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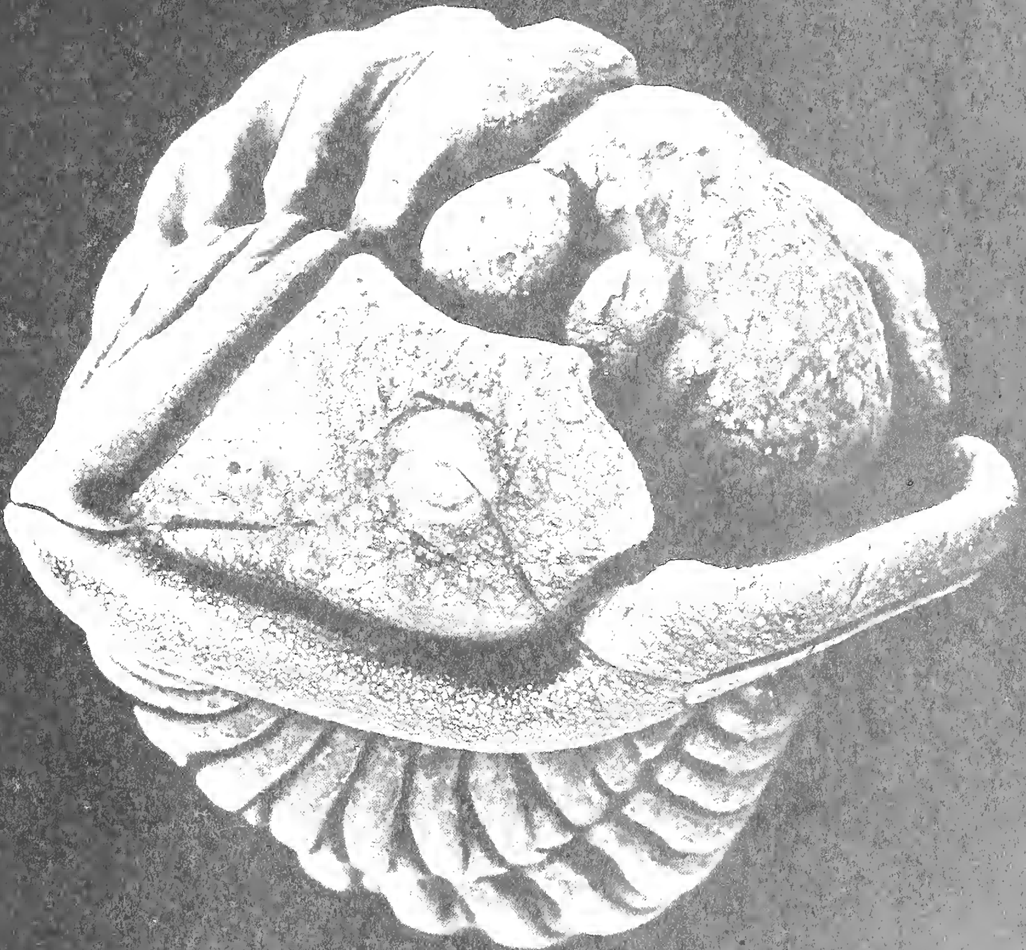

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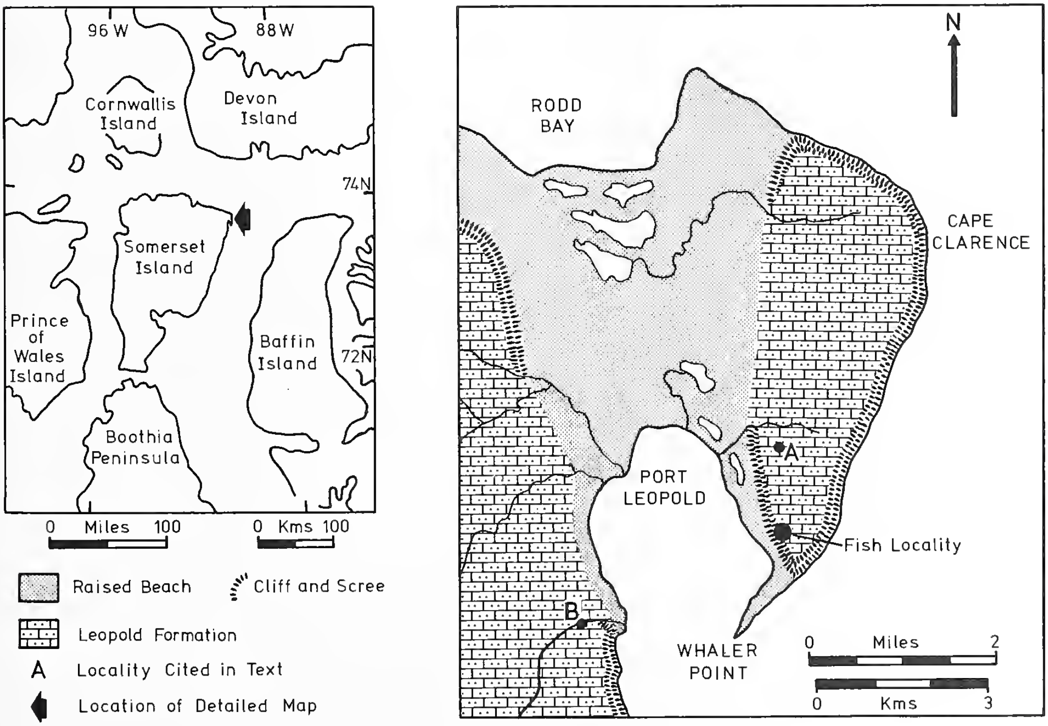
Cover: *Calymene frontosa* Lindström, from Visby Beds (Silurian) of Gotland, Sweden.
Specimen Ar 27038 from Naturhistoriska Riksmuseet, Stockholm, photographed by
Dr. D. J. Siveter, Trinity College, Dublin.

AN OSTRACODERM FAUNA FROM THE LEOPOLD FORMATION (SILURIAN TO DEVONIAN) OF SOMERSET ISLAND, NORTH-WEST TERRITORIES, CANADA

by E. J. LOEFFLER *and* B. JONES

ABSTRACT. An ostracoderm fauna, comprising *Archegonaspis* cf. *A. schmidti* (Geinitz), *Homalaspidella* cf. *H. borealis* Denison, Cyathaspididae indet., and Heterostraci indet., occurs in the Leopold Formation on north-eastern Somerset Island. The associated invertebrate faunas indicate a Pridolian (upper Silurian) or Gedinnian (lower Devonian) age for the ostracoderm horizon; this is the youngest substantiated report of *Archegonaspis*.

THE ostracoderms described in this paper were collected from a unit near the top of the cliffs at the southern end of the peninsula at Port Leopold, Somerset Island (text-fig. 1). This locality was discovered by one of the authors (B. J.) during a detailed study of the carbonate rocks of the area. The collection made at that time (1971) was sufficiently interesting to warrant further collecting; this, by both authors, took



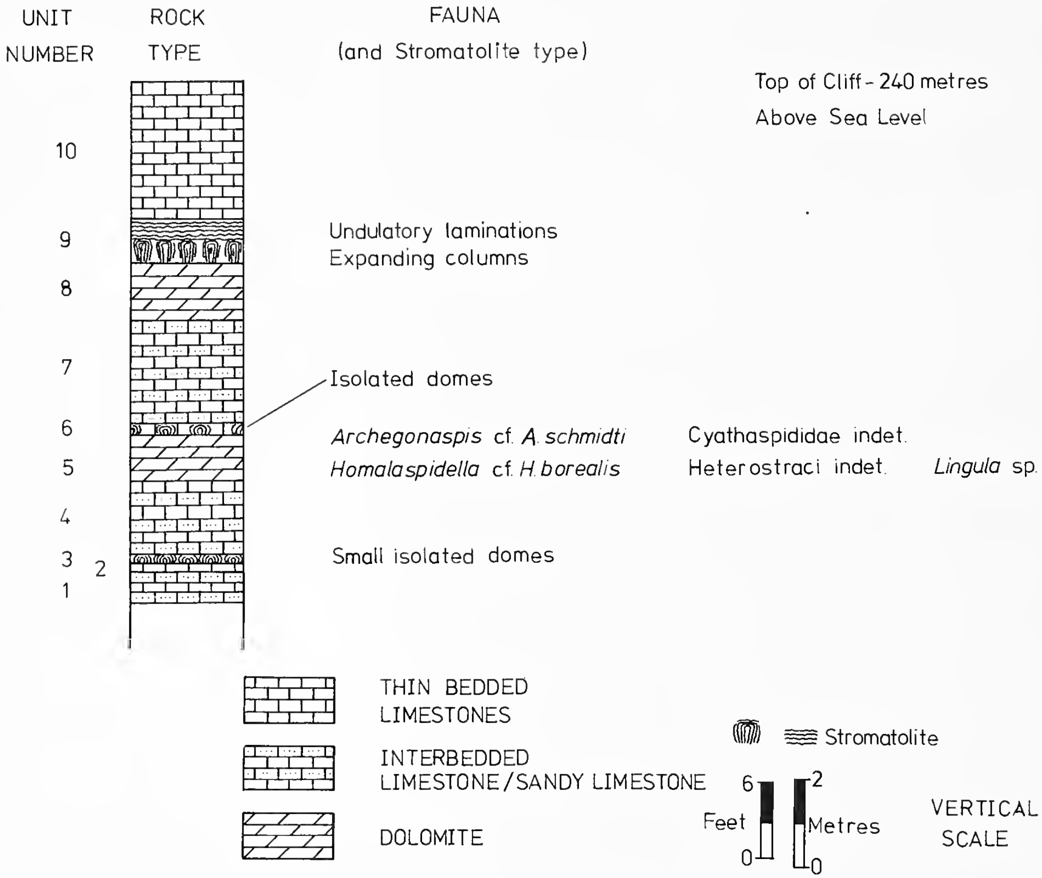
TEXT-FIG. 1. Locality map.

[Palaeontology, Vol. 19, Part 1, 1976, pp. 1-15, pls. 1-2.]

place in 1973. In the following discussion the stratigraphic and sedimentological information and age assessments were prepared by Jones; Loeffler described the vertebrates and discussed their significance.

