius, 1971; Bornhold and Milliman, 1973; ten Hove, 1974).

The purpose of this paper is to describe variations in both the functional and rudimentary opercula of *H. elegans,* as these variations may lead to confusion in the identification of the species. The observations presented here are the result of studying approximately 800 specimens taken from settlement panels submerged for between 2 weeks and 15 months in Wollongong and Port Kembla Harbours. Specimens of each different type of opercular arrangement were identified by Dr H. ten Hove, University of Utrecht.

OPERCULAR VARIATIONS

Individuals of *Hydroides elegans* bear two opercula which normally are dissimilar in structure and size. The larger of the two opercula, termed the functional operculum (Schochet, 1973a), consists of two goblet-shaped structures, one sitting inside the other (Fig. 1). This double-cupped structure is attached to a long smooth pedicle. The lower or inferior cup (goblet) of this structure is dish-like in appearance and has 16-28 crenulations around its perimeter. Arising from its centre is the upper or superior cup which bears 15-18 spines. Each main spine, which often has a small spike protruding from its inner surface, possesses 2-4 lateral spines (Fig. 1). In harbours and areas where water turbidity is usually high these features may be hidden as the superior cup is often covered by a thick layer of sediment. The functional operculum may be attached to either the right or left branchial circlet where it acts as a tube plug (Fig. 2**a**). It is

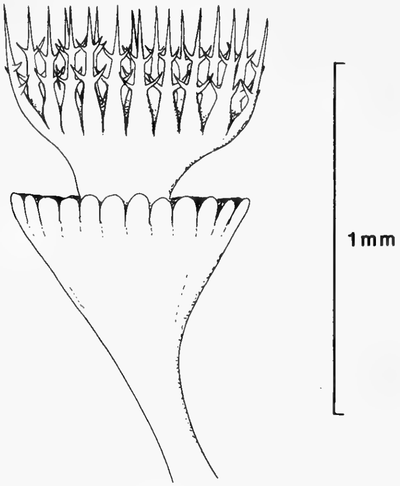

Fig. 1. Double-cupped functional operculum of *Hydroides elegans.*

thought also that the operculum is employed in a defensive capacity (Schochet, 1973a). The other operculum, termed the rudimentary operculum (Schochet, 1973a), is located on the side opposite to the functional operculum. It is a small bulbous structure of undifferentiated tissue which is attached to a short pedicle (Fig. 2**a**).

Although specimens of *Hydroides elegans* typically have only one functional operculum which is usually quite conspicuous, it is possible to find individuals which have two, fully developed, functional opercula. Dew (1958) found that individuals of *H. elegans* (identified as *H. norvegica* by Dew) may possess two double-cupped opercula, one of these having developed from the rudimentary operculum. In most instances this structure was noted to be shorter than the other functional operculum. Individuals with this type of opercular arrangement were found to occur in the fouling communities in both Port Kembla Harbour and Wollongong Harbour (Fig. 2**b**). In addition to observing that two double-cupped opercula may occur in the same tube, Dew (1958) also noted several other variations in the structure of the rudimentary operculum which corresponded to different stages of its development into a functional operculum.

Studies of individuals in Port Kembla and Wollongong Harbours have identified a further three different types of opercular arrangement in *H. elegans,* which result from changes in the structure of the rudimentary operculum and also the functional operculum. These three types have not been described before.

Several specimens were found which possessed a functional operculum that consisted of a single-cupped structure attached to a long pedicle (Fig. 2**c**). This opercular structure was very similar to the inferior cup of a normal functional operculum since it was dish-shaped and had approximately the same number of crenulations around its perimeter (16-25). Whereas in these specimens the rudimentary operculum was undeveloped (Fig. 2**c**), one individual was discovered to have two single-cupped opercula of dissimilar length in the one tube (Fig. 2**d**). In addition, a number of bi-operculate specimens of *Hydroides elegans* were found which contained a single-cupped operculum as well as a double-cupped operculum (Fig. 2**e**). Each of the opercula was associated with either the left or right branchial circlet. Usually in each individual tube the two opercular types were of different lengths. In some specimens the double-cupped operculum was longer whilst in others the single-cupped structure was found to be greater in length.

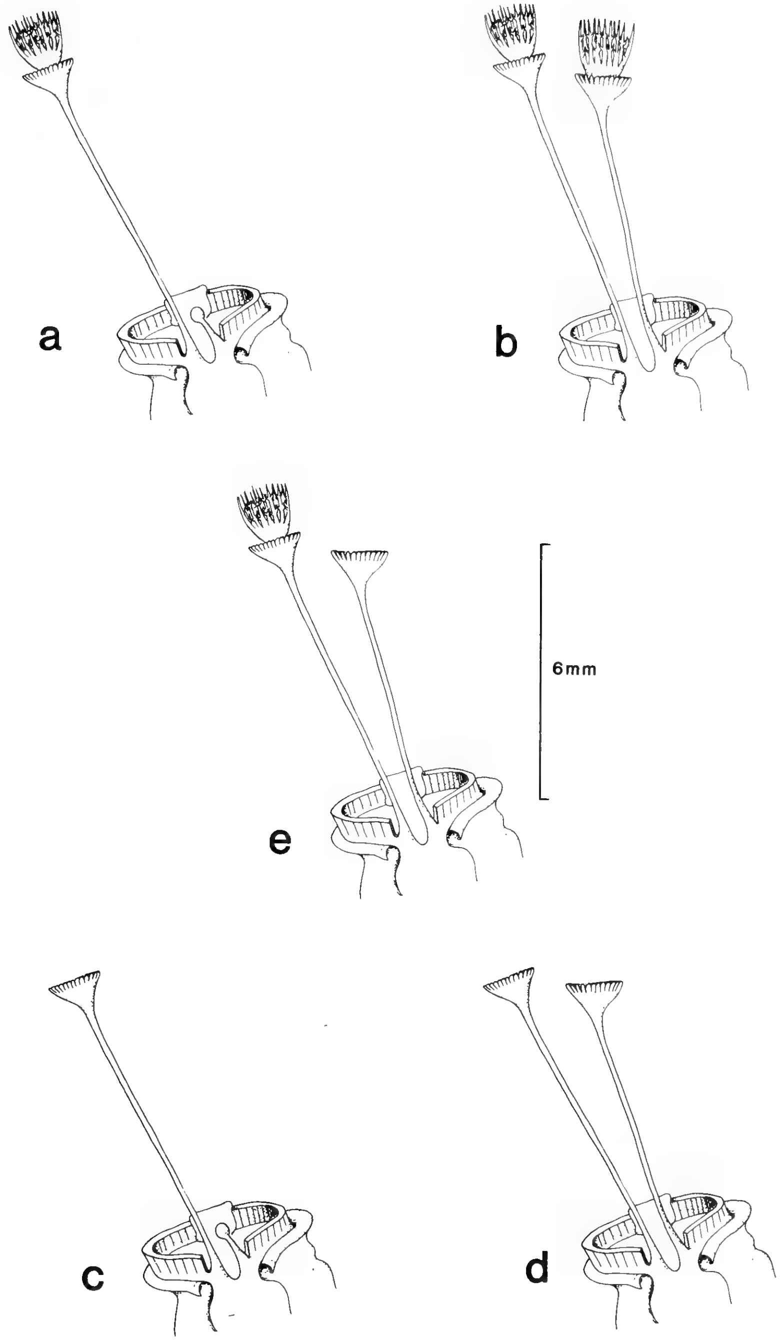

Fig. 2. Variability in the opercular structures of *Hydroides elegans.* Branchial filaments not shown. **a:** Functional operculum with single undeveloped rudimentary operculum. **b:** Two double-cupped functional opercula. **c:** Single-cupped functional operculum with undeveloped rudimentary operculum. **d:** Two single-cupped functional opercula. **e:** Double-cupped functional operculum with a single-cupped functional operculum.

DISCUSSION

A detailed account of opercular development has been given for *Hydroides dianthus* (Verrill 1873), (Zeleny, 1905, 1911; Schochet, 1973a) and *Hydroides norvegica* (Wisely, 1958). Initially, individuals of both these species are 'right-handed'. That is, the first functional operculum is attached to the right branchial circlet. However, 'left-handed' as well as 'right-handed' individuals have been found in adult populations, suggesting that the functional operculum is able to change its position, from one branchial circlet to the other, as the animal matures. This has been demonstrated for *Hydroides dianthus* (Zeleny, 1905; Schochet, 1973a); *Hydroides norvegica* (Wisely, 1958) and *Hydroides ezoensis* (Ichikawa and Takagaki, 1942). This is quite likely, since experiments have shown that amputation of the functional operculum results in the development of the rudimentary operculum (Ludwig and Ludwig, 1954; Schochet, 1973b). After the amputation, the functional operculum regenerates into a rudimentary structure, thus producing a reversal in the positions of both opercular types. This may occur several times during the lifetime of an individual (Schochet, 1973a). Coordination between the two types of opercula is thought to be governed by the functional structure. Puccia and Durante (1973) isolated a chemical substance which inhibited the development of the rudimentary operculum in specimens of *Hydroides norvegica.* The substance (5′ adenosine monophosphate) was found to be in greatest quantities in the functional operculum suggesting that this structure was responsible for preventing the development of the rudimentary structure.

Such information accounts for the variability observed to occur amongst individuals with one functional operculum, unfortunately it does not explain the occurrence of individuals with two functional opercula. A number of theories have been put forward to account for the occurrence of such specimens. For example, Rioja (1919) considered that such animals were atavistic and had reverted to an early ancestral form which was symmetrical, however it is most likely that individuals with two functional opercula are a result of either natural ontogenetic processes or due to damage to the functional operculum.

Schochet (1973a) considered that these animals did not provide evidence of atavism but concluded that they are indicative of opercular reversal. According to Schochet, individuals with two functional opercula occur when the rudimentary operculum develops after overcoming the inhibitory effects of the functional operculum. The resultant symmetrical state is largely unstable and generally the more mature operculum is spontaneously cast off and the individual reverts to a single opercular state. Dew (1958) on the other hand, has proposed that if a rudimentary operculum developed in response to damage to a functional operculum and the functional operculum recovered from this injury, then the animal would eventually possess two double-cupped opercula.

The occurrence of individuals with single-cupped opercula cannot be accounted for by the theories described above. However, since this structure was noted to be very similar to the lower cup of a normal functional operculum the single cup structure is probably a functional operculum which has lost its superior cup or crown. It could also be a primary functional operculum (see Zeleny, 1905, 1911; Wisely, 1958; Schochet, 1973 a,b), which is a funnel-shaped structure formed very early in the development of the organism. However this is unlikely since the single-cupped structures were found in adult specimens.

Loss of the superior cup from a normal functional operculum could be a natural event and it may be shed just before the whole operculum is autotomized during opercular reversal. Also, since the superior cup is attached to the inferior cup by what appears to be only a small, narrow base, then perhaps it is prone to being dislodged by natural physical disturbances, such as during times of storms and heavy seas.

Opercular structure in most instances, is a reliable taxonomic character to use when identifying serpulids. It is particularly useful when undertaking a census in which large numbers of serpulids are present, since it is a less time-consuming method of identification than employing features which require careful microscopic analysis. Unfortunately, problems may be encountered in the identification of *Hydroides elegans* because of the high degree of variability in its opercular structures. Indeed, specimens with single-cupped opercula could be confused with *Serpula* species, particularly *Serpula vermicularis* Linnaeus 1767. It has been suggested that *Hydroides* species are superficially similar to *Serpula* species except for the fact that they have a second crown on top of an otherwise funnel-shaped operculum (Lewis, 1982). Problems associated with the identification of individuals with single-cupped opercula may be resolved by considering a number of specimens, in order to determine whether they exhibit a diverse range of opercular structures. If this is the case, then the single-cupped individuals probably form part of a 'normal' population of *Hydroides elegans.* If considerable variation in opercular structure is not found amongst surrounding individuals then other more time-consuming taxonomic methods such as referring to the structure of setae, need to be undertaken.

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Two new Chiggers from Australian Marsupials (Acari: Trombiculidae)

LEITH N. LESTER

(Communicated by R. DOMROW)

LESTER, L. N. Two new chiggers from Australian marsupials (Acari: Trombiculidae). *Proc. Linn. Soc. N.S.W.* 107 (4), (1983) 1984: 493-499.

Ascoschoengastia deficiens, n.sp. is described from a native cat, *Dasyurus hallucatus* Gould (Marsupialia: Dasyuridae), in Western Australia; and *Guntheria insueta,* n.sp. from a marsupial mouse, *Sminthopsis crassicaudata* (Gould) (Dasyuridae), in South Australia. *Microtrombicula* Ewing, 1950 = *Ascoschoengastia* Ewing, 1946, n.syn.; *Zyzomyacarus* Goff, 1979 = *Guntheria* Womersley, 1939, n. syn.

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Two new chiggers from isolated Australian localities are described below. The *Ascoschoengastia* was studied through the courtesy of Dr P. J. A. Presidente, Veterinary Clinical Centre, University of Melbourne, Werribee; the *Guntheria* was kindly provided by Mr D. C. Lee, South Australian Museum, Adelaide, with details from Dr I. Beveridge, Institute of Medical and Veterinary Science, Adelaide. The hosts are given after Ride (1970).

Genus *ASCOSCHOENGASTIA* Ewing

Ascoschoengastia Ewing, 1946: 71 (type-species *Neoschoengastia malayensis* Gater).

Microtrombicula Ewing, 1950: 297 (type-species *Microthrombidium minutissimum* Oudemans), n.syn. See notes below.

For definition see Nadchatram and Dohany (1974).

Ascoschoengastia deficiens, n.sp.