STRATIGRAPHIC LOCATION

The ostracoderms occur in a one-metre-thick unit of dolomite approximately 240 m (800 ft) above sea level, 8 m (26 ft) below the top of the cliff (text-fig. 2) and approximately 220 m (670 ft) above the base of the Leopold Formation. From the southern extremity of the peninsula, the unit can be traced northwards for about 60 m (190 ft) before the exposure ends. Indeterminate ostracoderm fragments, in a similar lithology, were also found in the scree to the north (locality A, text-fig. 1) suggesting that the unit continues northward beneath the scree. Another ostracoderm fauna, which will form the subject of a separate paper, has been found on the west side of the bay at Port Leopold (locality B, text-fig. 1).



TEXT-FIG. 2. Section measured on cliffs on the east side of the bay at Port Leopold, showing lithological subdivisions and the position of the ostracoderm horizon.

McMillan (in Fortier *et al.* 1963, p. 130) assigned the strata of this area to the Read Bay Formation. However, detailed sedimentological study of the area (Jones 1974; Jones and Dixon 1975) has shown that the strata cannot be assigned to the Read Bay Formation since the lithologies and fauna do not correspond to the definition of the formation given by Thorsteinsson (1958, p. 47). Jones and Dixon (1975) have, consequently, assigned the strata to the Leopold Formation.

DEPOSITIONAL ENVIRONMENTS

The dolomite unit which contains the ostracoderms occurs in a succession in which stromatolitic units are common (text-fig. 2). Although the stromatolites have various forms (text-fig. 2), they collectively suggest intertidal environments (Logan *et al.* 1964). The textural relationship of the dolomite to small patches of micritic calcite in the rock suggests that the dolomite is of secondary origin and that it formed at an early stage. Such dolomite formation in Recent environments is most commonly associated with high intertidal and supratidal environments (Illing *et al.* 1965; Deffeyes *et al.* 1964). The presence of the brachiopod *Lingula* in unit 5 (text-fig. 2) also suggests shallow water. Craig (1952) noted that this brachiopod is commonly associated with tidal flat areas.

Based on the evidence outlined above and on evidence obtained from other sections in the area, the depositional environment has been interpreted as a tidal flat area with a seaward margin occupied by stromatolites (Jones and Dixon 1975).

The vertebrate remains in unit 5 comprise isolated dorsal and ventral shields, together with isolated scales. The ostracoderms probably did not live in the tidal-flat environment, since it is doubtful that they could have survived under such conditions. They may well have been washed on to the tidal flat during a period of strong current action, possibly during a storm. With decay of the soft tissues under aerobic conditions, the various elements of the skeleton would have become separated and subsequently incorporated in the sediment as isolated shields and scales.

AGE OF THE OSTRACODERM HORIZON

While the macrofauna of rare brachiopods (*Lingula*, *Kirkidium*?, and *Howellella*), rare coral fragments (*Coenites*), and abundant eurypterids (of *Eurypterus remipes* group) suggests an upper Silurian age for the strata, it does not permit distinction of the Ludlovian or Pridolian series (Jones and Dixon 1975). The ostracods (*Bairdiocypris*, *Beyrichia* (*Beyrichia*) aff. *arctigena*, *Leperditia jonesi*) suggest correlation with the upper part of the Read Bay Formation and/or the lower part of the Peel Sound Formation (Copeland 1973, pers. comm.). Elsewhere on Somerset Island the upper part of the Read Bay Formation and the lower part of the Peel Sound Formation are of Pridolian age (Jones 1974). The conodonts, *Ozarkodina confluens* (Branson and Mehl) (late form) and '*Ozarkodina*' *ortuformis* Walliser, from the basal 20 m (63 ft) of the Leopold Formation indicate a Pridolian age (*eosteinhornensis* Zone) (Uyeno 1974, pers. comm.).

Since the ostracoderm unit is approximately 220 m (670 ft) above the base of the

Leopold Formation, a Pridolian or younger age is indicated for the ostracoderm fauna.

SYSTEMATIC PALAEONTOLOGY

The ostracoderms described in this paper are the property of the National Museum of Canada and bear their catalogue numbers (prefixed NMC); they will eventually be housed in that institution.

Order HETEROSTRACI Lankester, 1868
Family CYATHASPIDIDAE Kiaer, 1932
Subfamily CYATHASPIDINAE Denison, 1964
Genus ARCHEGONASPIS Jaekel, 1927
Archegonaspis cf. *A. schmidti* (Geinitz, 1884)

Plate 1, figs. 1, 2, 3; Plate 2, fig. 1

Material. Sixteen dorsal shields (NMC 21574–21587, 21589, 21590, 21595) and three ventral shields (NMC 21597–21599).

Occurrence. Approximately 220 m above the base of the Leopold Formation, on the east side of the bay at Port Leopold, Somerset Island, North-west Territories, Canada (text-fig. 1).

Dimensions. Ranges are based on the measurement of ten dorsal and three ventral shields, few of which are complete; parameters selected for measurement are the same as those used by Denison (1964, fig. 93).

	Range	Mean	No. measured
Dorsal Shield:			
Median length	32·2–38·0 mm	33·9 mm	10
Maximum width	20·0–23·0 mm	21·2 mm	10
Orbital width	15·0–17·0 mm	15·9 mm	8
Orbital length	5·0–6·3 mm	5·9 mm	9
Pineal length	8·4–10·0 mm	9·3 mm	10
Postbranchial length	8·5–10·3 mm	9·2 mm	7
Width ratio	0·58–0·64	0·62	10
Orbital width ratio	0·44–0·48	0·46	7
Orbital length ratio	0·15–0·19	0·17	8
Pineal length ratio	0·25–0·29	0·27	10
Postbranchial length ratio	0·24–0·30	0·27	7
Ventral Shield:			
Median length	25·8–28·6 mm	27·0 mm	3
Maximum width	16·6–18·1 mm	17·3 mm	3
Width ratio	0·63–0·67	0·64	3

EXPLANATION OF PLATE 1

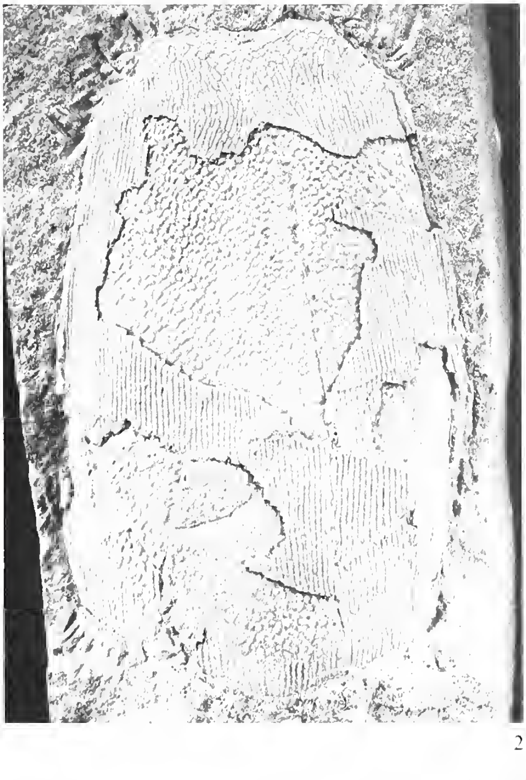
Archegonaspis cf. *A. schmidti* (Geinitz)

Fig. 1. Latex cast of external moulds of three dorsal shields; NMC 21582 (left), NMC 21581 (bottom centre), NMC 21583 (top right). Magnification ×2.

Fig. 2. Ventral shield, NMC 21598A, partly preserved as an internal mould. Magnification ×3.

Fig. 3. Latex cast of external mould of ventral shield, NMC 21598B. Magnification ×3.

1



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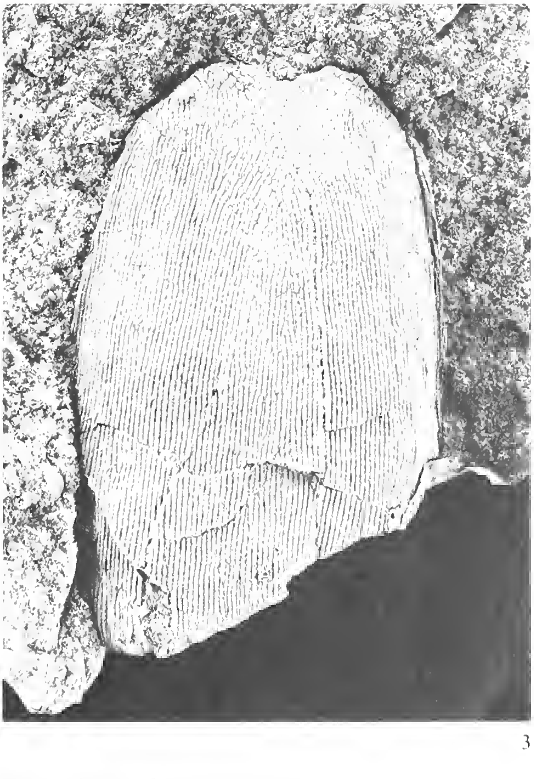

3

LOEFFLER and JONES, Ostracoderms from Canada

Remarks. Division of the dorsal shield into distinct epitega, the presence of transverse ridges on the rostral epitegum, the short, irregular ridges of the postrostral field, and the absence of a median rostral process suggest that these specimens belong to the genus *Archegonaspis* Jaekel. Comparison of size and proportions with those of established species of *Archegonaspis* (see Novitskaya 1970) shows that the specimens from Port Leopold are generally rather smaller, but of similar proportions. Dimensions are closest to those of *A. schmidti* (Geinitz), the width ratio and orbital width and length ratios of the holotype falling within the range of values calculated for the specimens from Port Leopold; the pineal length ratio of the holotype of *A. schmidti* is larger (0·31) and the postbranchial length ratio is not known.

Since the holotype is the only specimen of *A. schmidti*, and since it is not readily available for comparison, it is considered more valid to refer the Canadian specimens to *Archegonaspis* cf. *A. schmidti* (Geinitz) than to establish a new species for their reception.

Dorsal ornamentation comprises uniformly high, round-crested dentine ridges with a density of approximately four per mm. Their arrangement is typically transverse on the rostral epitegum, showing a gradation from continuous ridges anteriorly to short ridges and tubercles adjacent to the boundary with the postrostral field. On the postrostral field, ornamentation is mainly of short ridges with a fanned or irregular arrangement, but this is replaced anteriorly by small tubercles (text-fig. 3); dentine ridges on the rest of the central epitegum are long and longitudinal, although short ridges are commonly present toward the posterior margin. The single, median, scale-like area of short ridges, which is present on the posterior margin of the dorsal shield (Pl. 2, fig. 1), may represent a ridge scale which has been incorporated into the shield.

The three ventral shields ascribed to *Archegonaspis* cf. *A. schmidti* (Geinitz) are relatively slender, with a conspicuous median notch in the anterior margin (Pl. 1, fig. 3). The lateral margins are convex and the posterior margin slightly drawn out. Dentine ridges, which have a density of four per mm, are long and longitudinal over much of the ventral shield, but short and fanned anteriorly. Both the dorsal and the ventral shields are vaulted, the ventral more than the dorsal.

The lateral line system of *Archegonaspis* is known only from the holotype of *A. bimaris* Novitskaya, where the pattern of canals was deduced from the distribution of sensory pores (Novitskaya 1970). Although sensory pores are not conspicuous in the specimens from Port Leopold, the canals can be made visible through the somewhat transparent shields by immersion in glycerol. Viewed in this way the lateral line system of the dorsal shield is seen to consist of short segments of canal (text-fig. 4*a*, *b*) arranged in a simple network which includes medial dorsal canals, supraorbital canals,

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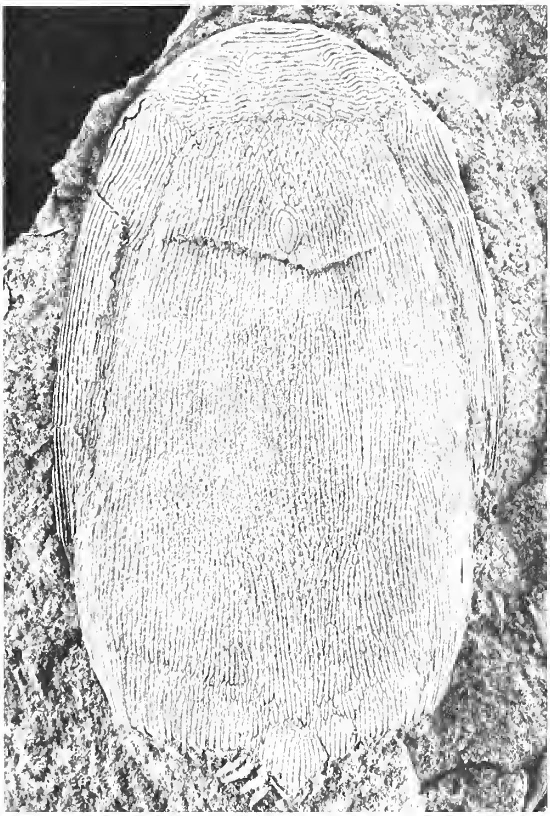
EXPLANATION OF PLATE 2

Fig. 1. *Archegonaspis* cf. *A. schmidti*. Latex cast of external mould of dorsal shield, NMC 21580. Magnification ×3.

Fig. 2. *Homalaspidella* cf. *H. borealis*. Incomplete dorsal shield. NMC 21596. Magnification ×3.

Fig. 3. Cyathaspididae indet. Dorsal shield. NMC 21588. Magnification ×3.

Fig. 4. Heterostraci indet. Indeterminate shield fragment. NMC 21571. Magnification ×2.



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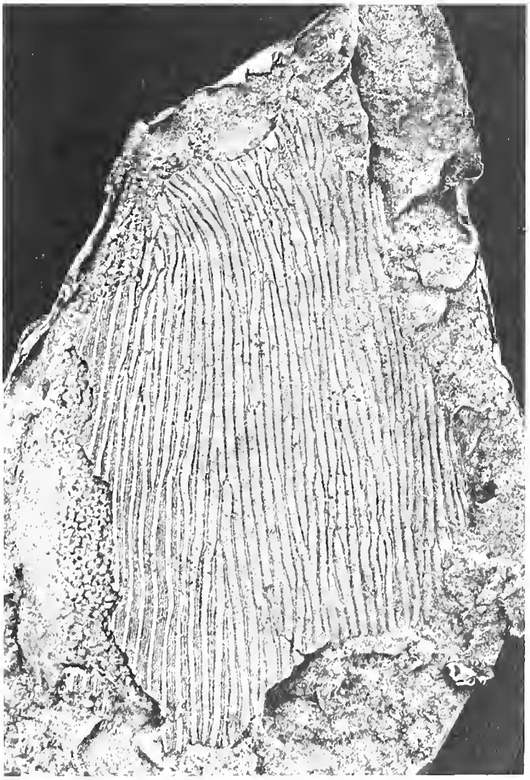

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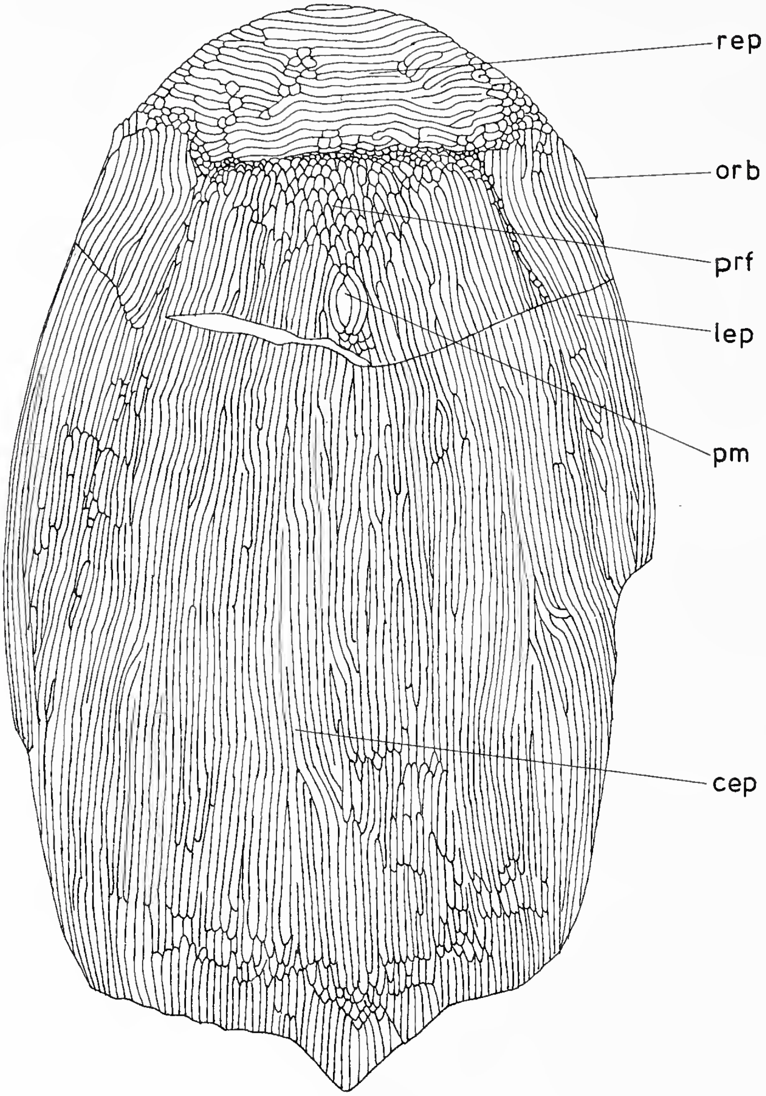
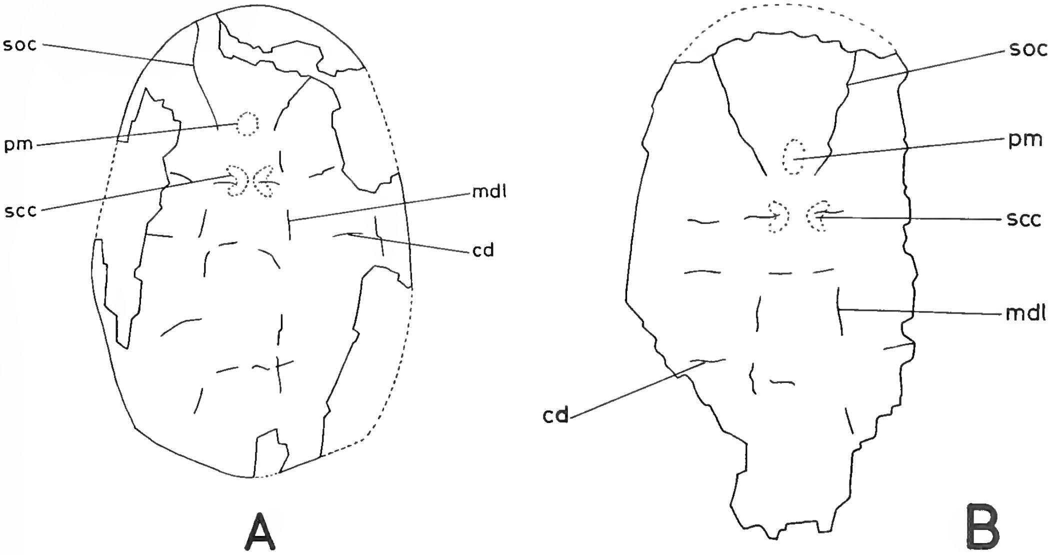
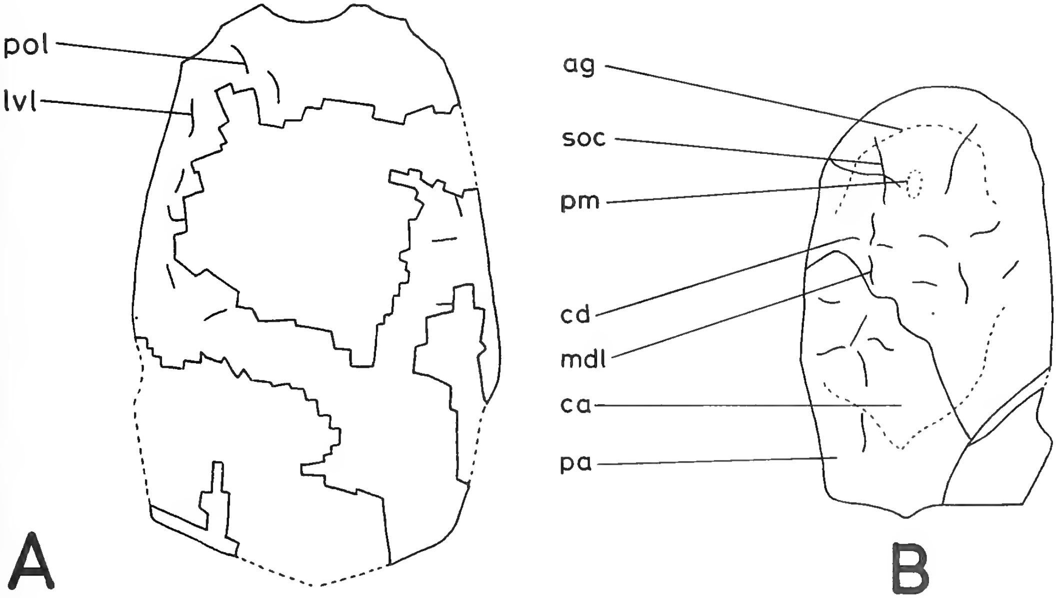
LOEFFLER and JONES, Ostracoderms from Canada and transverse commissures. The lateral line canals of the ventral shield are also divided into segments (text-fig. 5*a*). Segmented lateral line canals, which are also known in *Tolypelepis* and *Americaspis*, were regarded by Denison (1964) as the primitive condition in the Heterostraci.