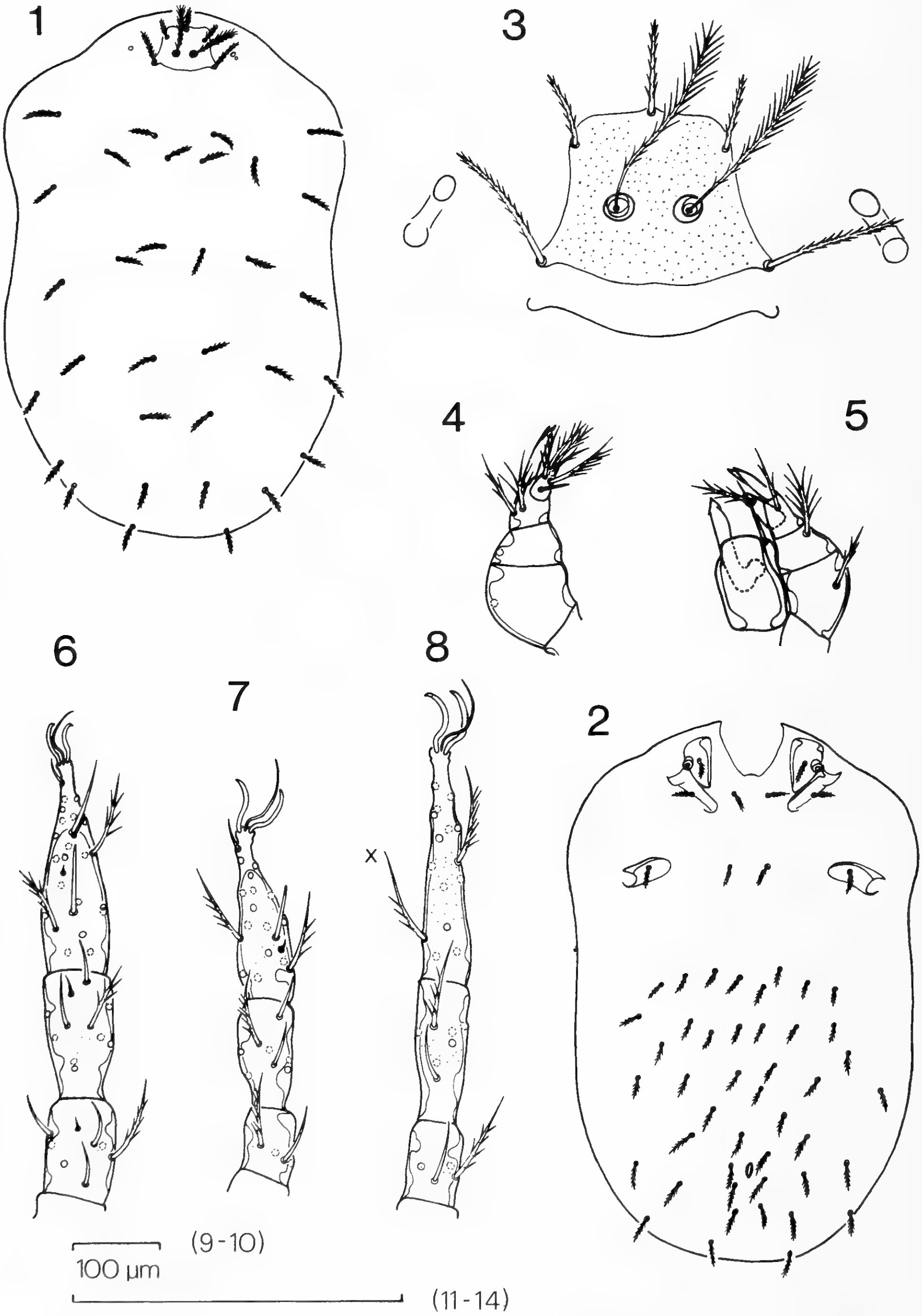
(Figs 1-8)

Material: Holotype larva and 110 paratype larvae, ear meatus of little northern native cats, *Dasyurus hallucatus* Gould (Marsupialia: Dasyuridae), Debatable Point, Mitchell Plateau, W.A., 17-18.vii.1982, P. J. A. Presidente. Holotype and 30 paratypes in Western Australian Museum, Perth; remaining paratypes divided between Bernice P. Bishop Museum, Honolulu; British Museum (Natural History), London; and Queensland Institute of Medical Research, Brisbane.

A soft oily or waxy deposit on these chiggers (removable with toluol) may indicate that they live deep in the ear meatus, as noted by Audy (1956) for *A. malayensis* (Gater).

Larva: Palpi (Figs 4-5) of usual proportions, with femur rounded externally; setation b.B.bbb.6B + T; claw two-pronged. Chelicerae unarmed except for usual tricuspid cap, bases unexpanded posterolaterally. Galeal setae N. Capitular setae B.

Body (Figs 1-2) slightly constricted behind shoulders when engorged; cuticle annulate. Dorsal setae typically arranged 2.8.6.6.4.4.2 = 32; first row varying from 6 to 10 (6 in 8/50 paratypes, 7 in six, 8 in 31, 9 in five; one specimen commencing 2.10.7 in another 60 paratypes examined only casually), with third and sixth setae in first row



Figs 1-8. Ascoschoengastia deficiens, larva. 1-2. Idiosoma, dorsal and ventral. 3. Scutum and eyes. 4-5. Palp and chelicera, ventral and dorsal. 6-8. Setation of legs I-III, about dorsal ('x' indicates a rarely present 15th seta).

TABLE 1

Standard data in µm of larval scutum of A. deficiens

AW	PW	SB	ASB	PSB	SD	AP	AM	AL	PL	Sens
46	71	20	29	24	53	32	35	25	41	61
46	71	22	29	24	53	32	34	26	42	61
46	67	19	29	27	56	34	34	25	46	64
49	64	18	27	27	54	30	34	27	47	64
48	68	20	30	24	54	34	34	23	46	64
49	68	18	27	24	51	29	34	25	41	65
47	63	18	28	25	53	30	34	25	43	60
44	65	18	30	26	56	31	37	25	43	65
48	71	19	30	23	53	32	34	23	42	61
44	66	19	29	24	53	35	36	25	42	60
47	67	19	29	25	54	32	35	25	43	63

moved forward as in *A. indica* (Hirst), except when only 6 are present. Intercoxal setae 2 + 2. Ventral setae about 44.

Scutum (Fig. 3, Table 1) subquadrate; anterior margin slightly sinuous, with distinct anterolateral shoulders; lateral margins slightly concave; posterior margin slightly, but variably convex; surface minutely punctate except behind sensillary bases and AM seta; PL > AM > AL, all with short ciliations; AL behind AM, on shoulders; PL on extended corners (two rather widely separated PL on one side of one paratype); sensillae set well in front of PL, filiform, strongly ciliated, especially in distal half. Eyes 2 + 2, posterior pair indistinct.

Legs 7.7.7-segmented. Specialized setae: Leg I (Fig. 6) with three genualae (anterobasal, anterodistal, posterodistal), microgenuala; two tibialae, microtibiala; tarsala, microtarsala (set distad of tarsala), subterminala, parasubterminala, pretarsala. Leg II (Fig. 7) with genuala; two tibialae; tarsala, microtarsala, pretarsala. Leg III (Fig. 8) with genuala; tibiala. Ordinary setae (none wholly nude, or long and outstanding; tarsus III with dorsobasal seta tending to be thinner and less strongly ciliated, but not a frank mastiseta): coxae 1.1.1; trochanters 1.1.1; basifemora 1.2.2; telofemora 5.4.3; genua 4.3.3; tibiae 8.6.6; tarsi 21.16.14 (rarely 15 when seta marked 'x' is present). Claws equal; empodia slender, without ciliations.

Notes: I now formalize the synonymy of *Microtrombicula* Ewing, 1950 and *Ascoschoengastia* Ewing, 1946 suggested by Domrow (1957) and Nadchatram and Dohany (1974). Womersley (1952) and Vercammen-Grandjean (1965) provided useful accounts of the species now included in the genus. In Womersley, the new Australian species keys out near a group of three Oriental species. It is sharply separated from *A. batui* (Philip and Traub) in having multi-branched sensillae, and from *A. munda* (Gater) and *A. spicea* (Gater) by the dorsal setal pattern commencing 2.8.6 and the strongly branched palpal setae.

The other Australian and Papuan species of *Ascoschoengastia* (Nadchatram, 1970; Nadchatram and Domrow, 1964) show clavate sensillae, with one exception. This is the hirsute *A. setosa* Goff, 1979a, from which the new species is readily distinguished by its unisetose coxa III and scutal proportions.*

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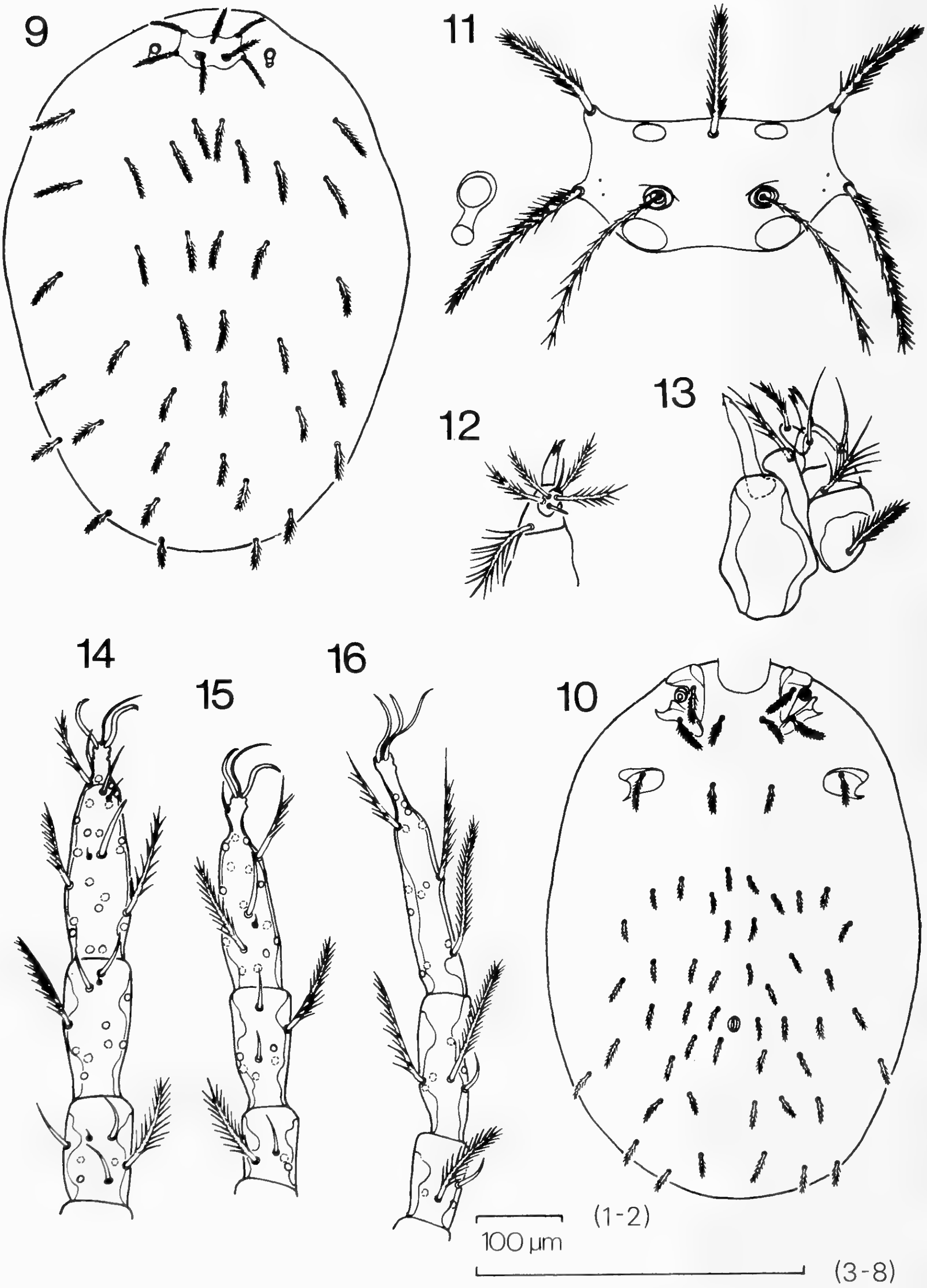
* The original description of *A. setosa* stated that two genualae I were present but there are, in fact, three as in the new species (Goff *in litt.*, 23.ii.1983).



Figs 9-16. Guntheria insueta, larva. 9-10. Idiosoma, dorsal and ventral. 11. Scutum and eyes. 12-13. Palp and chelicera, ventral and dorsal. 14-16. Setation of legs I-III, about dorsal.

Euschoengastoides Loomis, 1954 (see also Loomis, 1971) also shows sensillae ranging from filiform to the frankly clavate.

The new specific name is the Latin adjective *deficiens* (wanting, lacking), and refers to the depleted setation of tarsi I (21B) and III (14B). Most chiggers have 22 and 15, respectively, though 14 is common on III in *Ascoschoengastia.*

Genus *GUNTHERIA* Womersley

Guntheria Womersley, 1939: 157 (type-species *Neoschoengastia kallipygos* Gunther).
Zyzomyacarus Goff, 1979a: 82 (type-species *Zyzomyacarus arguri* Goff), n.syn. See notes below.

For definition see Domrow (1960, 1971) and Goff (1980).

Guntheria insueta, n.sp.

(Figs 9-16)

Material: Holotype larva and twelve paratype larvae, fat-tailed dunnart, *Sminthopsis crassicaudata* (Gould) (Dasyuridae), Partacoona Station, near Hawker, Flinders Ranges, S.A., 13.xii.1972, D. Hayman. Holotype and eight paratypes in South Australian Museum, Adelaide; four paratypes in Queensland Institute of Medical Research, Brisbane.

Larva: Palpi (Figs 12-13) of usual proportions, with femur rounded externally; setation B.B.NNB.5BS + T; claw three-pronged. Chelicerae unarmed except for usual tricuspid cap, bases unexpanded posterolaterally. Galeal setae B. Capitular setae B.

Body (Figs 9-10) ovoid when engorged; cuticle annulate. Dorsal setae arranged 2.8.6.6.6.4.2.2 = 36. Intercoxal setae 2 + 2. Ventral setae about 46.

Scutum (Fig. 11, Table 2) rectangular; anterior margin sinuous, without shoulders; lateral margins concave; posterior margin clearly biconvex; surface without punctae except for two distinct pairs adjacent to PL; 'windows' present behind anterior margin and scutum with signs of thinning behind SB. PL > AM > AL, all with strong ciliations; AL in front of AM, not on shoulders; AL and PL on extended corners; sensillae set slightly behind PW, filiform, with ciliations somewhat longer distally. Eyes 2 + 2, anterior pair larger, but both pairs distinct.

Legs 7.7.7-segmented. Specialized setae: Leg I (Fig. 14) with three genualae (anterobasal, anterodistal, posterodistal), microgenuala; two tibialae, microtibiala; tarsala, microtarsala (set beside tarsala), subterminala, parasubterminala, pretarsala. Leg II (Fig. 15) with genuala; two tibialae; tarsala, microtarsala, pretarsala. Leg III (Fig. 16) with genuala; tibiala. Ordinary setae (none nude, or long and outstanding): coxae 1.1.1; trochanters 1.1.1; basifemora 1.2.2; telofemora 5.4.3; genua 4.3.3; tibiae 8.6.6; tarsi 22.16.15. Claws equal; empodia slender, without ciliations.

Notes: The first new species described above is one argument against maintaining the Trombiculini and Schoengastiini on sensillary shape alone (filiform *vs* expanded).

The second new species may well provide another. Although it has filiform sensillae, it fails to meet the detailed diagnoses to genera of Trombiculini in Vercammen-Grandjean (1960) and Nadchatram and Dohany (1974). Further, on a strict reading of Womersley's earlier key (1952) to the Oriental-Australian fauna, it runs out (depending on one's interpretation of couplet 68) near two species from India and Sri Lanka — *Trombicula gliricolens* (Hirst) and *T. jayewickremei* Womersley — which show characters of *Leptotrombidium* Nagayo *et al.,* 1916, *e.g.* palpal tarsus 7B and two genualae I (Vercammen-Grandjean and Langston, 1976). Nor does it relate closely to subsequently-described Australian species of Trombiculini, *e.g.* those of Domrow (1959, 1964) and Goff (1979a, b). Most of these are specialized parasites of bats (Chiroptera), though some are from rats (Muridae).

TABLE 2

Standard data in µm of larval scutum of G. insueta

AW	PW	SB	ASB	PSB	SD	AP	AM	AL	PL	Sens
71	91	30	29	19	48	25	37	35	52	—
77	86	33	29	19	48	26	39	36	54	—
74	86	32	30	20	50	27	39	37	55	61
74	88	31	30	18	48	28	41	37	54	—
72	84	31	29	19	48	25	41	34	53	—
70	82	29	30	18	48	26	39	34	56	—
70	82	30	28	18	46	24	40	35	59	—
68	80	30	27	19	46	25	40	33	53	—
72	85	31	29	19	48	26	39	35	54	61

Conversely, although the second new species' filiform sensillae argue against its placement in the Schoengastiini, it is among these genera that it fits more comfortably. Thus it shares many characters with species of *Guntheria* Womersley, 1939 such as *G. newmani* (Womersley) and *G. peregrina* (Womersley), including: palpal setal formula B.b.NNb.5BS + T, palpal claw 2- to 3-pronged, dorsal setae commencing 2.8.6, scutum of similar proportions (transverse, with biconvex posterior margin, PL > AM > AL, SB set behind PL), three genualae I and hosts largely marsupials (never bats). The new species is closest to *G. newmani* in Domrow (1960, 1978), but can at once be separated by its filiform sensillae.

Zyzomyacarus, raised recently by Goff (1979a) for two species from an 'old-endemic' Australian rodent (Muridae), differs from *Guntheria* only in its very narrowly expanded sensillae (the other two distinguishing characters mentioned by Goff — eyes free, leg III lacking attenuated, finely ciliated, apically nude setae — in fact separate only a few species of *Guntheria* from *Zyzomyacarus*), and one can readily point to species of *Guntheria* which share many characters (*e.g.* palpal setal formula P.B.BBB.5B + T, galeal setae barbed, dorsal setae commencing 2.8.6, sensillae slenderly clavate, dorsal shield deeply convex posteriorly and two genualae I) with *Zyzomyacarus: G. dasycerci* (Hirst), *G. shieldsi* (Gunther) and possibly *G. bamaga* Domrow, *G. pertinax* Domrow and *G. pseudomys* (Womersley). I therefore synonymize *Zyzomyacarus* with *Guntheria.*

The new species can be separated from *G. arguri* (Goff), n.comb. and *G. napierensis* (Goff), n.comb. by having a palpal subterminala and three genualae I.

The new specific name is the feminine form of the Latin adjective *insuetus* (unusual).

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I am grateful to Dr M. L. Goff, University of Hawaii at Manoa, Honolulu, and Mr M. Nadchatram, National University of Science, Singapore, for their opinions on the two new species; to Dr R. Domrow for his patient and generous guidance; and to the Australian Research Grants Scheme for financial support.

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On 'Bridging the Gap between Race and Species': The Isolation Concept and an Alternative

D. M. LAMBERT and H. E. H. PATERSON
(Communicated by T. G. VALLANCE)

LAMBERT, D. M., & PATERSON, H. E. H. On 'Bridging the gap between race and species': The isolation concept and an alternative. *Proc. Linn. Soc. N.S.W.* 107 (4), (1983) 1984: 501-514.

This contribution examines some aspects of the current state of studies on species and speciation. In particular, the role which Dobzhansky's Isolation Concept has played in the development of theories is briefly reviewed and the validity of some current commonly-accepted views are examined. A new species concept, the Recognition Concept, is discussed in the light of serious objections to these current views. We examine some aspects of the reinforcement model, especially the relationship between this model of speciation and the Isolation Concept of species. Some predictions of the Recognition Concept are detailed, and contrasted wherever possible, with alternative predictions of the Isolation Concept. Finally, it is suggested that the testing of these alternative predictions is of paramount importance.

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INTRODUCTION

It is twenty-three years since the publication of Theodosius Dobzhansky's paper 'Bridging the gap between race and species', in the Proceedings of the Linnean Society of New South Wales (1960). This was the second Sir William Macleay Memorial Lecture, and Dobzhansky, firmly recognized as one of the leading evolutionary biologists of the time, presented a knowledgeable and authoritative account of current evolutionary research. In this paper Dobzhansky recounted his understanding of the relationship between races and species and made important comments on the nature of species and of speciation. After twenty-three years, and eight years since the death of this most influential biologist it seems an appropriate time to reflect on the current theoretical corpus, and consider what changes may have occurred in our thinking since that time.

THE CURRENT PARADIGM

Theodosius Dobzhansky, by his succession of classic books (1937, 1951, 1970) and his innumerable articles, greatly influenced the genetic study of evolutionary biology for approximately four decades (Ruse, 1981: 810). Ernst Mayr (1970) described him as the '. . . foremost architect of evolutionary genetics of today'. Dobzhansky left behind him, besides the residues of his own personal influence, a large number of students of particular ability. Many of these students have helped to further develop Dobzhansky's original ideas, and the well-known textbook 'Evolution' (1979), written with a number of co-workers, summarizes much of the general thinking of the 'Dobzhansky School'.

Amongst his most significant innovations Dobzhansky will be remembered for his introduction of the term 'Isolating Mechanisms' (Dobzhansky, 1937). It is perhaps not immediately apparent the degree to which this term has influenced the development of our ideas. However, on reflection, this is the basis of the Isolation Concept of species, as Paterson (1980) has named it, and the listing of 'premating and postmating Isolating Mechanisms' (Mecham, 1961) gave biologists one of the most useful conceptual frameworks on which to hang ideas and use as a basis for data collection.

Dobzhansky viewed a species as any group of individuals which is 'reproductively isolated' from any other group. This inevitably influenced his concept of speciation which is, logically, the development of these 'Isolating Mechanisms'. Although Dobzhansky (1960) commented that '. . . the means whereby speciation is accomplished, i.e. whereby reproductive isolating mechanisms are established between diverging populations, are not the same in all organisms', he nevertheless argued consistently over many years, for one particular model of speciation. This model has been referred to as 'Speciation by Reinforcement' (Grant, 1966).

Reinforcement requires the evolution of 'premating isolating mechanisms' through the direct action of natural selection. This is supposed to occur when populations secondarily overlap and hybrids between individuals of the two groups are disadvantageous. Selection then favours individuals that mate only with their own group, since those which crossmate are reproductively penalized owing to the reduction in fitness of hybrids. This is what Dobzhansky meant when he said '. . . the hybrid sterility caused by the peculiar cytoplasmic effects was probably the primary, and the sexual isolation the secondary, reproductive isolating mechanism in *D. paulistorum*' (1960). Ayala (1975) agreed with this view, and in his discussion of the subject commented: 'The process of speciation is being completed between the semi-species. Sexual Isolation is being superimposed over the pre-existing hybrid sterility and is nearly complete in many cases . . .'

It cannot be emphasized too strongly that there is a distinct logical nexus between the term 'Isolating Mechanism' and the Reinforcement model of speciation. If natural selection directly causes the evolution of divergent courtship patterns for the function of isolation, then these should indeed be considered 'Mechanisms' (*sensu* Williams, 1966) to isolate. If one does not necessarily accept that particular model of speciation, then the term is inconsistent and hence inappropriate. For example, if one agrees that there is overwhelming evidence that species arise as a result of allopatric divergence, and that secondary overlap of population is not a prerequisite for speciation, then characteristics such as courtship behaviour and the structure of male and female genitalia should not be considered logically as 'Isolating Mechanisms'.

Dobzhansky's speciation model is discussed in some detail in his Macleay Lecture and he uses the results of his own work on *Drosophila paulistorum,* together with those of his colleague Lee Ehrman, to illustrate the concept. Since that time a number of other workers, and in particular Ehrman, have gone on to detail this interesting case and to establish it as a classical case in speciation studies (Ehrman, 1960, 1965; Dobzhansky *et al.,* 1969; Malogowokin *et al.,* 1965; Ayala, 1975). *Drosophila paulistorum* was described by Dobzhansky as a 'ring' species. He explains this as '. . . a series of races, the adjacent members of which resemble each other closely, and are often connected by intermediates in the geographically intermediate zones. But the terminal members of the "ring" live together, sympatrically, differ usually more strongly than do neighbouring races elsewhere in the "ring", and yet do not interbreed and do not form intermediates'. Dobzhansky (1960) referred to these six races as being '. . . mostly allopatric, occurring in different countries'. Today, however, these six 'semispecies' are known to overlap considerably (see fig. 2, Ayala, 1975). The example is no longer considered a case of a 'ring' species. However, it is accepted by many authors as a classic example of Dobzhansky's much advocated speciation model.

Although Dobzhansky's paper is twenty-three years old, his basic comments on *D. paulistorum* are still accepted by a great many biologists (e.g. Bush, 1975; Grant, 1963;

White, 1978). He set the scene for much future research and gave a broad framework within which many biologists would work for at least two decades.

We contend that essentially very little has changed in this aspect of evolutionary theory since that time. The advent of techniques for the analysis of enzyme variability for example may be considered by some to have been a significant change in direction. In retrospect, however, many discussions such as that of Ayala (1975), and Avise (1974), considering genetic differentiation during the speciation process, show that these data are merely plugged into the framework which Dobzhansky left behind.

The central concept considered by Dobzhansky in the paper under discussion, that of the relationship between species and races, is an old one. As he points out, Darwin considered species to be merely highly-developed varieties. This is perhaps one of the most basic ideas in speciation theory; that populations adapt to different environments and that speciation is a gradual process which is an indirect consequence of the process of differential adaptation. This is essentially the 'Dumbell Model' of speciation (White, 1978). A large population becomes divided, perhaps by some extrinsic barrier, and the two separated populations slowly diverge. Hence these populations go through the stages of varieties, to sub-species and finally distinct species. It was the presence of varieties and races which so impressed Darwin and which seemed to him to form a logical connecting link between populations of the one species and completely distinct species. Dobzhansky completed his paper by commenting, with respect to the *D. paulistorum* species, 'In any case, we have a beautiful demonstration of Darwin's argument that . . . species are only strongly marked and permanent varieties, and that each species first existed as a variety'. Herein lies a logical inconsistency in Dobzhansky's argument. Whilst he argues for the evolution of *D. paulistorum* species via reinforcement he immediately suggests that Darwin's gradualist speciation arguments are compatible with this view. These two speciation models are logically distinct and incompatible. Dobzhansky and his co-workers have however consistently argued that these views are indeed compatible. Dobzhansky (1970), for example, remarks 'The two hypotheses (reinforcement and allopatric change) are not mutually exclusive. Needless disputes have arisen because they were mistakenly treated as alternatives'. Some years later Dobzhansky *et al.* (1977) made essentially the same statement.

We disagree: Either natural selection *is* or *is not* capable of causing the evolution of complete divergence in 'premating isolating mechanisms' of individuals of different populations.

After having argued very strongly against the reinforcement model in his earlier book (Mayr, 1942), Mayr (1963) changed his view and argued for a limited role for reinforcement. Thus he said, when considering hybrids 'Such hybrids, being sterile cannot reproduce and thus there is no danger of a breakdown of the species barrier. However, there will be strong selection in favour of the acquisition of additional isolating mechanisms to prevent such wastage of gametes' (p.551). This view is one held by many biologists — that of a limited role of natural selection in the perfection of isolating mechanisms. Mayr (1963: 551) says 'Nevertheless natural selection does play a role in the improvement of some of the isolating mechanisms, only it concerns subsidiary isolating mechanisms. The primary, basic one must be fully efficient when contact is first established'. However here lies the crux of this seemingly 'reasonable' view to hold. If the primary basic isolating mechanism is 'fully efficient' then where is the selective pressure to cause a change? Certainly if premating mechanisms are 'fully efficient' then there are no crossmatings and hence no immediate pressure to direct the development of further isolating mechanisms. Mayr argues that this is so since he discusses species in which reproductive isolation is maintained exclusively by the differences in display song. Since hybrids in the case he discusses (that of *Chortippus brunneus* and *C. biguttulus* (Perdeck (1957) quoted in Mayr, 1963) are quite fertile 'The function of this ethological isolating mechanism must have been virtually perfect before contact was established, because the essentially fully viable hybrids would serve as a channel of gene flow between the two species, if they occurred at all frequently'.

Hence we see that Mayr is indeed advocating essentially the same process as Dobzhansky. The argument is simply that this is a refining process which 'sharpens up isolating mechanisms'. We point out that when there is very little hybridization there is consequently very little selective pressure to cause divergence. If there is no divergence in the mate recognition systems of two populations then hybrids will form 50% of the F_1 generation and presumably a large percentage of subsequent populations. However if hybrids form only 1% of the population there is very little selective pressure to cause a change in the mate recognition systems. This remains an important problem, and one which is not addressed by advocates of reinforcement (Lambert *et al.,* 1984).

We would suggest that it is an appropriate time to re-analyse the direction that evolutionary theory has taken, consider the influence of Dobzhansky's school of thought and consider some recent developments.