TEXT-FIG. 3. *Archegonaspis* cf. *A. schmidti*, dorsal shield, NMC 21580. *cep*, central epitegum; *lep*, lateral epitegum; *orb*, orbital notch; *pm*, pineal macula; *prf*, postrostral field; *rep*, rostral epitegum. Magnification approximately ×4.



TEXT-FIG. 4. Dorsal lateral line system in *Archegonaspis* cf. *A. schmidti*. A, NMC 21581. Magnification approximately × 2. B, NMC 21590. Magnification approximately × 2·5. *cd*, dorsal transverse commissure; *mdl*, medial dorsal canal; *pm*, pineal macula; *scc*, semicircular canal; *soc*, supraorbital canal.



TEXT-FIG. 5. Lateral line systems. A, *Archegonaspis* cf. *A. schmidti*, ventral shield, NMC 21598. Magnification approximately × 3. B, Cyathaspididae indet., dorsal shield, NMC 21588. Magnification approximately × 2·5. *ag*, anterior groove; *ca*, central area; *cd*, dorsal transverse commissure; *lvl*, lateral ventral canal; *mdl*, medial dorsal canal; *pa*, peripheral area; *pm*, pineal macula; *pol*, postoral canal; *soc*, supraorbital canal.

Subfamily PORASPIDINAE Denison, 1964

Genus HOMALASPIDELLA Strand, 1934

Homalaspidella cf. *H. borealis* Denison, 1963

Plate 2, fig. 2

Material. An incomplete dorsal shield (NMC 21596).

Occurrence. Approximately 220 m above the base of the Leopold Formation, on the east side of the bay at Port Leopold, Somerset Island, North-west Territories, Canada (text-fig. 1).

Dimensions.

Median length	26·0 mm	Postbranchial length	6·6 mm
Maximum width	—	Orbital length ratio	0·15
Orbital width	—	Pineal length ratio	0·26
Orbital length	3·8 mm	Postbranchial length ratio	0·26
Pineal length	6·7 mm		

Remarks. Reference of this specimen to *Homalaspidella* Strand is suggested by the rather narrow proportions of the shield, the lack of epitega, the shallowness of the orbital notches, and the absence of a median rostral process. The size of the shield, together with the size and pattern of the dentine ridges, implies a closer affinity with *H. borealis* Denison than with *H. nitida* (Kiaer).

Although there are some differences between the specimen from Port Leopold and *H. borealis* (Denison 1963), it is regarded as inappropriate to erect a new species for the reception of a single incomplete specimen. The most noticeable differences are in the smaller size of the shield and the coarseness (4–5 per mm) and simplicity of the dentine ridges of the specimen from Port Leopold. Although the orbital notches are rather more posteriorly placed than in *H. borealis* (orbital length ratio = 0·10–0·12), the position of the pineal region is similar.

The pattern of ornamentation of the specimen from Port Leopold is very simple; the uniformly high dentine ridges are long and longitudinal posteriorly but converge anteriorly to form a broad curve in front of the pineal macula (Pl. 2, fig. 2; text-fig. 6).

Of the lateral line system, only the supraorbital canal and several short segments of transverse commissure are distinguishable. The supraorbital canal is marked by a slight discordance of the dentine ridges (text-fig. 6), but lateral line pores are not readily visible.

CYATHASPIDIDAE indet.

Plate 2, fig. 3

Material. A dorsal shield (NMC 21588).

Occurrence. Approximately 220 m above the base of the Leopold Formation, on the east side of the bay at Port Leopold, Somerset Island, North-west Territories, Canada (text-fig. 1).

Dimensions.

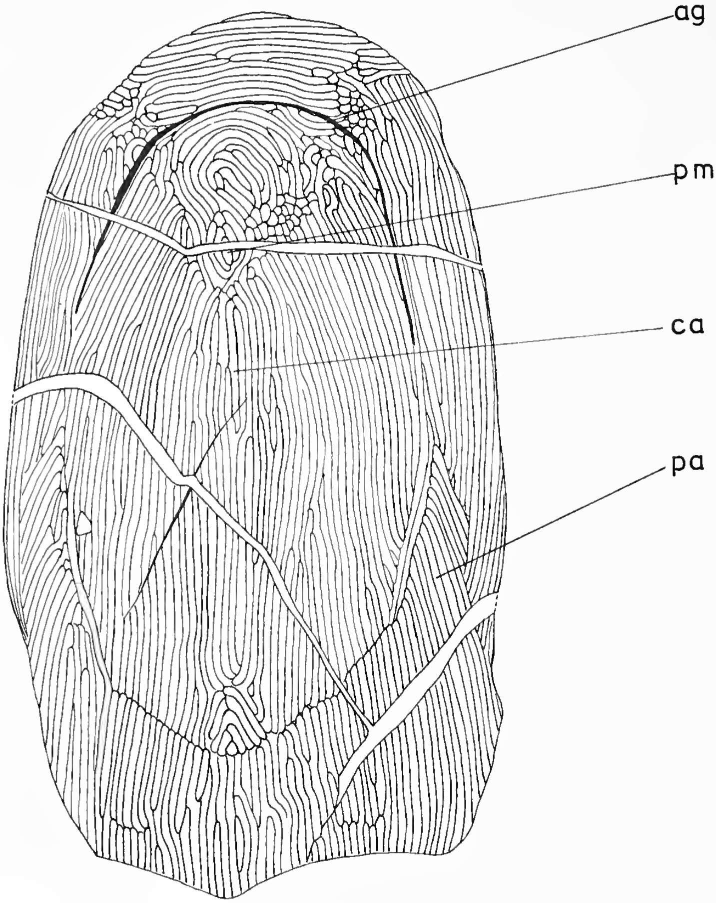
Median length	24·3 mm	Width ratio	0·58
Maximum width	14·0 mm	Orbital width ratio	0·45
Orbital width	11·0 mm	Orbital length ratio	0·10
Orbital length	2·5 mm	Pineal length ratio	0·26
Pineal length	6·2 mm	Postbranchial length ratio	0·24
Postbranchial length	5·8 mm		

TEXT-FIG. 6. *Homalaspidella* cf. *H. borealis*, dorsal shield, NMC 21596. *orb*, orbital notch; *pm*, pineal macula. Magnification approximately × 5.

Remarks. The small dorsal shield lacks a median rostral process, has moderately well-developed branchial lobes and, although the pineal macula occupies a posterior position, the orbital notches are unusually far forward. The posterior margin of the shield is transverse, except for a small median lobe.

The dorsal shield exhibits an unusual subdivision into an oval central area and a peripheral area (text-fig. 7). The anterior and anterolateral margins of the central area coincide with the normal position of the anterior boundary of the central epitegum in a typical cyathaspidinid, and are marked by a distinct groove and a discontinuity of ornamentation; the posterior and posterolateral margins of the central area are delimited by a discordance of ornamentation only. The peripheral area includes those parts of the shield that would normally form the rostral and lateral epitega but, in this specimen, there is no boundary between the rostral and lateral epitega, nor between the latter and the posterior part of the shield.

Ornamentation consists of uniformly high, flat-topped dentine ridges with a density of five ridges per mm. Within the oval central area the ridges are whorled in front of the pineal macula but largely longitudinal elsewhere. In the mid-line of the posterior margin, the ridges are arranged in an anteriorly pointing V. In the peripheral area the ridges are transverse on the rostrum, parallel to the lateral margins of the shield laterally, and longitudinal posteriorly (text-fig. 7).



TEXT-FIG. 7. Cyathaspididae indet., dorsal shield, NMC 21588. *ag*, anterior groove; *ca*, central area; *pa*, peripheral area; *pm*, pineal macula. Magnification approximately ×5.

Although lateral line pores are not distinguishable, canals are visible under glycerol. Both the medial dorsal canals and the transverse commissures are made up of short segments of canal (text-fig. 5*b*); no lateral dorsal canals are distinguishable.

Since this specimen is unique, it is difficult to determine whether or not it is an example of an abnormal individual and, if it is, whether it belongs to a new or an established taxon.

Similar anomalous subdivision of the shield has been recognized in *Americaspis* (Denison 1964), *Archegonaspis* (Novitskaya 1970), *Vernonaspis* (Broad and Lenz 1972), and *Pionaspis* (undescribed material from Arctic Canada). Although Denison (1964) considered the superficial subdivision of the shield of his specimen to be the result of injury prior to mineralization, both Novitskaya (1970) and Broad and Lenz (1972) established new species for their material which they considered to differ in ontogenetic development from closely related forms. Studies on cyathaspidids from the Delorme Formation of Western Canada (Loeffler 1974) indicate that the superficial layer of the shield underwent incremental growth which, if interrupted by disease or adverse conditions, could have resulted in the formation of anomalous areas. The variation in relative size of these anomalous areas in the specimens ascribed to *V. epitegosa* (Broad and Lenz 1972) supports this interpretation.

Unfortunately, since the border between the central and peripheral subdivisions obscures the region where epitegal subdivisions would be apparent, it is not possible to refer this specimen to a smaller taxonomic unit than Cyathaspididae indet.

HETEROSTRACI indet.

Plate 2, fig. 4

Material. Four shield fragments (NMC 21571–21573, 21594).

Occurrence. Approximately 220 m above the base of the Leopold Formation, on the east side of the bay at Port Leopold, Somerset Island, North-west Territories, Canada (text-fig. 1).

Remarks. Four shield fragments bearing similar ornamentation of coarse elevated ridges and finer interstitial ridges are referred to the Heterostraci, but cannot be ascribed with certainty to a smaller taxonomic unit.

The largest of the specimens, NMC 21571 (Pl. 2, fig. 4), appears to be part of a large median plate. Near its lateral margin, ornamentation is of long coarse ridges (0·2 mm wide) separated by interspaces (0·4 mm wide) occupied by up to five narrow ridges. Toward the centre of the plate there is a gradual change in ornamentation; the coarse ridges become broader (up to 0·4 mm), flatter, and more closely spaced, while the interstitial ridges become progressively fewer in number and are completely absent from the central region of the plate. The dentine ridges have an over-all longitudinal arrangement, but fan out anteriorly.

The three remaining plate fragments bear similar ornamentation to that of the lateral margins of the large plate fragment (NMC 21571). In these specimens, however, the elevated ridges are no wider than 0·2 mm and the interspaces, which are from 0·4 to 0·8 mm wide, contain 5–12 interstitial ridges. Although most of the coarse ridges are long, all of the fragments have at least some short ridges, around which the interstitial ridges are curved. Both the coarse and the fine ridges are minutely serrated along their lateral margins.

From the similarity of ornamentation of these specimens it is probable that the single median plate is a ventral shield and that the smaller fragments are parts of the dorsal armour of the same species; the coarse medial ornamentation of the ventral shield may be an adaptation to continued abrasion.

Similarity in ornamentation to the cyathaspidid genus *Cyathaspis* Lankester is probably not indicative of a close relationship; *Cyathaspis* is much smaller and does not have coarse ventral ridges.

SIGNIFICANCE OF THE VERTEBRATE FAUNAS

The discovery of *Archegonaspis* in Pridolian or Gedinnian strata at Port Leopold is the first reliable evidence for extension of the range of the genus beyond the lower and middle Ludlovian. Although Denison (1964) recorded an occurrence of *Archegonaspis* sp. in the ?early Devonian of Wales, Novitskaya (1970) questioned the identification of the specimen, which was originally listed as a Ludlovian occurrence (White 1958, p. 218). *A. schmidti* is known only from an erratic of the Graptolithengestein, which is of early Ludlovian age (Denison 1964).

This is not the first record of *Archegonaspis* from Canada; Thorsteinsson (1967) has reported the genus from the early Ludlovian and possibly the late Wenlockian intervals of the Cape Phillips Formation of Cornwallis Island, but the material has not been figured or described.

Two species of *Homalaspidella* are known; *H. nitida* occurs in the early Devonian of Spitsbergen (Kiaer 1932) and *H. borealis* in the upper Silurian of south-eastern Yukon (Denison 1964). At the type locality of the latter species, the ostracoderm horizon is overlain by strata containing the graptolite, *Monograptus dubius* (Hovedebo *et al.*, in Denison 1963), which is considered by Broad and Lenz (1972) to range from Wenlockian to Pridolian; that the ostracoderm horizon is of upper Silurian age is suggested by the presence of *Conchidium*? in the same beds (Hovedebo *et al.*, in Denison 1963).

Homalaspidella, or forms closely resembling it, have been reported from the late Wenlockian and early Ludlovian intervals of the Cape Phillips Formation on Cornwallis Island (Thorsteinsson 1967).

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CARBONIFEROUS CHONETACEAN AND PRODUCTACEAN BRACHIOPODS FROM EASTERN AUSTRALIA

by JOHN ROBERTS

ABSTRACT. Chonetacean and productacean brachiopods are amongst the most useful groups in defining the nine Carboniferous brachiopod zones of Eastern Australia. The current revision of the zones has led to the recognition of many new taxa and the clarification of a number of previously described species. Three new chonetaceans and fourteen new productaceans, nearly half the known productacean fauna, are described. Chonetaceans include *Trichochonetes perpendicularis* gen. et sp. nov., *Leiochonetes salisburyensis* gen. et sp. nov., and *Megachonetes alatus* sp. nov.; and productaceans include *Pharcidodiscus boulderensis* gen. et sp. nov., *Spinorugifera chichesterensis* gen. et sp. nov., and the new species *Productina striata*, *P. macdonaldi*, *P. morrisi*, *Krotovia procidua*, *Stegacanthia leviatha*, *Rugauris*? *brookeri*, *Eomarginifera megalotis*, *Inflatia engeli*, *Scoloconcha geniculata*, *Marginicinctus reticulatus*, *Antiquatonia spinulicosta*, and *Reticulatia cinctifera*. The morphological relationships between *Retichonetes kennedyensis*, *Rugosochonetes magnus*, *R. careyi*, and *R. gloucesterensis* are clarified, and *Spinocarinifera kennedyensis* and *Marginatia patersonensis* are revised. The affinities of the species provide new evidence for the ages of some zones: the *Tulcumbella tennuistriata* Zone is confirmed as early Tournaisian; the *Delepinea aspinosa* Zone is, mainly from ammonoid evidence, late Viséan; and the *Levipustula levis* Zone is shown to be Namurian to Westphalian in age.

THE sequence of eastern Australian Carboniferous brachiopod faunas, which ranges in age from Tournaisian to possibly Stephanian, has been divided into nine zones (text-fig. 3; Campbell and Roberts 1969; Jones *et al.* 1973; and Roberts 1975). Recent biostratigraphical studies by Roberts (1975) have linked the Early Carboniferous zones to reference sections within well-known stratigraphical sequences. This has clarified both the faunal composition of each zone and the relationships between zones. Work is currently in progress to revise the zonal sequence in the Upper Carboniferous. During the course of these revisions new taxa have been recognized, and it has also been necessary to revise the concept of a number of existing taxa.

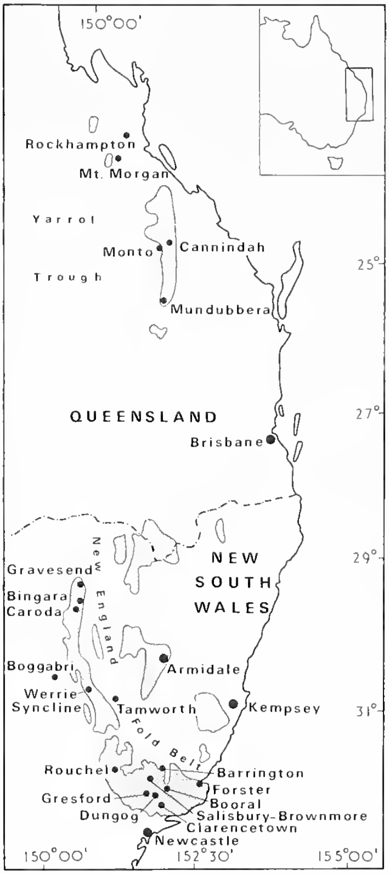
This paper provides a large part of the systematic basis for the revision of early Carboniferous zones, and includes the description or revision of a large proportion of the Early Carboniferous chonetacean fauna and half the known Carboniferous productacean fauna. The seven chonetaceans include two new genera, *Trichochonetes* and *Leiochonetes*, and the sixteen productaceans the new genera *Pharcidodiscus* and *Spinorugifera*.

Material from both New South Wales and Queensland is housed in three museums: the Australian Museum, Sydney; the Geological Survey of Queensland, Brisbane; and the Department of Geology, University of Queensland, St. Lucia. Details of localities, including locality number, grid reference, and the name of the topographic sheet, of material used in the systematic descriptions are listed at the end of the paper. Most of the locality numbers cited in the occurrences of species refer to collections held in the School of Applied Geology, University of New South Wales (for example, 88-3); other locality numbers refer to collections in the Geology Departments at the University of Newcastle (L402 U Newcastle), the University of New England (L35 UNE), the Australian National University, Canberra (L10024 ANU), and the University of Queensland (L1288 UQ), and to collections at the Geological Survey of Queensland. Precise locality data can be obtained from each of these institutions.

[Palaeontology, Vol. 19, Part 1, 1976, pp. 17–77, pls. 3–13.]