THE RECOGNITION CONCEPT OF SPECIES

For a number of years Paterson (Paterson and James, 1973; Paterson, 1976, 1978, 1980, 1981, 1982) has argued that the term 'Isolating Mechanism' is inappropriate and misleading. He has suggested an alternative species concept, the *Recognition Concept* and contrasted it to the Isolation Concept. The Recognition Concept emphasizes that species are groups of organisms which are tied together by a common *Specific-Mate Recognition System* (SMRS).

The SMRS is a communication system which results in conspecific fertilization: a subset of a broader category, Fertilization Mechanisms. Paterson's argument is that the phenomena known as 'Isolating Mechanisms' were not moulded by natural selection for the *function* (*sensu* Williams, 1966) of isolating one species from another, but should more appropriately be viewed as communication phenomena that result in fertilization. According to this view species are not the direct products of natural selection to isolate, they are incidental consequences of change in the SMRS of individuals of a population. Students of the Recognition Concept agree that species are 'isolated' from other species; however, this is purely an incidental effect of differences in the SMRS's and therefore, of little direct evolutionary importance.

The SMRS is a species-specific communication system comprising a unique signal-response chain. Different signals in the chain may be auditory, tactile, visual or olfactory for example. A close examination of biparental species demonstrates that individuals, from unicellular algae to mammals, ensure fertilization by the operation of a SMRS of this basic nature. Such a communication system can be described as being maintained by stabilizing selection since any individual which is a deviant with respect to its signal or receiver is less likely to be recognized by, or recognize, a conspecific mate (Lambert *et al.,* 1982; Lambert and Paterson, 1982). This has previously been pointed out (Paterson, 1976, 1978) and subsequently recognized by others (Carson, 1978; Templeton, 1979). Striking evidence for the stability in the mate recognition system of *Drosophila melanogaster* has recently been presented (Henderson and Lambert, 1982). Individuals from worldwide populations of this species appear to possess mate recognition systems which are not detectably different. This lack of variation in the SMRS is in marked contrast to the variation in other genetical and morphometric characteristics of these populations (details in Henderson and Lambert, 1982). Perhaps this is a feature of many species. Geographic variation in characters such as bird and frog calls may *not,* in fact, be evidence for variation in mate recognition characteristics. Individuals almost certainly do not recognize the *call* as a mate recognition character but some *component* of that call. More intense study may show that certain parameters are quite geographically stable. The stability of the SMRS in large natural populations is amply demonstrated by experiments using sterile male insects released in order to eliminate target populations. One reason for the failure of control programmes of this type is changes in the mating behaviour of released males (Bush, 1978). Such altered males are not accepted for mating by females of the target population.

A VIABLE ALTERNATIVE?

The Isolation Concept has been a useful one for a long period of time in that it stimulated much biological research. However, if the phenomena described as 'Isolating Mechanisms' are not the products of natural selection moulded to keep species apart, but intraspecific communication phenomena, a reinterpretation of much previous thinking is needed. New questions must be asked. For example, how do communication systems operating between male and female individuals change? Is this not the essential problem of speciation? What are the laws which govern the transformation of one SMRS to a new and stable SMRS? Why is it that at speciation other species specific communication systems often appear to change also?

Immelmann's (1967) studies on Australian finch species yield an interesting example in this regard. In all these species chicks have patterning inside the mouth which are recognized by the adult bird and this system enables accurate placing of food in the mouths of young (see Immelmann, 1967: 8-9). Immelmann comments that these patterns are '. . . very distinct for a species, and for a group of closely related species, they are important features in the study of the bird systematics'. Adults of each species are 'attuned' to the conspecific patterning and this elicits the feeding response. It seems likely that the patterns are so constant because any chick deviant in its marking pattern will produce a weaker feeding response by the female and hence have less chance of surviving. Adults producing such a deviant chick will also suffer a reduction in their reproductive success.

In speciation events in this group of finches, not only has the SMRS changed, but this offspring-adult communication system also commonly changes. Perhaps studies dealing with other communication systems may yield important information regarding this general phenomenon.

If the SMRS remains stable as evidence indicates, then it is unlikely to change gradually over long periods of evolutionary time. Even if two large populations were gradually to change as a result of different environmental conditions, will the SMRS necessarily change? The condition most conducive to change in the SMRS appears to be small population size. Is then the process of speciation really reflected in the presence of varieties and subspecies? It may well be that large geographically separated populations which are commonly recognized as subspecies are not in the process of gradually changing their SMRS's and hence are not speciating. Whatever distinctness they may show could have occurred while the population was small, prior to its expansion.

The question might reasonably be asked: If the SMRS is so stable, how can it change at speciation? Under conditions of small population size changes in the SMRS can and do occur (Powell, 1978; Arita and Kaneshiro, 1979). Selection may, however, act to maintain the SMRS, and one sex may be selected to recognize the signals from individuals of the altered sex. This could then result in efficiency of communication. Such a process will cause changes in the SMRS of some small isolated populations such that recognition between individuals of the parental and daughter populations does not occur. A speciation event has then occurred.

The Recognition Concept resolves problems that have been noticed by other authors. Levin (1979) for example is dissatisfied with the ability of the Isolation Concept to explain the nature of plant species. He has commented 'It is important to recognise that isolating mechanisms do not exist as properties of single species or single populations'. It is true that isolation is a characteristic only of at least two species never of one. Indeed, species in terms of the isolation concept is a 'relational concept' (Mayr, 1963). Mate recognition, however, is an individual phenomenon and therefore has meaning regardless of the presence of closely related species. Littlejohn (1981) has also recently argued against the concept of reproductive Isolating Mechanisms. Inherent in the Recognition Concept is that species are not in themselves deliberate adaptive devices of the biological world as some have believed (Dobzhansky, 1976; MacArthur and Connell, 1966; White, 1978) but incidental effects of the evolution of sexual reproduction. An examination of the Recognition Concept reveals its basic emphasis on the intraspecific nature of the male-female communication phenomenon. Any characteristic of species which is incidental to this important intraspecific phenomenon is also incidental to the essence of species. Since 'postmating isolating mechanisms' such as hybrid sterility cannot have been directly selected for (Darwin, 1859; Mecham, 1961; Paterson, 1976), despite invoking selection to this end by some authors (e.g. Grant, 1966). Therefore they are not 'mechanisms' (*sensu* Williams, 1966) and their nature is an effect of allopatric change. Here again is a basic difference between the Isolation and Recognition concepts.

Dobzhansky (1960) believed that species arise via secondary overlap of populations which have acquired, in isolation, 'postmating isolating mechanisms'. He maintained that natural selection will directly cause the evolution of species. This will be achieved because individuals from the one group which mismate with individuals of another will have offspring which are disadvantageous (hybrid inviability). Over successive generations selection will favour individuals which recognize mates belonging to their own group and mate only with them. These 'mechanisms' which ensure that individuals do not mismate with members of another group will eventually be perfected by selection and at this time perfect 'isolation' will be achieved and the speciation event completed.

Dobzhansky's reinforcement model has recently been under critical examination from a number of authors. Paterson (1978) has argued that another important factor, that of heterozygote disadvantage, has not been considered and that this can conceivably lead to an alternative outcome. Moore (1957) and Mayr (1942) have criticized this model for a number of theoretical reasons and Futuyma and Mayer (1980), Jackson (1973), Loftus-Hills (1975), Paterson (1978), Roberts (1976), and Walker (1964), have recognized a scarcity of convincing cases in the literature. Moore's (1957) serious general criticisms have never been satisfactorily answered. Littlejohn (1981) appears to accept Moore's argument that genes which have been selected for divergent SMRS's in the zone of secondary overlap will be disadvantageous in allopatry. Indeed, as recognized by Wallace (1968: 377-378) the criticism raised by Moore is satisfied in the model of speciation by small population size developed by Carson (1955, 1975). Littlejohn's (1981) suggestion that reinforcement might still be possible when one population is completely surrounded by another and hybrids are disadvantageous, needs to be examined while taking into account the force of heterozygous disadvantage. The much more likely outcome of such a situation would be elimination of the rarer population (when S = 1 for hybrids) or a cause of the disadvantage (when 0

$<S<1$) (Paterson, 1978, 1981). Harper and Lambert (1983) have recently presented experimental verification of the power of negative heterosis.

Despite the fact that Littlejohn (1981) did not consider the effects of negative heterosis on the vital process of selection for divergence, he apparently nevertheless considers the process can feasibly result in the evolution of distinct species (see his p.328). Littlejohn regards the following studies as detailed and requiring discussion: Blair, 1955; Littlejohn, 1965; Fouquette, 1975 and Ralin, 1977. We will now discuss these.

Fouquette, 1975:

Fouquette (1975) described an analysis of mating calls of two species of the frog genus *Pseudacris* and reports 'divergence' in two components of calls: pulse rate and pulse number. Fouquette (1975:19) argues that '. . . only the differences in mating call can be identified as an effective mechanism operant in maintaining integrity of these species'. The author then goes on to argue that in order to be able to demonstrate character displacement in sympatry it must be possible to determine which characters are used in call discrimination and then to show that differences in these are significantly greater in sympatry than in allopatry. The proposed method by which call parameters are designated as important illustrates a basic circularity in argument. Referring to pulse rate (Pr) of calls Fouquette (1975) comments 'If separate localities are examined (fig. 2e), the slowest *feriarum* call is faster than the fastest *migrita* at all sympatric localities, by a factor of 2 or greater. *This suggests* that Pr is the critical component of mating call enabling females of this species — complex to recognise males of their own species' (our emphasis). The circularity here is that Pr is suggested to act as an isolating mechanism because, in sympatry, there is divergence in this character. However Fouquette's basic argument is that these data are evidence for the reinforcement of isolating mechanisms because the character shows divergence in sympatry. Clearly it must be possible to 'illustrate' reinforcement while using this logic. Whenever one finds a character which shows some evidence for divergence in sympatry it is therefore designated as an isolating mechanism and hence this is consequently evidence for divergence of an isolating mechanism in sympatry. Since divergence is the criterion on which it is designated as an isolating mechanism, to subsequently argue that this is now evidence for reinforcement is unreasonable.

In posing the general problem '. . . can character displacement be demonstrated in call components that are critical in enabling females to identify the call of their own species?' (Note that he has framed this in the positive or recognition format), he goes on to say 'To answer this we must determine what parameters are used in call *discrimination,* and ascertain if differences in these are significantly greater in sympatry than in allopatry' (our emphasis). The latter comment illustrates that Fouquette considers that certain call parameters will indeed be used not to recognize conspecifics as mates but to act as isolating mechanisms and allow the individual to discriminate against non-group members (an isolationist view). Fouquette admits however that 'No direct data are available for Chorus Frogs to indicate which part of the call may be utilized in discrimination . . .'

We agree with Fouquette that characters of calls which exhibit high variability are unlikely to be those involved in mate recognition. It is agreed that we must look for characters of rather low variability. However it is quite possible that one species e.g. *nigrita* uses pulse rate as a component of the mate recognition system and that *feriarum* uses some other component. Pulse rate cannot then be an isolating mechanism since, according to this scheme, individuals of *feriarum* do not use it to 'discriminate' against *nigrita* individuals. In general it is an isolationist assumption that two species will use the *same* call character to ensure there will be no cross matings. On the contrary it seems likely that, of two closely related species, one might use one call parameter in mate recognition and the other might use a different parameter.

In conclusion because of Fouquette's circular reasoning and his lack of any evidence regarding which call parameters are used in mate recognition we argue that this cannot be regarded as evidence for reinforcement.

Ralin, 1977:

The study of Ralin (1977) discusses evidence for reproductive character displacement between populations of the North American frogs *Hyla chrysoscelis* and *H. versicolor.* Ralin (1977) argues that there are three results which are *sufficient* to infer that reproductive character displacement is occurring. These are (1) that call parameters '. . . differ significantly from sympatry to allopatry'; that (2) those same parameters '. . . differ in directions that increase the sympatric differences between two species' and (3) that they '. . . differ in a pattern that cannot be explained as the result of alternative factors'.

First we would however point out that evidence must be presented that these characters are involved in mate recognition. With respect to the particular case concerned, Ralin suggests that there is evidence for the reinforcement of pulse rate and call duration between these frog species. With respect to pulse rate he admits that females of the *H. chrysoscelis — H. versicolor* complex '. . . are capable of species specific discrimination at the level of the difference in mean pulse rates of any two populations of *H. chrysoscelis* and *H. versicolor* whether *sympatric* or *allopatric*' (our emphasis). If this is so there cannot be any pressure to cause sympatric divergence because there can be no mismating. Ralin hence goes on to produce an argument, unconvincing to us, that *chrysoscelis* females might still mate with *versicolor* males and hence reinforcing selection is argued to be possible. Although Ralin suggests that differences in call duration are being reinforced in sympatry he also acknowledges that there is a great deal of overlap in this call parameter between the two taxa.

Unlike Littlejohn (1978), Ralin (1977) does not consider the work of Blair (1955) as a convincing case of reinforcement. He considers only Littlejohn's work on the *Litoria ewingi* group, and the work of Fouquette (1975) (already discussed) are convincing cases.

Littlejohn, 1965:

The most widely-known case of reproductive character displacement is that of Littlejohn (1965), Loftus-Hills and Littlejohn (1971). The significance and importance of the study is reflected in its discussion in such textbooks as Brown (1975), Wilson (1975), White (1978), Futuyma (1979), Shorrocks (1979). However the same circularity of reasoning applies in this case as in the others previously discussed. Littlejohn (1965) remarks that since sympatric populations exhibit a marked difference in characters such as pulse repetition frequency 'It is suggested that the marked differences between sympatric populations have resulted from the direct action of selection . . .' He goes on to suggest '. . . that pulse repetition frequency, because of its similarity in the allopatric populations, and difference in the sympatric populations . . . is the critical information bearing component of the mating call on which efficient and specific discrimination depends'. Hence the same argument appears. Pulse repetition frequency is the discriminator because there is divergence in this character in sympatry, and because there is divergence in sympatry then this is evidence for reinforcement.

In contrast to previously discussed cases however Littlejohn in association with Loftus-Hills went on to test the assertion that pulse repetition frequency is the premating isolating mechanism which keeps species distinct. Loftus-Hills and Littlejohn (1971) conducted two choice discrimination trials using synthetized calls with different pulse repetition rates. The authors reported that in 28 discrimination trials involving eight responsive *Hyla (Litoria) ewingi* females, and seven responsive *H. verreauxi* females, the females were able to discriminate between the two synthetic signals and were attracted by the signal with the pulse repetition rate corresponding to that of their homospecific mating call. However in the production of the synthetic signals the call parameter of pulses per note also changed. The number of pulses in a note of the synthetic *ewingi* call was 15 with 30 pulses per note in the synthetic *verreauxi* call. Loftus-Hills and Littlejohn reject the proposition that this difference provided the basis for call discrimination. They argue that this call parameter will seem to increase as the subject approaches the sound source, making such criteria unsuitable for 'interspecific discrimination'. However such a call parameter as the *rate* of change of pulses per note as an individual approaches, could be a quite satisfactory mate recognition signal. It is also quite possible that *L. ewingi* uses pulse repetition rate in the SMRS of that species. If this were so then the results obtained by Loftus-Hills and Littlejohn (1971) would also be obtained.

Blair, 1955:

In this classic paper Blair (1955) began an approach which was to be used in a number of later studies including the ones discussed previously. This is, however, probably the weakest case discussed. In his discussion of the calls of the North American frog species *Microhyla olivacea* and *M. carolinensis,* Blair shows no conclusive evidence that call duration and mid-point frequency of the calls of these species show conclusive evidence for divergence in the overlap zone. Blair is, in fact, quite cautious in his comments: he says (p.477) 'The greater difference in mating call of the two kinds of frogs in the overlap zone, where there is some hybridization, than where the two do not occur together is possibly explained as the result of selection against hybridization'. Later he remarks 'The striking divergence in mating call in overlap zone suggests selection against hybridization' (p.478).

Again the same problem arises here as in the previous cases. Divergence automatically means that the call parameters being considered are isolating mechanisms and this is then seen as evidence for reinforcement. The general point needs to be made that, just as ecological character displacement cannot occur if the two populations do not compete for a particular environmental variability the same applies to reproductive character displacement. If two species do not use the same call parameter in mate recognition then there can be no possible reinforcement. Each of the studies discussed assume that a particular call parameter is 'premating isolating mechanism', i.e. both species actively utilize this parameter in order to ensure that they do not interbreed with members of another species. For this reason, amongst others discussed, it seems to us that there is, at present, no compelling evidence for speciation by reinforcement.

The essential point is this: if there is no good evidence that 'postmating isolating mechanisms' can directly bring about the evolution of 'premating isolating mechanisms' by selecting against individuals which mismate with members of another group, and consequently have less fit offspring, then, speciation is indeed most appropriately seen as a reorganization of the system of communication between conspecific males and females.

The so-called semispecies of *D. paulistorum* are then not species in *'statu nascendi'* but distinct species. That hybrids between them are fertile to some degree, does not necessarily mean that they are 'capable of exchanging genes', since Dobzhansky himself agrees that there appears to be no exclusive evidence that crossing occurs in the wild (Dobzhansky, 1972). Dobzhansky (1972) was later to remark that 'A cogent argument can be made, that *D. paulistorum* is really a set of five species'. Dobzhansky

(1972) preferred the interpretation that *'Drosophila paulistorum* is a superspecies which still conserves a common, although deeply fissured, gene pool'. This interpretation then allows for the role of natural selection in producing 'complete premating isolating mechanisms'.

PREDICTIONS OF THE RECOGNITION CONCEPT

The conceptual uniqueness of the Recognition Concept of species is reflected in a set of concise predictions. The testing of these predictions, and any contrasting predictions of the Isolating Concept, is of paramount importance in discussions of the relative merits of these two diametrically opposed concepts. Some of the more important predictions of the Recognition Concept are outlined here.

(a) Signals and receivers will be structured for efficiency of communication.

To result in fertilization signals and receivers of individuals of the same species, will be co-ordinated that is, receivers will be 'tuned' so as to 'recognize' conspecific signals. Considerable illustration of this phenomenon has been provided. For example, the studies by Carde and Roelofs (e.g. Carde *et al.,* 1977) on the SMRS's of moths provide details of the use of chemical components in the female sex phenomenon. Males are, however, always 'maximally attracted to a species-specific blend' of these different chemical components.

This prediction is not in absolute conflict with the isolation concept, only that according to the latter view, isolation must result and this may be at the expense of efficiency of communication.

(b) Stabilizing selection acts on both signals and receivers.

Individuals which are deviant with respect to either their signal or receiver characteristics are less likely to be recognized as conspecifics and hence will suffer a selective disadvantage. There is considerable evidence for this prediction. In *Drosophila melanogaster,* for example, mutants such as 'yellow' and 'white eye' result in males with deviant courtship (Reed and Reed, 1950; Bastock, 1956) and these are rejected by conspecific females. Similarly, many genes are known to affect the SMRS and these are apparently selectively eliminated from natural populations, as they arise.

(c) At speciation signals must result in fertilization in the habitat to which the individuals are restricted.

This basic prediction of the Recognition Concept is in contrast to that of the Isolation Concept. The latter predicts that the design features of signal receiver systems will be primarily dependent upon ensuring effective isolation from other species, i.e. it is the presence of other species in the zone of secondary overlap that is the main force moulding the characteristics of the 'Isolating Mechanisms'.

(d) The SMRS is expected to show little variation geographically.

Since the SMRS is co-ordinated and under stabilizing selective pressure minimum variation is expected between geographically distinct populations. Good evidence for this prediction exists from studies on populations of *Drosophila melanogaster* (Henderson and Lambert, 1982; Petit *et al.,* 1976). Similarly Anderson and Ehrman (1967) have shown similar geographic stability in the SMRS of populations of *Drosophila pseudoobscura.*

It should be pointed out that any illustration of geographic variation in frog or bird calls, for example, is not evidence for geographic variation in the SMRS. Recognition is mediated by particular characteristics of the call and these may remain stable despite variation in other components. Emlen's (1972) analysis of playback experiments in Indigo Buntings, together with the results from four other major studies of bird species, stimulated him to comment 'In all five species, recognition depends upon song features that are among the most constant and unvarying in the species repertoire'. Emlen (1972) also concluded that components of calls which appeared to be involved in individual recognition were extremely variable. Hence variability in calls may be due to the fact that a number of functions are involved.

(e) The SMRS of any species is likely to remain stable through time.

The basis for this prediction is essentially the same as that for *(d)*. Once a distinct SMRS has evolved and become fixed, such that individuals from the one group do not recognize those from the original group, and the population then increases in size, we can expect it to remain stable.

(f) The complexity and specificity of the SMRS will not be dependent upon the presence of sympatric closely related species.

Isolating Mechanisms need to be more efficient in situations where crossmatings with closely related relatives are possible. Hence, where groups of closely related species occur, selection will strengthen these mechanisms. Alternatively where single species are geographically separated from their relatives, selection will be relaxed. Lack (1974) for example, when discussing plumage of ducks on remote islands, remarked 'There is presumably much less need for such recognition marks on remote islands with only one resident duck species than on the mainland where several species usually occur together'. Mayr (1963: 109) and Sibley (1961) also make similar comments.

In contrast, the Recognition Concept predicts that courtship in such species needs to be equally specific for normal conspecific fertilization to result.

A review of the data available on this point reveals little support for the isolationist expectation. The Black Swan *(Cygnus atratus)* indigenous to Australia, and not sympatric with any other swan species, appears, by all obvious criteria, to possess as complex a courtship as other swan species (Johnsgard, 1965). Even better examples perhaps are the Hawaiian Goose or nene *(Branta sandvicenis),* and the Cape Barren Goose *(Cereopsis novae-hollandiae).* Although each of these species has no close relatives, and appears to have long since split from some ancestral stock, they seem not to lack any of the courtship characteristics of other Geese (Johnsgard, 1965). For further discussion see Paterson (1978).

(g) Species will remain stable without significant gene flow between populations.

The suggestion that many species appear to have surprisingly small amounts of gene flow between demes, but retain their species specific characteristics, has worried a number of authors (Ehrlich and Raven, 1972; Grant, 1980; Mayr, 1975). The 'orthodox viewpoint' (Grant, 1980) that 'The steady and high genetic input caused by gene flow is the main factor responsible for genetic cohesion among the populations of a species' (Mayr, 1963: 521-522) is argued to be incorrect. Many species characteristics, including the SMRS, are stable because they are composed of two interdependent parts, i.e. because of their structure. Since the co-ordination between signals and receivers is stable this also results in the stability of species. This stability is so obvious that it has been recognized by non-biologists (Macbeth, 1971).

The Recognition Concept has already been misinterpreted by one author. Templeton (1979) has commented 'The *raison d'être* of a mate recognition system is to prevent matings with other sympatric *Drosophila*', to which Paterson has replied (1980), 'The *raison d'être* of an SMRS is to ensure effective syngamy within a population occupying its preferred habitat'. This basic difference carries with it a different view of the nature of species, how species arise and, indeed, the basic nature of biological diversity.

In conclusion, Dobzhansky's Isolation Concept provided the basis for our genetic investigations of species; perhaps, however, it is time for the adoption of a new framework. The Recognition Concept is a scientifically valid alternative, free of many of the difficulties inherent in the isolation concept and thus deserves serious consideration and testing. It is important to consider this viewpoint because 'The expectations of theory colour perception to such a degree that new notions seldom arise from facts collected under the influence of old pictures of the world. New pictures must cast their influence before facts can be seen in different perspective' (Eldredge and Gould, 1972).

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Related Species of *Tridideмnum* in Symbiosis with Cyanophyta

PATRICIA KOTT

KOTT, P. Related species of *Tridideмnum* in symbiosis with Cyanophyta. *Proc. Linn. Soc. N.S.W.* 107 (4), (1983) 1984: 515-520.

A new species of *Tridideмnum* from the Great Barrier Reef in apparently obligate symbiosis with Cyanophyta is described. It appears to be closely related to *T. clinides* Kott, known from the same habitat. Differences in colony form, in the size, shape and distribution of spicules and in the size of the zooids and larvae, distinguish the species from one another.

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INTRODUCTION

Ten of the 20 didemnid species previously known to be associated with prokaryotic plant cells are contained in the genus *Tridideмnum* (Kott, 1982). Four species of *Lissoclinum,* 3 species of *Diplosoma,* 2 species of *Didemnum* and one species of *Echinoclinum* are known to have similar symbionts (see Kott, 1982). The large number of *Tridideмnum* spp. with associated plant cells is more surprising in view of the relatively small number of *Tridideмnum* spp. in the tropical environment when compared with the diversity of the genus *Didemnum* (see Kott, 1981). The symbiosis is most often obligatory, although non-obligate symbionts occur in patches on the surface of some species (Kott *et al.,* 1984).

In the majority of cases the plant cells involved in symbiosis with *Tridideмnum* are *Prochloron,* although Cyanophyta are also known to occur (see Kott, 1982).

Two closely related species of *Tridideмnum* with obligate prokaryotic symbionts are discussed below and compared with one another. One, a new species described for the first time, has only Cyanophyta in the test. The other, *T. clinides* Kott, 1977, recorded previously from a wide geographic range, has both Cyanophyta and *Prochloron* (*pers. comm.* G. C. Cox). It is redescribed in order to clarify its relationship to the new species. These two related species differ from most other small algae-bearing species of this genus in having an atrial siphon rather than a sessile opening. *In situ* the species look almost identical and occupy the same habitat on weed and under rubble near the low tide mark, behind the reef crest. Their symbionts are embedded in the test as in the equally small species *T. miniatum* Kott, 1977, that is also recorded from similar habitats in the Great Barrier Reef. *Tridideмnum miniatum* is readily distinguished by its small spherical spicules and sessile atrial aperture.

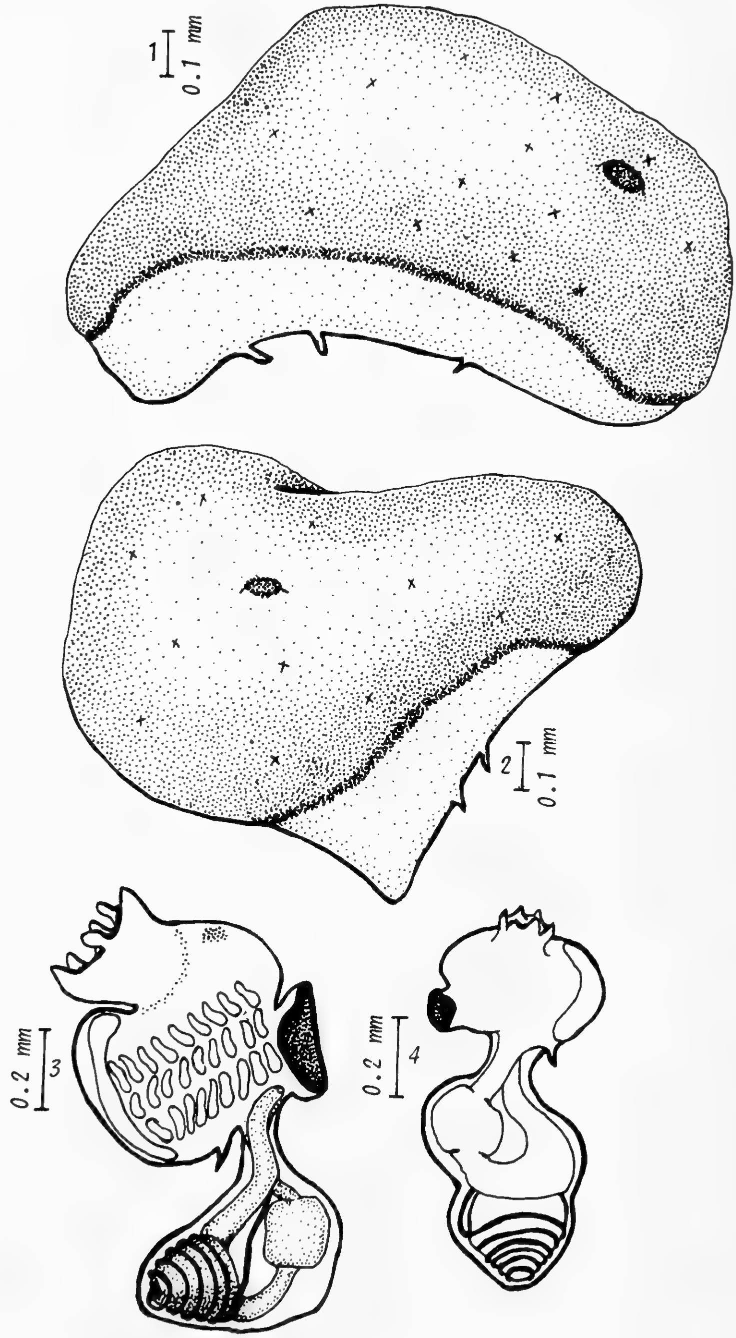
Types of both species are located in the Queensland Museum (QM).