BIOSTRATIGRAPHY AND AGES OF THE ZONES

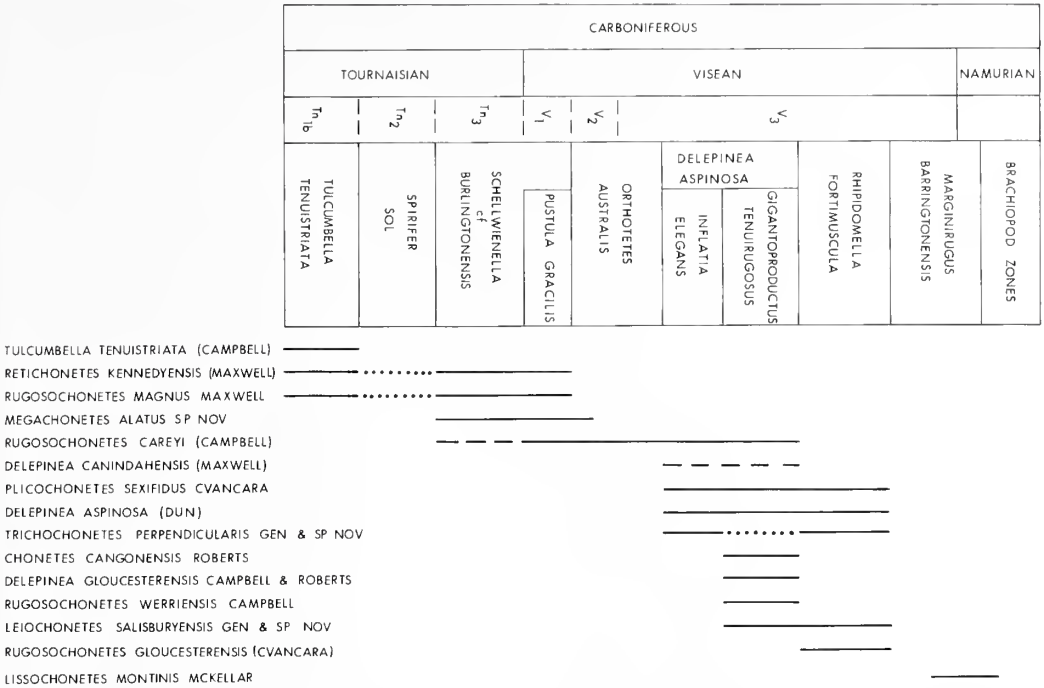
The stratigraphical ranges of all known Early Carboniferous chonetaceans and Carboniferous productaceans described from eastern Australia are shown in text-figs. 2 and 3 respectively. The ranges are plotted against the eastern Australian brachiopod zones, which in turn are correlated with the standard European stages. Correlations with Europe are based mainly on evidence from ammonoids and to a smaller extent on conodonts and brachiopods (Jones *et al.* 1973). Jenkins (1974), from work on conodonts, suggested alternative ages for some of the zones, particularly the *Orthotetes australis* and *Delepinea aspinosa* Zones. His proposals are examined, and rejected, in the following discussion on the ages of some of the zones. Brachiopod faunas do not appear to be as precise as ammonoids or conodonts in determining correlations between Australia and northern hemisphere continents, possibly because of the geographic separation of the two areas (Smith *et al.* 1973, fig. 11). A number of the productaceans described in this paper, however, are sufficiently close morphologically to overseas species to give 'indications' of age.



TEXT-FIG. 1. Locality map showing main areas of outcrop of Carboniferous rocks in eastern Australia.

The early Tournaisian age of the *Tulcumbella tenuistriata* Zone, previously derived indirectly (Jones *et al.* 1973), is confirmed by the close morphological relationship between *Spinocarinifera kennedyensis* (Maxwell) and *S. adunata* Roberts. *S. adunata* comes from rocks in the Bonaparte Gulf Basin, north-western Australia, dated by conodonts and brachiopods as early Tournaisian (Roberts 1971).

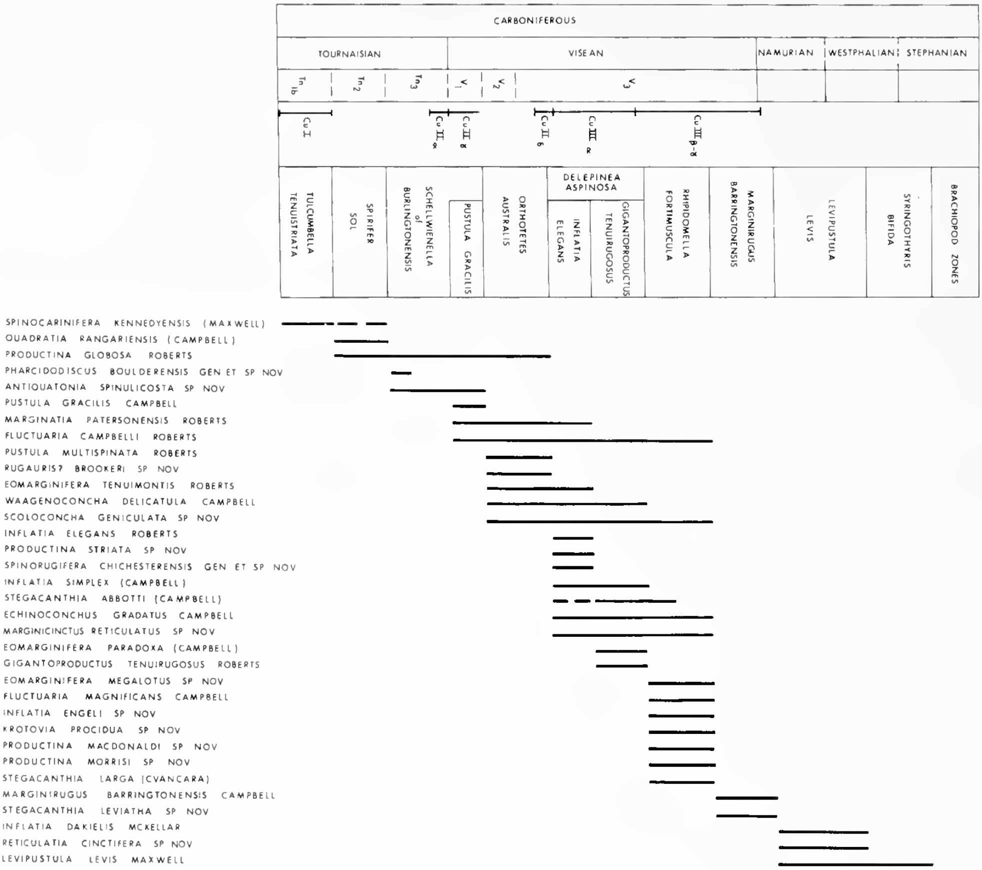
The *Delepinea aspinosa* Zone has long been considered to be late Viséan in age (Roberts 1965*a*; Campbell and McKellar 1969; Jones *et al.* 1973). Brachiopods from the zone do not give precise indications of age because species with which they are compared have long stratigraphical ranges, but ammonoids from immediately adjacent zones determine the maximum and minimum ages of the zone. The lower limit is provided by an ammonoid fauna from the *Orthotetes australis* Zone at Trevallyn (Roberts 1965*a*, *b*; Brown *et al.* 1965), and the upper limit by ammonoid faunas in the *Rhipidomella fortimuscula* Zone in both New South Wales and Queensland (Jones *et al.* 1973; Campbell and Brown, unpublished). Conodonts from the *Gigantoproductus tenuirugosus* Subzone of the *Delepinea aspinosa* Zone in the Flagstaff Sandstone at Brownmore led Jenkins (1974) to suggest younger ages for both the *Orthotetes australis* and *D. aspinosa* Zones. Jenkins's *Patrognathus*? cf. *capricornis* Zone at Brownmore was dated as early Viséan because of the associa-



TEXT-FIG. 2. Ranges of Early Carboniferous chonetaceans plotted against eastern Australian Brachiopod Zones. Specimens have not been collected from dotted portions of the stratigraphical ranges.

tion of *Gnathodus bulbosus* with *Taphrognathus varians*. The latter species ranges into the late Viséan *Apartognathus scalenus-Cavusgnathus* Zone in the Mississippi Valley (Collinson *et al.* 1971) and hence the age is based essentially on *G. bulbosus*, which was considered to be short-ranging and to be confined to the early Viséan. More recent sampling of limestones in eastern Australia by Jenkins (pers. comm.) indicates that *G. bulbosus* has a longer range than previously recognized. The species has so far been recorded from the *Pustula gracilis* Subzone in the Waverley Formation at Rouchel, New South Wales; from both the *O. australis* and *D. aspinosa* Zones in the Woolooma Formation at Rouchel; and fragments have been recovered from the *Marginirugus barringtonensis* Zone in the Killala Creek Formation, Queensland. In Australia, therefore, the range of *G. bulbosus* is so large that the species cannot indicate a precise correlation. It is perhaps noteworthy that Collinson *et al.* (1971, pp. 380–381) suggested that the *G. bulbosus* Zone in Missouri 'may be the result of a local biologic phenomenon of little biostratigraphic significance'.

Jenkins (1974) also questioned the identifications of *Prolecanites* sp. (Roberts 1965*b*) and the generic assignment of *Beyrichoceras trevallynense* (Brown *et al.* 1965) which provide the basis of the $CuII_\delta$ or $CuIII_\alpha$ age for the *O. australis* Zone and hence the maximum possible age for the *D. aspinosa* Zone. Additional specimens of *Prolecanites* sp., identical with those from Trevallyn, have been collected from the lowermost part of the *Inflatia elegans* Subzone of the *D. aspinosa* Zone at Rouchel, New South Wales (Roberts and Oversby 1974). These possess a ventral lobe intermediate between those of *Prolecanites* and an informal taxon termed Genus B by



TEXT-FIG. 3. Ranges of Carboniferous productaceans plotted against eastern Australian Brachiopod Zones.

Weyer (1972*b*, fig. 2). According to Weyer, *Prolecanites* ranges throughout the late Viséan and into the E_2 Zone of the Namurian, and Genus B first appears in the latest part of the late Viséan and also ranges into the E_2. The authors of *Beyrichoceras trevallynense* cannot see any valid reason for changing the generic assignment of the species. They still consider it closest to *B. submicronotum* Bisat, and, where it is associated with *Prolecanites* sp., to indicate an equivalence with subzones 3 and 4 of the *Beyrichoceras* Zone. This level is unaffected by the hiatus in the German ammonoid succession (Weyer 1972*a*), implied by Jenkins (1974) to be relevant to the age of the Trevallyn fauna, and the ammonoids still provide the soundest basis for the age of the *O. australis* Zone and hence the lower limit of the *D. aspinosa* Zone. The conflict with the early Viséan age indicated by *G. bulbosus* is resolved by its extended range in Australia compared with that in North America or Europe.

The affinities of the brachiopods in the *D. aspinosa* Zone are given by Roberts (1965*a*) and Jones *et al.* (1973). Two species described in this paper provide additional information: *Scoloconcha geniculata* sp. nov., which is relatively long-ranging (text-fig. 3), is morphologically close to *S. indianensis* (Hall) from the Salem Limestone, U.S.A., and is younger than early Viséan; and *Marginicinctus reticulatus* sp. nov. resembles *M. projectus* (Muir-Wood), which ranges from the C_2 to the D_2 in Britain, and is also younger than early Viséan in age.