Tridideмnum tegulum n.sp.

Figs 1-3; 5

DISTRIBUTION

Records: Heron I. low tide under boulders, on weed and rubble. Holotype QM GH1492. Paratypes, QM GH892, GH1337, GH1350, GH1493, GH1494, GH1495.



Figs 1-4. **1, 2.** Colonies of *Trididemnum tegulum* n. sp. **3.** Zooid of *Trididemnum tegulum*. **4.** Zooid of *Trididemnum clinides*.

DESCRIPTION

Colony: The colonies are small, firm, almost cartilaginous cushions up to 10 mm in greatest dimension and up to 6 mm thick. The upper surface is almost hemispherical and the diameter narrows to the sometimes pointed base. Larger colonies are elongate and appear to lobulate. Zooids are arranged in a single or at most two circles around the outside of the upper rounded surface. There is a large, but only slightly protruberant common cloacal opening in the centre of the upper surface, or in elongate colonies 2 to 3 common cloacal openings are present, equidistant from one another along the length.

In the living specimen, the highly-arched surface is brownish-black. This gradually fades to white about half way down the sides of the colony.

The test is firm but easily cut. There is a superficial layer of bladder cells all around the upper surface, the sides and base of the colony. On the upper half of the colony, spicules are moderately crowded to sparse in a thin layer beneath the superficial bladder cell layer. In the thick basal test beneath the abdominal common cloaca they are always rather evenly spaced and are not crowded into a layer beneath the bladder cells either around the borders or base of the colony. Occasionally spicules are also present at abdominal level. However they are very sparse, or absent altogether from the fleshy test at thoracic level. Clumps of spicules are present in the test around the branchial apertures and these are the only spicules that protrude through the bladder cell layer. There is a small group of spicules where each atrial aperture opens into the common cloacal cavity. Prokaryotic plant cell symbionts, 0.01-0.015 mm diameter, are embedded in the bladder cell layer and throughout the test at the level of the thoraces, although they become progressively less crowded away from the surface. They are not present beneath the cloacal cavity. Minute dark rounded or oval cells about 0.005 mm in diameter are present throughout the upper layer of test (beneath the bladder cells and lining the cloacal cavity) and in large oval reservoirs in the basal test. This dark pigment, scattered through the deep thoracic layer of the test is the cause of the black opaque pigmentation of the upper half of the colony, while the lower half is off-white, owing to the embedded spicules and the absence of dark pigment cells. The dark pigment usually masks the symbionts, unless they are especially numerous in the upper layer of test.

In preservative, the colour of the symbionts fades more rapidly than the black of the ascidian cells and the upper half of the colonies remain grey-black, only a slightly lighter shade than they are in their natural habitat. Occasionally small spherical or rod-shaped pink cells (0.007-0.009 mm) are present in the test amongst the green symbionts.

In the smaller colonies the central test is uninterrupted from the base of the colony to just beneath the cloacal aperture where it sometimes forms a plug projecting up into the aperture. The cloacal cavity slopes deep into the colony around this central core and breaks into canals around the zooids at abdominal level. The firm uninterrupted central core of test, and thick surface layer around the thoraces in the periphery of the colony maintain the conspicuously arched contour of the upper surface of these colonies. In elongate colonies, before lobulation, there is a shallow cloacal cavity that extends their whole length and slopes off into the abdominal canals around the sides.

The spicules are 0.02-0.05 mm in diameter. They are very variable. More than half are of the usual stellate form with about 9 conical rays in optical transverse section. However there are also burr-like spicules with very fine needle-like rays and others with very numerous blunt and/or pointed rays.

Zooid: Zooids are just over 1 mm long. The branchial siphon is large with 6 very conspicuous lobes. The atrial aperture is on a short and conspicuous funnel-shaped

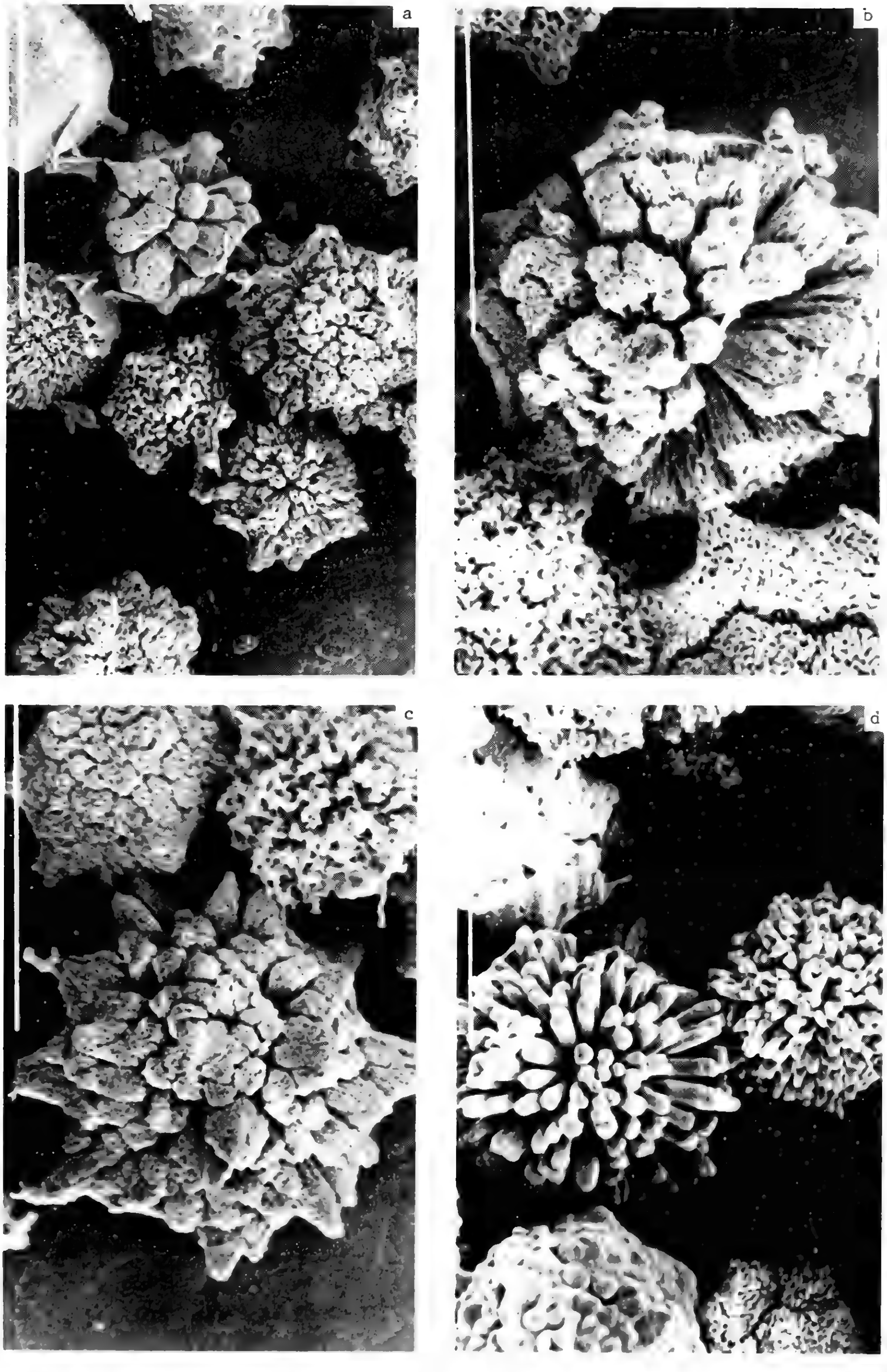


Fig. 5. Spicules of *Trididemnum tegulum* (small scale line = 0.0005 mm).

siphon from the posterior third of the dorsal surface. There is a long prebranchial area and 3 rows of 9 long, oval stigmata. The thorax is over half the length of the body. There are fine longitudinal thoracic muscles, but the retractor muscle is very small, projecting only slightly from the thorax, at the base of the endostyle.

The stomach is small and yellow and the gut forms a rounded loop, flexed ventrally. The ♂ follicle on the dorsal or under side of the gut loop is pointed and there are 5.5. coils of the vas deferens.

Larva: The numerous colonies collected in January 1982, 1983 and August 1982 had no embryos, and only a single larva was present in a colony collected in June 1982. The trunk is 1 mm long and is completely enveloped in symbiotic algal cells, these being absent only from a small area above the larval sense organs. The three adhesive organs also protrude through the plant cells.

Remarks: The species is distinguished from *T. clinides* by its highly-arched upper surface, large zooids and larvae, abdominal cloacal canal, and by its larger and more variable spicules and their distribution, being found principally in the lower half of the fleshy colonies. The thick surface layer of test that extends the full length of the thoraces has dark pigment that is not obscured by the spicules which are principally confined to the basal layer of test beneath the common cloacal cavity and cause only the lower half of the colony to be off-white. This is apparent from the outside of the thick colony, contrasting with the brown-black pigment in the zooid-bearing upper part.

Trididemnum clinides Kott, 1977.

Fig. 4

Trididemnum clinides Kott, 1977: 671; 1980: 5 and synonymy; 1982: 109.

DISTRIBUTION

Records: Philippines, Eniwetok, Guam, Heron I.

DESCRIPTION

Colony: The colonies are small (up to 5 mm in diameter and not more than 3 mm thick). Preserved specimens are usually flat on the upper surface, the border sometimes slightly raised. The surface contour of the preserved specimens is a result of the relatively thin layer of surface test that is depressed over the thoracic cloacal cavity, while the borders of the colony are supported by the crowded layer of spicules that usually occurs just beneath the bladder cell layer around the borders of the colony. The surface layer of test, limited by the position of the cloacal cavity, is relatively thin and has a thin bladder cell layer and a thin layer of spicules, that are often very sparse except over the anterior end of the zooids where these open to the surface. The basal layer of test, beneath the cloacal cavity, is thick and contains the embedded abdomens and moderate to sparsely distributed calcareous spicules. The spicules are evenly distributed except around the base and borders of the colony, where they are crowded together beneath the thin bladder cell layer. They are also present in small groups where the atrial aperture opens into the cloacal cavity. Spicules are 0.03-0.04 mm in diameter with 9-11 rounded or conical rays. Prokaryotic symbiotic algae are present in the surface and basal layer of test, very much reduced in numbers beneath the cloacal cavity. Eukaryotic (Chlorophyta) green algae are also usually present in the test.

Zooid: The zooids are arranged around the periphery of the colony, opening onto the upper surface around a central cloacal aperture. They are never more than 1 mm long, usually less, and their small size is emphasized by the fact that the thorax is always contracted in fixed specimens. There are 5-6 stigmata in each row. The thorax is always smaller than that of *T. tegulum.* The retractor muscle is minute, as in *Trididemnum tegulum.* In both species the branchial siphon is large and has conspicuous pointed lobes. The abdomen does not differ appreciably from that of *T. tegulum.*

Larva: Larvae are small, the trunk being 0.6 mm long. They otherwise resemble larvae of *T. tegulum* with a complete envelope of algal cells exposing only the larval sense and adhesive organs. It is not known if the symbiotic cells that surround the larval trunk are *Prochloron* or Cyanophyta or both.

Remarks: In this species the greater part of the thickness of the colony is beneath the shallow thoracic cloacal cavity. The spicules present in this basal layer of test are especially crowded superficially and create the bright white border and base of the colony by which this species can be readily distinguished from *T. tegulum.*

Since analysis of pigments is based on whole colony extracts, the presence of *Prochloron* is masked by the Chlorophyta which usually occur in the test of *T. clinides* (see Kott, 1982). The presence of Chlorophyll a and b and phycobilin pigments indicates the presence of Cyanophyta and of *Prochloron* and/or Chlorophyta. The presence of *Prochloron*, in addition to the Chlorophyta known to occur, must be determined by studies on the morphology of the prokaryotic cells present.

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On the Philosophy and Methods used to reconstruct Tertiary Vegetation

HELENE A. MARTIN

MARTIN, H. A. On the philosophy and methods used to reconstruct Tertiary vegetation. *Proc. Linn. Soc. N.S.W.* 107 (4), (1983) 1984: 521-533.

Historical interpretations may be offered from plant geography, phylogeny and other studies on living plants as well as the fossil record. Lange (1982) considers that in theory, palaeovegetation reconstructions should result in a single interpretation satisfactory to all, but in practice this is not the case.

This paper examines the lines of evidence used to reconstruct Tertiary vegetation, what each method can do, and just as important, what each method cannot do. It does not present a reconstruction of the Tertiary vegetation; that may be found in Martin (1982). The application of the principle of uniformitarianism with respect to analogy and to basic physical and biological processes is also discussed. This evidence is crucial to the interpretation of fossil evidence.

The fossil record, when used to reconstruct Tertiary vegetation, can do three things which no other line of evidence can do, viz., (1) provide a time control, for fossils can be dated by any of a number of methods, (2) reveal extinct taxa and lineages, and (3) show that taxa have occupied regions where they no longer grow. All three are essential in the reconstruction of Tertiary vegetation.

Plant geography, phylogeny, growth rhythms and other lines of evidence from living plants may be used to suggest hypotheses which require testing by independent evidence. If the hypothesis is an historical one, then the fossil record is an important source of independent evidence. The reconstruction of the Tertiary vegetation from fossil evidence is a speculative process, but to use these other lines of evidence from living plants for such reconstructions is to speculate upon mostly untested hypotheses, and this is not acceptable.

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INTRODUCTION

There is an intrinsic interest in how the present state of the flora and vegetation came to be. It is well recognized that historical factors play an important part, but how does one deduce the history of a flora and vegetation? On one hand, studies from a wide range of botanical disciplines have, at some time, offered historical hypotheses as an explanation of the observations being reported. This practice is most frequent in biogeography and plant ecology, but it also occurs in phylogeny, taxonomy, cytology and plant physiology (e.g. growth rhythms). The historical hypotheses postulate changes through time although the evidence is gleaned from a single instant of time, the present. On the other hand, palaeobotanists present historical hypotheses from fossils which are records of life during past ages. Lange (1982) considers that theoretically, the reconstruction of the Tertiary vegetation should result in a single interpretation which is satisfactory to all, but in practice, this is not so. The hypotheses generated from the different disciplines are frequently at some variance with each other.