The *Rhipidomella fortimuscula* Zone is characterized by many short-ranging brachiopods (Roberts 1975), a number of which indicate a late Viséan age. *Inflatia engeli* sp. nov. is morphologically close to *I. inflata* (McChesney) from the Chesterian Fayettville Formation, Oklahoma. *Krotovia procidua* sp. nov. is closest to *K. spinulosa* (J. Sowerby) which occurs mainly in the D_2 and D_3 of Great Britain (Thomas 1914), although Brunton (1966) records it from low in the D Zone in Ireland. Two species are morphologically related to forms in the Upper Kohlenkalk of Germany: *Eomarginifera megalotis* sp. nov. to *E. frechi* Paeckelmann; and *Productina morrisi* to specimens incorrectly referred by Paeckelmann (1931) to *P. pectinoides* (Phillips). Ammonoids from the *Rhipidomella fortimuscula* Zone indicate correlation with the $CuIII_\beta$ of Germany (Jones *et al.* 1973). Additional ammonoids of late Viséan aspect from the *R. fortimuscula* Zone in Queensland are being studied by K. S. W. Campbell and D. A. Brown at the Australian National University.

Jones *et al.* (1973) suggest that the *Marginirugus barringtonensis* Zone spans the interval $CuIII_\gamma$ to early Namurian. *Stegacanthia leviatha* sp. nov. is closest to *S. strigis* Roberts from the late Viséan to early Namurian *Anthracospirifer milliganensis* Zone in the Burvill Beds in the Bonaparte Gulf Basin, north-western Australia (Roberts 1971).

The *Levipustula levis* Zone was considered by most workers (Campbell 1961; McKellar 1965; Jones *et al.* 1973) to be Westphalian in age because of the close morphological relationship between *L. levis* Maxwell, *L. piscariae* (Waterlot), and *L. rimberti* (Waterlot); the latter species are from the Westphalian B and basal Westphalian C respectively of Europe (McKellar 1965). *L. levis* is also found in Argentina where it is associated with ammonoids and trilobites. The ammonoids indicate a Pennsylvanian (Desmoinesian) age, but they may not have been *in situ* (Amos *et al.* 1960). *L. levis*, however, has a long stratigraphic range, and in New South Wales first appears in the Namurian. At Kempsey *L. levis* is found on two horizons (Lindsay 1969), approximately 2000 m stratigraphically apart, in the Kullatine and Taits Creek Formations. These horizons bracket beds containing *Cravenoceras kullatinensis* Campbell, indicative of a Namurian, probably E_1, age (Campbell 1962). Lindsay's (1969) initial report of *L. levis* from below *C. kullatinensis* has been confirmed by recent field work. The Namurian age for the base of the zone is supported by field evidence from Yagon Gibber near Forster, New South Wales, where in a conformable sequence exposed along the coastline the *L. levis* Zone first appears only about 50 m above the *M. barringtonensis* Zone. The large productacean, *Reticulatia cinctifera* sp. nov., which occurs with *L. levis* in the Branch Creek Formation, Queensland (Maxwell 1964; McKellar 1967), and at Yagon Gibber in New South Wales, supports a Westphalian age for the *levis* Zone. *R. cinctifera* is closely related morphologically to specimens identified by Demanet (1943) as *Productus* (*Dictyoclostus*) aff. *americanus*, which are from the same horizon as *L. rimberti* in the Westphalian C of Belgium; and to specimens identified as *Tolmatchoffia demaneti* by Böger and Fiebig (1963) from the Westphalian C of Germany. Because of the ammonoid evidence, the range of the *levis* Zone on the correlation chart of Jones *et al.* (1973) should be lowered to almost meet the *M. barringtonensis* Zone. Apart from brachiopod evidence there is no information available to reliably date the top of the *levis* Zone, and in text-fig. 3 the zone is shown to extend into the Westphalian. *L. levis* has also been collected by the author from the *Syringothyris bifida* Zone near Booral, New South Wales, and that unit is shown to be also partly Westphalian; there is no evidence of age for the top of the *S. bifida* Zone.

SYSTEMATIC DESCRIPTIONS

Superfamily CHONETACEA Bronn, 1862
Family CHONETIDAE Bronn, 1862
Subfamily ?STROPHOCHONETINAE Muir-Wood, 1962
Genus TRICHOCHONETES nov.

Type species. Trichochonetes perpendicularis gen. et sp. nov. from the Flagstaff Sandstone near Brownmore, New South Wales.

Diagnosis. Shell gently concavo-convex, and ornamented by fine capillae; pedicle valve with spines at 90° to the hinge, and a short median septum; brachial valve having twin divergent septa, and a cardinal process with a posterior face bearing three concave lobes; lateral septa and brachial markings absent.

Remarks. The assignment of *Trichochonetes* to the subfamily Strophochonetinae is based on the presence of twin septa in the brachial valve and long spines projecting at 90° to the hinge of the pedicle valve. However, because strophochonetoid genera have not previously been recorded outside the time range of ?Late Ordovician, Early Silurian–Early Devonian (Muir-Wood 1962) the ancestry of *Trichochonetes* is doubtful, and the genus is therefore tentatively placed in the Strophochonetinae. The only other group of chonetaceans in which some genera possess twin dorsal septa is the Anopliidae Muir-Wood, 1962. *Trichochonetes* cannot be assigned to the Anopliidae because of its large size, transverse outline, and low concavo-convex profile.

The name of the genus is derived from the Greek *trichos*, hair, and refers to the fine hair-like capillae ornamenting the shell.

Trichochonetes perpendicularis gen. et sp. nov.

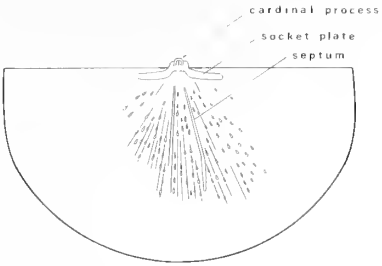
Plate 3, figs. 10–21

1975 Chonetoid gen. et sp. A, Roberts, Table 1.

Diagnosis. Shell wider than long, semi-elliptical in outline, and bearing 24–28 capillae per 3 mm at 5 mm from the umbo; pedicle valve with up to two hinge spines on either side of the umbo; ventral umbo low; internal surface ribbed in the pedicle valve, and finely spinose in the brachial valve.

Description. External. Shell moderately concavo-convex, and widest just behind the mid-length; hinge line usually slightly less than the greatest width; capillae occasionally irregular over the mid-part of the shell, and increasing by bifurcation or intercalation; micro-ornament not observed; specimens ranging in size up to 15 mm wide and 0·5 mm long. Pedicle valve highest around the middle of the valve; umbo low, projecting a short distance behind the hinge, and barely rising above the level of the lateral slopes; lateral slopes usually evenly convex, but in some cases becoming flat at the postero-lateral extremities; hinge line straight, and bearing up to two long spines on either side of the umbo; delthyrium wide, triangular, and apparently open; cardinal area low and apsacline. Brachial valve deepest around the mid-point; lateral slopes becoming flat on the postero-lateral extremities.

Internal. Pedicle valve. Median septum extending one-quarter the length of the valve; ventral muscle scars poorly differentiated, but forming a smooth impressed muscle field; adductor muscle scars possibly subovate and bordering the median septum; diductor muscle scars triangular, and in some specimens bounded postero-laterally by ridges; teeth not observed; inner surface of valve finely ribbed except for a patch of small endospines immediately in front of the median septum. Brachial valve (text-fig. 4). Socket ridges mainly parallel with the hinge, but medially curving abruptly posteriorly and supporting the cardinal process; cardinal process with three concave lobes on the posterior face; the floor of the valve immediately in front of the cardinal process is depressed, but does not actually form an alveolus; dorsal septa comprise two thin delicate divergent blades which extend from in front of the depression to about two-thirds the length of the valve; lateral septa and brachial markings not observed; internal surface of the valve, particularly the medial portion, bearing radial rows of fine endospines.



TEXT-FIG. 4. Dorsal interior of *Trichochonetes perpendicularis* gen. et sp. nov. showing twin septa. Drawn from the holotype F56943 AM. Approximately × 3.

Remarks. Other than the type species, only one species is tentatively referred to *Trichochonetes.* The finely ribbed *Rugosochonetes delicatus* Brunton (1968, pp. 62–66, pl. 9, figs. 3–15) from the D Zone at Bunnahone Lough, Northern Ireland, resembles *T. perpendicularis* in having a comparable over-all shape and profile, a short, slender, ventral median septum, and in lacking a dorsal median septum; because of these similarities, *delicatus* is tentatively referred to *Trichochonetes. T.*? *delicatus* differs from *T. perpendicularis* in having an indistinct capillate ornament at the umbo, up to four pairs of spines on either side of the umbo, divergent socket ridges, and lateral septa in the brachial valve.

The specific name *perpendicularis*, Latin for upright or at right angles, refers to the spines at right angles to the ventral hinge.

T. perpendicularis ranges from the *Inflatia elegans* Subzone of the *Delepinea aspinosa* Zone to the *Rhipidomella fortimuscula* Zone, but has not been recorded from the *Gigantoproductus tenuirugosus* Subzone of the former zone; it is late Viséan in age.

Occurrence. Locality 86-2 (the type locality) in a quarry alongside the Dungog–Salisbury road; locality 100-5, Native Dog Creek; locality 100-13, Byron's Quarry on the Dungog–Chichester road; locality 106-15, Chichester River; all in the Flagstaff Sandstone. Locality 88-3, Quartpot Creek, in an unnamed formation. Localities L404, Nooroo, and L437, North Coast Railway Line east of Dungog, in the Wootton Beds; and L402, north of Clarencetown in unidentified sediments; all University of Newcastle localities.

Material. F56938–F56945, Australian Museum. Holotype F56943; paratypes F56938, F56939, F56941, and F56942.

Subfamily RETICHONETINAE Muir-Wood, 1962
Genus RETICHONETES Muir-Wood, 1962

Type species. Chonetes armatus Bouchard-Chantereaux *in* de Verneuil 1845.