This paper examines the philosophy behind the methods used to reconstruct Tertiary vegetation. It examines the strengths and weaknesses of the different lines of evidence. Selected examples are used to illustrate the principles discussed. It is not intended to present a reconstruction of the Tertiary vegetation in this paper, but this may be found in Martin (1982).

Throughout this paper, speculation is used in the sense that it is based on evidence; inference is used in a sense that it is not so constrained. Inference may draw upon several lines of argument which appear reasonable but for which direct connection has not been demonstrated.

UNIFORMITARIANISM

All aspects of palaeobotany and palaeoecology, and indeed all historical sciences, rely on the principle of uniformitarianism, i.e., the present is the key to the past. However, there is evident confusion as to how this principle should be applied. On the one hand, basic physical and biological processes are assumed to have remained the same through time and an understanding of the past is sought in terms of these modern processes (Rymer, 1978). On the other hand, analogy is used to match past patterns of distribution with those of today. In attempting to use analogy, Quaternary palaeoecologists have found that some plant communities of 10,000 years ago have no modern counterparts (Davis, 1978). Tertiary plant communities, the youngest of which are two million years old, are unlikely to exist today without significant modification. Some Tertiary environments may have been quite unlike any experienced today and are likely to have produced plant communities with features not known today. Clearly, analogy has severe limitations in reconstructing the Tertiary vegetation.

The question of Tertiary forests in the high latitudes, before the poles became glaciated, provides an illustration of the two ways the principle of uniformitarianism may be applied. The inhospitable polar regions are quite unsuitable for tree growth today, so there are no modern analogues. The Early Tertiary fossil record, however, is unequivocal. Silicified wood and stumps show that trees once grew in both arctic and antarctic regions. On Ellesmere Island (present and palaeo-latitude about 77-82°N, i.e. latitudes in these regions of the northern hemisphere have not changed), the Early Tertiary angiosperm trees were deciduous and petrified wood shows sharply-defined rings caused by seasonal growth. An unusual leaf gigantism is inferred from modern studies to result from almost continuous photoperiod. There is also relatively low diversity in these assemblages (Hickey, 1981). Reptilian assemblages indicate an equable climate with winters that rarely suffered freezing temperatures (Estes and Hutchinson, 1980). Angiosperms predominate in Early Tertiary floras of Spitsbergen (present and palaeo-latitude about 76-80°N) and they are almost entirely broadleaved, deciduous species. A bivalve and the foraminifera indicate a cool temperate climate with occasional wintery snowfall and light frosts. The coniferous flora divides into two groups: (1) those genera which are frost tolerant but cannot reproduce under a cool temperate climate, and (2) genera which are extremely sensitive to cold so that the younger branchlets are killed by light frosts (Schweitzer, 1980).

The basic biological problem involved here is survival during the long polar winter. The evidence indicates that temperatures were not severely limiting in the Early Tertiary but months of almost continuous darkness would be a serious constraint. However, dormancy would allow the plants to avoid these adverse conditions. Mammalian and reptilian faunas are found also in the Early Tertiary Ellesmere Island deposits. Animals become dormant during adverse conditions as well. Winter dormancy is considered energetically more practical for reptiles (even for those whose modern relatives do not practise it) than is the ability to function under optimal temperatures lower than that found in those groups today (Estes and Hutchinson, 1980).

Evidence of Tertiary vegetation in the high southern latitudes is limited (for a review of antarctic vegetation, see Truswell, 1982), but there is a remarkable Early Cretaceous fossil forest, where stumps and trees have been preserved *in situ* by volcanic muds, at palaeo-latitude 69-75°S (Jefferson, 1983). These are all gymnospermous trees for angiosperms were just evolving about this time, but the basic biological processes for tree growth are the same as for angiosperms, and, indeed, the silicified wood has been examined according to the standard methods of tree-ring analysis.

Undoubtedly, there is much to be learned about life in the polar regions when they were unglaciated and this topic is not without controversy. However, analogy can do little to further our knowledge which will rely on the application of basic biological processes. It is just as important to apply basic biological processes to less extreme examples, such as the Tertiary in lower latitudes, for even if an apparent analogue is found, the comparisons are, at best, superficial. Experimentation into these basic processes under simulated environmental conditions could prove fruitful.

The physical environment of a relatively warm polar climate has no analogue today. On the one hand, some extraordinary mechanisms have been invoked to account for this extraordinary climate. A change in the inclination of the earth's axis of rotation is one such mechanism. Wolfe (1978) advocates such a mechanism but admits that the changes required to produce the temperatures indicated by the Eocene fossils in polar regions would have had very serious consequences on the earth's crust. In addition, with no inclination, there would be no seasonality, and at the poles, the sun would have been about a dozen or so degrees above and below the horizon on each day and night which, coupled with a forested landscape, would have resulted in very low light intensities on the forest floor (McKenna, 1980). It has also been suggested that the solar radiation received by the earth has been greater in the past, although the solar 'constant' has only varied within about 1% of its present value during the last century. However, in order to produce the Eocene temperatures indicated by fossils in polar regions, the increase in solar radiation would be such that the tropics would be baked to death (McKenna, 1980). Clearly, extraordinary propositions of this kind create more problems than they solve.

On the other hand, the warmer polar climates may be explained in terms of physical processes which operate today, for example, heat transfer from the equator to the poles via oceanic currents. The models of Frakes and Kemp (1973) indicate that the warm equatorial currents could penetrate to higher latitudes along the eastern coasts of the continents during the Early Tertiary, before the southern circumpolar current became established. Their estimates of high latitude Eocene temperatures do not conflict with those indicated by the fossil plants (Frakes and Kemp, 1973). Barron *et al.* (1980) model the effect of changes in continental position on the distribution of land and sea and its influence on the energy budget through altered albedo. Their models indicate that small variations in the radiation balance result in dramatic climatic changes. Climatic modelling is in its infancy, but it is based upon processes which may be observed and measured in operation today, and should prove fruitful to the understanding of environments totally outside of present experience.

In practice, both ways of applying the principle of uniformitarianism are necessary, although the limitations of analogy should be obvious. The attribution of ecological tolerances of modern representatives to the fossil taxon is probably an unavoidable analogy, although numerous examples of closely-related modern taxa with different ecological tolerances could be quoted. However, if the ecological tolerances of each taxon in the fossil assemblage are considered together with all the abiotic information of the sediments, and together with the basic physical and biological processes approach, a sound reconstruction of the fossil ecosystem can be achieved.

THE NATURE OF FOSSIL EVIDENCE

The use of basic physical and biological processes to reconstruct past floras and vegetation results in a more general and less specific interpretation (Rymer, 1978) which cannot match the precision of results from the study of living plants. This may be seen at almost every level. For example, fossil populations may be circumscribed and form-species described, but they are rarely equivalent to natural species. With pollen, the fossil form-species may be equivalent to a genus but more frequently, it encompasses several related genera, although not necessarily all the species in these genera. Pollen may be identifiable only to family or a higher level of the taxonomic hierarchy. In other words, the fossil unit, the form-species is not equivalent to any unit in a natural classification of living plants. The type of vegetation may be deduced from the fossil pollen assemblage, but only to a fairly general level, e.g. the formation or vegetation-landform unit (Birks and Birks, 1980).

Fossil assemblages may be dated with varying degrees of certainty/uncertainty. For Tertiary plants in Australia, the most common method of dating involves identification of the pollen assemblage with a described palynological zone which has been dated using independant evidence. An absolute chronology, i.e. radiometric dating (usually potassium-argon) is rarely possible for it requires basalts and fossiliferous sediments to be interbedded. Such requisites are rarely fulfilled in Australia.

The fossil record is often dismissed because it is incomplete. Admittedly, it is incomplete and will remain so, even after many more new discoveries and studies. Paul (1982) shows that the fossil record is much less incomplete than generally accepted. Its incompleteness is largely irrelevant if reconstructions are confined to the known organisms. In any case, every branch of science is incomplete as new evidence will come to hand and old evidence will be viewed with new insight. The fossil record is no different from any other branch of science in this respect. Its incompleteness should not be used as an excuse to dismiss the fossil evidence.

LINES OF EVIDENCE

Palaeobotany/palynology

Fossil spores and pollen are abundant, widely dispersed, and can be recovered in sufficient quantities for routine quantitative evaluation. Many sediments, including those obtained from boreholes, are suitable for palynology; relatively few can be used for analysis of macrofossils for which outcrops are usually required. Once recovered, the fossils (leaves, pollen, wood etc.) must be identified, and there are many pitfalls associated with this procedure. Such identifications produce a fossil assemblage that is an indicator of the floristics for the region. The major problem is in the interpretation of such fossil assemblages into the type of vegetation that might have existed. The interpretation of pollen assemblages relies primarily on species composition and comparisons with living relatives, whereas leaf assemblages may indicate the type of vegetation through a foliar physiognomic classification (e.g. that of Webb, 1959), quite independent of floristics.

There is a wealth of experimental and observational data on modern pollen production, liberation, dispersal, deposition, sedimentation, preservation, deterioration and redeposition which is used as a basis for the interpretation of Quaternary pollen diagrams (see West, 1971; Birks and Birks, 1980). While the examples in these references are almost entirely from the Quaternary of the northern hemisphere, many of the general principles are applicable to Australia and to the Tertiary. Specific examples applying to Australian taxa may be found in almost all of the papers on Australian Quaternary pollen analysis and there are some studies devoted entirely to modern pollen deposition (e.g. Kershaw and Hyland, 1975).

Papers on New Zealand Quaternary and modern pollen studies also contain much that is relevant to the Australian Tertiary (see Martin, 1984).

Quaternary palaeoecologists reconstruct plant communities using one or more of the following broad methods (Birks and Birks, 1980: 231):

(1) The statistical approach leading to the delineation of recurrent groups.

(2) The application backwards in time of known ecological and sociological preferences of taxa. Those with a well-defined narrow ecological tolerance can be used as indicator species.

(3) The comparison of fossil pollen spectra with modern pollen studies from known vegetation types.

The last two methods rely on finding modern analogues. The reconstruction of Tertiary vegetation utilizes mainly the second method, but in a more general way than that used in the Quaternary. The statistical approach, where a mathematical method is used to calculate some measure of interspecific association may be used quite independent of modern analogues, or if analogues are used then this method may show the fossil assemblages for which there are no analogues (see Birks, 1976). Luly *et al.* (1980) have used this method to delimit recurrent groups in the Australian Tertiary, and wisely, without any attempt to match them with modern analogues.

There appear to be no similar 'guide lines' for the interpretation of macrofossil assemblages. Relatively little experimental work has been done to elucidate the extent of, or the processes involved in, the transport, sorting, degradation and deposition of macrofossils. Spicer (1981) considers that much has been taken for granted in the interpretation of macrofossil assemblages and even the most basic assumptions must be tested.

Spicer (1981) chose a small lake with a stream forming a delta advancing over the lake bottom, for a detailed investigation of leaf deposition. Leaves accumulate on the bottom of the lake. The stream entering the lake transports leaves into it, but because of the difference in settling rates, most of the mineral particles settle first and the leaves settle out on top. In this way, two leaf beds of different provenance are being formed at the same time, viz. (1) the lake leaf bed, with leaves from species growing around the margin and leaves blown off the top of the canopy and (2) the delta leaf bed, with leaves from species growing on the delta and those transported in by the stream. These two leaf beds may contain different species assemblages. This is only one example of leaf accumulation, but it illustrates the importance of knowing the conditions under which macro-fossils accumulate.

Biological degradation is an important factor in the preservation of leaves. Invertebrates attack leaves already affected by microbial activity. Decomposition by fungi is more devastating than bacterial activity. There is evidence of differential attack, organisms of decay preferring leaves with a high nitrogen and phosphorus content. The content of lignin and antifungal compounds, e.g. condensed tannins, in leaves is also important in determining the rate of decay. Rapid burial by inorganic sediments ensures better preservation (Spicer, 1981).

Quaternary palaeoecologists may investigate macrofossils using much the same methods as those for pollen. These macrofossils are mainly fruits and seeds, and a 'seed diagram' may be constructed in much the same way as a pollen diagram. Surface samples of lake sediments are used to investigate modern representation and dispersal of the macrofossils. Where both pollen and macrofossils have been studied from the same sediments, each complements the other and a much better reconstruction of the vegetation is obtained.

Some macrofossil assemblages accumulate *in situ* and these afford excellent opportunities for reconstruction of the plant communities. Blackburn (1981) has reconstructed some Miocene swamp vegetation from macrofossils in the Latrobe Valley brown coals. Reconstructions from palynology (Luly *et al.,* 1980) contain much that is complementary and there is a core of evidence in general agreement. Hill (1982) has compared the Eocene macro- and micro-floras of Nerriga. Some of the evidence may be complementary, but the lack of taxonomic determinations make comparisons difficult. Of the 25 leaf taxa circumscribed, only 5 have been identified with living representatives and only one of the five is an angiosperm. Not all of the pollen is identifiable either. Part of the difficulty of identifying older Tertiary fossils involves the lack of relevant reference sets. However, Hill used leaves from several thousands of Australasian species of angiosperms for the one identification, so larger reference sets are unlikely to overcome this difficulty. It could be that many of the early Tertiary angiosperms are extinct, or that evolution has so altered the character of leaves that they cannot be identified with extant taxa. There is no reason to assume that evolution has proceeded at the same rate in pollen and leaves (Hill, 1982), particularly since pollen is believed to be 'conservative' in this respect.

With leaves, however, a foliar physiognomic classification is possible, e.g. that of Christophel and Blackburn (1978). The reference classification of Webb (1959) is based upon sun leaves, the smallest of the mature leaves. Fossil assemblages are likely to contain a mixture of sun and shade leaves, hence the degree of tropicality is likely to be somewhat inflated (Webb, *pers. comm.*).

The best reconstructions of the Tertiary vegetation will result from the investigation of both macro- and micro-fossils. Not all deposits are suitable for comprehensive investigations of this kind, indeed few are capable of producing the excellent evidence obtained from the Latrobe Valley brown coals. Nevertheless, evidence from less comprehensive investigations is of value, but it is important to remember its limitations and bias.

Plant geography

Classical plant geography seeks to explain the cause of present distributions from evidence inherent in these distributions. This practice is of very long standing and has relied on the area of origin and dispersal concept originally proposed by Darwin. In this model, a taxon spreads out from its area of origin by dispersal, expanding its distribution with time. This expansion may be stopped or channelled by barriers to dispersal. Recently this concept has been challenged by the vicariance model in which a widespread distribution becomes fragmented. The cause of this disjunction is frequently attributed to continental drift. (For a full account of these topics see Nelson and Rosen, 1981). Both models, however, rely primarily on the present distribution of the groups concerned. It is freely admitted (e.g. Stott, 1981) that many 'external' factors influence distributions, e.g. changes in climate, geology and other biotic factors, which would disrupt or obliterate the distributions expected on these theoretical models. There are, however, many phytogeographic studies which pay scant attention to such 'external factors'. Many of the studies also pay little attention to the environment and ecology, and historical explanations are offered for distributions which may be controlled by these factors.

Just how much the original premises and methods influence conclusions may be seen in two papers presented in the symposium 'Bridge and Barrier: The natural and cultural history of Torres Strait' (Walker, 1972). In the first, Hoogland (1972) interprets plant distributions by the classical historical biogeographic method, i.e. a monophyletic origin of a taxon and its subsequent increase in area which, theoretically would constitute concentric circles, but which are modified by topography and other features of the habitat. After an analysis of family, generic and species distributions for New Guinea and Australia, the latter sometimes divided along the Tropic of

Capricorn, Hoogland concludes that Torres Strait is a distinct barrier to dispersal and anomalous distributions which transgress the Strait are explained when habitat factors are taken into account. It is hardly surprising that these comparisons produce marked differences, since approximately half the area of Australia north of the Tropic of Capricorn falls within the arid zone, whereas New Guinea is mostly rainforest and has no arid zone.

In the second example, Webb and Tracey (1972) adopt an ecological approach. Structurally and physiognomically similar communities are believed to reflect equivalent physical environments, so pairs of communities occupying analogous habitats, one from northern Australia and one from New Guinea are compared. Within Australia the structural and floristic differences between adjacent rainforest and sclerophyll forest are far greater than related community pairs widely separated by Torres Strait. The infertile soils of Cape York Peninsula do not permit the growth of rainforest except in the most favoured and small habitats. Where rainforest does grow on Cape York Peninsula, it is closely related to that in New Guinea. Thus the major barrier is the change in soil type which, for the most part, coincides with Torres Strait. The water gap of the Strait is hardly any barrier to dispersal if there is a suitable environment for growth.

These two studies illustrate how an historical explanation may be offered for distributions which are really the result of ecological causes. The failure of many biogeographical studies to take account of ecology and the habitat is a serious shortcoming.

Traditionally, the tropical elements in northern Australia (i.e. many rainforest species), have been regarded as recent immigrants from the Indo-Malaysian area (the 'invasion theory' outlined by Barlow, 1981). On distribution alone, this appears a reasonable proposition, as many of the groups are much better represented in the island chain to the north. It is only recently that the long history and wide distribution of rainforest in Australia all through the Tertiary, as shown by the fossil record (Martin, 1978, 1981) has been accepted. Herbert consistently opposed the immigration view (Barlow, 1981) partly for ecological reasons and partly because of the fossil record. Writing fifty years ago, Herbert (1933) gave his reasons thus: the Australian palaeotropic (= tropical) element is easily recognizable as distinct from the typical Australian element. Its distribution is restricted primarily by climatic factors although it has a wide range in Australia. Formerly it covered a much greater area, as the fossil record from New South Wales and Victoria indicates, and its present area represents a considerable contraction of its territory (Herbert, 1933). It is interesting to note that the fossil record, inadequate as our knowledge of it was fifty years ago, still showed essentially the same general pattern as it does today, to those who were willing to consider it.

The practice of seeking to explain the cause of distribution from evidence inherent in present distributions (called the retrospective method by Stott, 1981) developed long before there was a fossil record worthy of the name. Even if a fossil record is available, its general nature frequently cannot provide answers to specific questions about the pattern of distribution of individual taxa. While a number of Australian phytogeographic studies have made use of the fossil record, the inclination to relegate the fossil record to a supportive role, or dismiss it if it proves inconvenient, still exists. Barlow (1981) admits that *Acacia* is known in the fossil record only since the beginning of the Miocene, but 'it undoubtedly has had a longer Tertiary history in Australia'. No evidence for its undoubted history before the Miocene, nor reasons why it should have been absent from the fossil record before this time are given. One suspects that the fossil evidence does not agree with the author's notions, and is therefore simply written off.

The distribution of any plant species or group is determined ultimately by its ability to survive under the existing environment. But in addition to these limitations, distributions are also the product of historical factors, including past climates, geographics and floristics. Studies based on very simple models, such as the area of origin/dispersal or the vicariance model are unrealistic if they ignore the complex multifactorial nature of plant distributions. However, plant distributions may be used to suggest hypotheses which require testing with independent evidence. Indeed, many of the interpretations of biogeography should be viewed in this light: they are hypotheses which require testing. Unfortunately, the untested nature of the hypotheses is too frequently forgotten. On the one hand, it may take a long time to produce the required independent evidence. For example, although many biogeographical tenets effectively supported the hypothesis of continental drift, a fulfilling testing of this hypothesis required geophysical evidence and a programme of deep-sea drilling, some 50 years later. On the other hand, the evidence may exist, but be ignored for 50 years or more; for example, the invasion theory of the tropical element, discussed above.

Phylogeny

From cytological studies, Smith-White (1959) found that certain patterns of change in chromosome number run parallel in different families. In general, herbaceous taxa show more variation in chromosome number than woody taxa. For these woody taxa, differences in haploid numbers are said to be characteristic of genera rather than species. Smith-White concluded that the genera date from the early Tertiary. This date, however, is based on the fossil record of the Proteaceae, but one of the families he studied cytologically. There is a marked difference at the specific level in the hardwood floras of western and southeastern Australia which is inferred to be the result of long-standing isolation. Crocker and Wood (1947) postulate minimum isolation during the warm, moist Miocene period, so Smith-White infers that isolation has been effective since that time; hence he concludes that the species are post-Miocene and the genera pre-Miocene in origin. (For a more detailed summary of Smith-White's hypotheses, see James, 1981). Essentially, Smith-White viewed these patterns of variation in chromosome number, or cytological evolution, as some relative measure of time, and by an integration of the geological history as he knew it, arrived at an evolutionary interpretation spanning the Cretaceous and Tertiary.

Lange (1982) accepts the hypothesis that a relative age is displayed by the pattern of variation of chromosome number and uses phylogeny as one of his lines of evidence to reconstruct the Tertiary vegetation. James (1981), however, considers evidence accumulated since Smith-White formulated his hypothesis and shows that some of his assumptions do not hold. Smith-White's principle of the constant number of chromosomes within genera, and the diversity of chromosome numbers between genera amongst woody components of the Australian flora does not apply in the Casuarinaceae or Dilleniaceae; it is scarcely relevant in Myrtaceae, it is quite obscure in Epacridaceae and Rutaceae; it almost applies in Papilionaceae and it holds up quite well only in Proteaceae.

James (1981) presents an alternative hypothesis that cytoevolutionary change is more relevant to understanding genetic systems than in providing a basis for deducing past selection intensities. Chromosomal variation is frequently associated with changes in the breeding system towards inbreeding which conserves adaptive gene arrays but reduces heterozygosity. On the other hand, complete or relative chromosome stability is associated with effective cross pollination, and by inference, a high level of heterozygosity.

This hypothesis of James may provide a genetic explanation of some of the observed features of the fossil record. For example, proteaceous pollen first appeared some 80 million years ago in the Late Cretaceous. In the Early Tertiary, there is a wealth of different forms, many of them undescribed. Many of these Early Tertiary forms became extinct by the end of the Eocene. There are some pollen forms, however, which occur in the Late Cretaceous, throughout the Tertiary and in living species (Martin, unpubl.). Some of the extinct forms may represent bursts of radiation in which adapted gene arrays are conserved, but because of their inbreeding tendencies, lack the genetic flexibility to survive change. Only the Proteaceae with relatively stable chromosome numbers, by virtue of their outbreeding and genetic flexibility, have survived to the present.

Other phylogenetic studies, such as that of the Proteaceae by Johnson and Briggs (1975), attempt to reconstruct the ancestral form of the family. The fossil record is far too inadequate for the reconstruction of a lineage, and they are thrown back on the comparative method using living forms. Their reconstruction of the phytogeographic history of the family makes as much use as is possible of the fossil record and the background of palaeogeography and palaeoclimatology, and should be regarded as an hypothesis about the place the family may have occupied in past ages.

At best, cytoevolutionary and other phylogenetic studies may suggest hypotheses which require testing by independent evidence. The fossil record is the most important source of independent evidence. Such hypotheses should not be used as though they are evidence for the reconstruction of the Tertiary vegetation. In any case, vegetation is not defined by the phylogenies of its component parts.

Growth rhythms

In a study of South Australian heath, Specht and Rayson (1957) found that the dominant species grew in the summer months, in contrast to the expected spring growth. This lead to the conclusion that the growth rhythm of the heath 'is markedly out of phase with the annual climatic cycle' (Specht and Rayson, 1957). The geological history indicates that there was once a more humid, and probably warmer climate, so Specht (1973) concludes that the 'mediterranean-climate' flora of southern Australia is probably a relic of tropical origin. Thus modern rhythms are being used as evidence of the origin of the flora.

Specht and Brouwer (1975) list the growth periods of a number of species from different types of vegetation. In this context growth means the elongation of the stem tips and expansion of new leaves. It should be noted that not all the species in the one community grow at the same time. There is considerable variation and some species have two periods of growth, one in spring and one in autumn.

Growth is not confined to the expansion of the new leaves, although this phase is the most conspicuous and it may be the time of maximum growth. There is an annual cycle (Specht, 1975). Leaf decomposition is greatest in late winter and spring. If the major period of growth then follows, as it does with many sclerophyllous species, it may be advantageous to mineral recycling. It is thought that exotics with a spring period of growth may have a competitive advantage for minerals, except that they usually cannot become established in such infertile soils as support these sclerophylls (Specht, 1975). Thus Specht has provided an alternative hypothesis for the observed growth rhythms: they have some adaptive advantage to these infertile soils.

In South African sclerophyllous communities, there is wide variation of growing season although most growth occurs from late winter to early summer (Kruger, 1981). The diverse phenologies (i.e. growth and other seasonal variation, such as flowering) are viewed as probably some means of maintaining community diversity in the face of seasonal drought, infertile soils and periodic fire. Thus Kruger regards the observed growth patterns as having some adaptive advantage.

Growth is a complex process, and the same end result may well be achieved by different means, under the one climate. A growth rhythm which developed under a different climate is likely to be maladapted to a changed climate. An inflexible growth rhythm is more likely to lead to extinction, once change occurs. Growth rhythms undoubtedly have a genetic component and are the product of a history, but the fact that they have survived climatic change, if one accepts that a summer growth rhythm originated in the tropics, should caution any who wish to attempt a backwards extrapolation.

The habitat

Lange (1982) includes the habitat as one of his lines of evidence for the reconstruction of the Tertiary vegetation. A considerable amount of information about the habitat is deduced from the fossil assemblage itself, hence the danger of a circular argument. Independent evidence about the habitat is found in the sediments themselves, the local depositional environment and the geological history of the region. Deductions about the habitat obtained from different fossil assemblages, e.g. animals, are a most valuable source of supporting speculation.

It appears, however, that Lange considers palaeogeography and oxygen-isotope palaeotemperatures as providing evidence of the habitat. These features are so general that their use in this way is rather like an ecologist defining habitat solely in terms of latitude and mean annual temperature. Such factors only constitute a background or regional setting. The more specific deductions about the habitat should be in general accord with the regional setting, but local factors may be of major importance in determining the overall specific character of the habitat.

DISCUSSION

Of all the lines of evidence, palaeobotany can do three things for the reconstruction of Tertiary vegetation which none of the others can do. These are:

1. Provide a time control, for fossils are datable,
2. Reveal extinct taxa and lineages, and
3. Show that taxa have occupied regions where they no longer grow.

Plant geography, phylogeny and other investigations from living plants can only suggest hypotheses which then require testing with independent evidence. If the hypothesis is an historical one, then the fossil record is the most important source of independent evidence. The reconstruction of vegetation from a fossil assemblage is a speculative process and it should be based on the evidence, viz, the fossils, the sediments, and the geological setting and history of the region where the fossils occur. To use investigations from living plants as evidence for the reconstruction of the Tertiary vegetation is to speculate upon mainly untested hypotheses, and this is not acceptable.

To plant geographers, phylogenists and others who wish to use the fossil record to deduce histories of the group(s) they study, the generalized nature of the fossil record will remain a problem. Even when a good record exists, rarely can it answer specific questions asked of it. For example, I am frequently asked when a specific taxon first appears in the fossil record. For the most part, I can only answer that the general pollen type is present, but it cannot be differentiated reliably from similar pollen, which may be found also in quite unrelated taxa, without the most detailed and intensive investigation.

Theoretically, the fossil record should pin-point the origin of a taxon in time and space, but there are practical difficulties to achieving this aim. If the taxon in question is found in isolated deposits, then the stratigraphic position and age may be difficult to establish. The 'resolution' in this case may be many millions of years, and it would appear that a taxon could become world wide in this time (for example, *Ilex,* a very distinctive pollen type, see Martin, 1977). Some deposits are extensive and continuous through a relatively long period of time, and it is possible to trace evolutionary changes, as with the Atlantic Coastal Plain of the U.S.A. which has been used to trace the early evolution of angiosperm pollen (see Doyle, 1973, 1978). The experience with pollen referred to here would apply to macrofossils as well.

The future will witness many advances over the present knowledge of the Tertiary vegetation. New evidence will come to hand and older evidence will be viewed with new insight. Some outstanding problems such as the reasons for the presence of abundant *Nothofagus* with the *brassii* type pollen but the absence of leaves of this section of *Nothofagus* in the Tertiary fossil record of Australia, remain to be solved. The most fruitful investigations are likely to result from thorough studies of micro- and macrofossils in the same deposits and the sediments in which they occur, though, as discussed previously, few deposits are suitable for such investigations. There is much scope for innovative methods and the adoption of those used by Quaternary palaeoecologists (discussed previously), as Luly *et al.* (1980) have shown. Above all, interpretations must be based on basic physical and biological processes, and recognition of the numerous variables of the environment that influence plant distributions.

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page 14 — *delete lines 20 and 21 and replace with:*

Islands, as well as an apparently undisturbed raised beach at 54 m, suggesting isostatic readjustment as the explanation for such a fresh beach at that altitude. There is also a

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