Remarks. Maxwell (1954) previously referred this material to *Rugosochonetes.* The small semicircular and concavo-convex nature of the shell, and prominent concentric growth lines crossing costellae are typical of Retichonetes. Internally, this material has a ventral median septum which extends to the apex of the umbo, whereas in the type species the septum is reported to be 'not continuous to the umbo' (Muir-Wood 1962, p. 63); fig. 13B of Muir-Wood (1962), however, suggests that the septum in *R. amatus* extends well into the umbonal region. The brachial valve of this material is known only from poorly preserved material, but it is clear that there is a median septum. The presence of a dorsal median septum indicates a lack of affinity with *Caenanoplia* Carter (1968), another small Early Carboniferous genus. *Caenanoplia* is characterized by weaker ribs, a lamellose ornament, larger ears, and a typically anopliinid dorsal interior.

Retichonetes kennedyensis (Maxwell)

Plate 4, figs. 12–20

1892 *Chonetes cracowensis* Etheridge Snr. *in* Jack and Etheridge, pl. 13, fig. 9.
1954 *Rugosochonetes kennedyensis* Maxwell, pp. 20–21, pl. 2, figs. 8–12.
non 1964*b* *Rugosochonetes kennedyensis* Maxwell; Roberts, pp. 181–182, pl. 2, figs. 1–7.
non 1971 *Rugosochonetes kennedyensis* Maxwell; Roberts, pp. 67–69, pl. 8, figs. 11–22.
1974 *Rugosochonetes kennedyensis* Maxwell; Roberts and Oversby, Table 1.
1975 *Rugosochonetes kennedyensis* Maxwell; Roberts, Table 1.

Diagnosis. Shell small, strongly concavo-convex, semicircular in outline, and wide at the hinge; costellae with a density of 18 per 5 mm at 5 mm from the umbo; pedicle valve having up to eight hinge spines, a small umbo, steep lateral and anterior margins, and small auriculate postero-lateral extremities; ventral median septum short and separating triangular adductor muscle scars; brachial valve with a deep alveolus, a median septum extending to the mid-length of the valve, and short divergent lateral septa.

Description. External. Shell globular and widest at the hinge; costellae strongly developed, increasing by both bifurcation and intercalation, and crossed by closely spaced concentric striae having a density of about 10 per 1 mm; postero-lateral margins lacking costellae and ornamented only by concentric growth lines; specimens ranging in size up to 9 mm wide and 6·5 mm long. Pedicle valve strongly convex, particularly at the umbo, and highest at about one-third the length of the valve; umbo small, barely projecting beyond the hinge line, and poorly differentiated from the body of the valve because of inflated umbonal shoulders; postero-lateral margins gently convex to flat, auriculate, and forming the widest part of the valve; ventral interarea short, apsacline to orthocline, and having a small delthyrium filled by a convex

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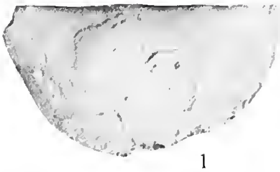
EXPLANATION OF PLATE 3

Figs. 1–9. *Leiochonetes salisburyensis* gen. et sp. nov. 1, 2, a mould and rubber cast of the dorsal exterior. F56933a, ×4. 3, rubber cast of the brachial valve interior, a counterpart of the specimen figured in 1 and 2. F56933b, holotype, ×4. 4, rubber cast of the exterior of the pedicle valve. F56934, paratype, ×4. 5, 6, rubber cast and a mould of the ventral interior. F56935, paratype, ×4. 7, 8, rubber cast and a mould of the ventral interior. F56936, paratype, ×4. Figs. 1–8 from locality 85-10. 9, rubber cast of a partly decorticated brachial valve exterior. F56937, ×4, from locality 90-2.

Figs. 10–21. *Trichochonetes perpendicularis* gen. et sp. nov. 10, 11, rubber casts of two pedicle valve exteriors. F56938 and F56939 respectively, paratypes, ×3. 12, 13, rubber casts of the ventral and dorsal exterior of F56940a and F56940b respectively, ×3. 14, rubber cast of the ventral interior of F56941, paratype, ×3. 15, 16, external mould and rubber cast of a brachial valve exterior. F56942, paratype, ×3. 17, 18, mould and rubber cast of the interior of F56943, holotype, ×3. Figs. 10–18 from locality 86-2. 19, 20, rubber cast and internal mould of the pedicle valve. F56944, ×2 and ×3 respectively. 21, internal mould of a pedicle valve. F56945, ×3. Figs. 19–21 from locality L437 U Newcastle.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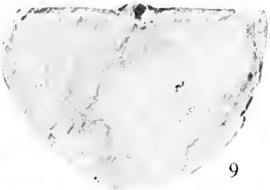
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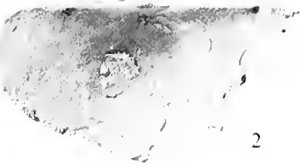
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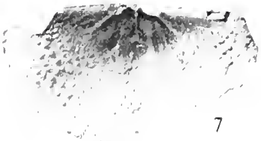
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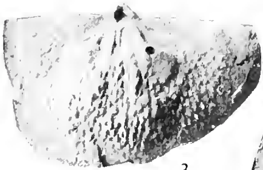
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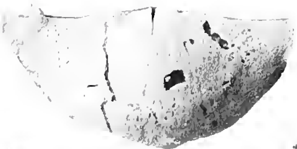
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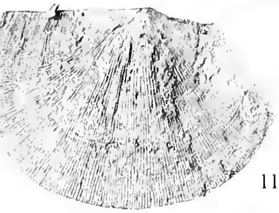
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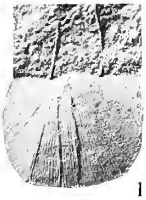
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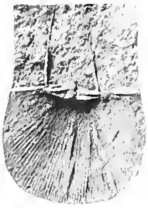
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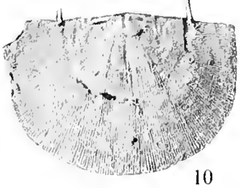
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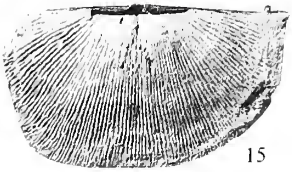
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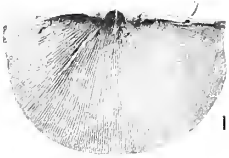
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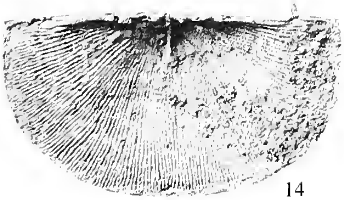
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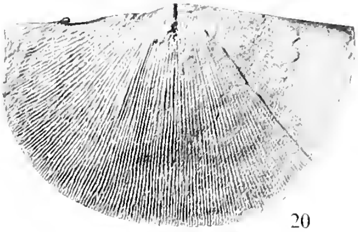
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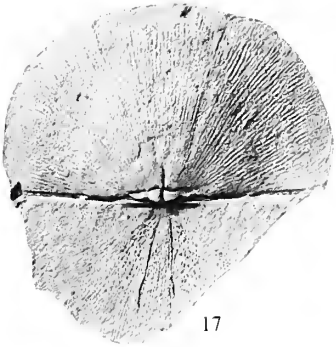
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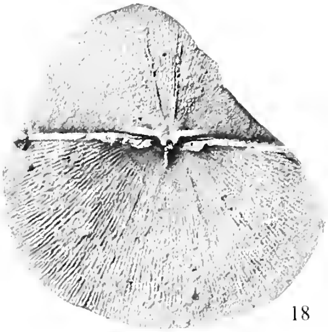
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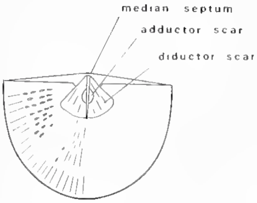
ROBERTS, Australian chonetaceans

plug-like deltidial plate; up to eight hinge spines projecting at 90° to the hinge. Brachial valve strongly concave, and deepest at about one-third the length of the valve; lateral slopes steep, and passing on to flat or gently concave postero-lateral extremities; interarea shorter than on the pedicle valve.

Internal. Pedicle valve (text-fig. 5). Median septum extending between one-quarter and one-sixth the length of the valve; adductor muscle scars moderately large, impressed, pointed posteriorly, and broader anteriorly; diductor muscle scars faint, and flabellate in outline; teeth not observed; internal surface ribbed and bearing radially arranged endospines.

Brachial valve. Median septum extending from in front of a large alveolus to the mid-point of the valve; lateral septa short, diverging from the median septum at about 30°, and separating poorly defined adductor muscle scars; cardinal process not observed; socket ridges elongate, subparallel with the hinge, and bordering narrow elongate sockets; internal surface of valve bearing radially arranged endospines; brachial markings not observed.



TEXT-FIG. 5. Ventral interior of *Retichonetes kennedyensis* (Maxwell) drawn from a topotype specimen from locality 121-2, Pond Formation, Queensland. The median septum extends to the apex of the valve. Approximately ×2·5.

Remarks. Retichonetes kennedyensis (Maxwell) was first compared with *R. amatus* by Maxwell (1954). Some of the similarities and differences between the two species have been discussed in the remarks on the genus. In addition, *R. amatus* is characterized by a more subcircular outline, and the possession of dorsal accessory septa and divergent hinge spines.

Several small chonetaceans from the United States are externally close to *R. kennedyensis.* Specimens identified as *Chonetes logani* Norwood and Pratten by Weller (1914, pp. 84–86, pl. 8, figs. 43–46) from the Kinderhook of Iowa are close in size, shape, and, according to the description, in the density of costellae. *C. logani* is assigned by Carter (1968) to *Caenanoplia.* Specimens referred to *Chonetes glenparkensis* Weller (Weller 1914, pl. 8, figs. 47–49) from the Chouteau Limestone of Missouri, and believed by Carter (1967, p. 280) to be conspecific with *C. logani,* differ from *kennedyensis* in the auriculate nature of their postero-lateral extremities.

R. kennedyensis (Maxwell) ranges from the *Tulcumbella tenuistriata* Zone to the *Schellwienella* cf. *burlingtonensis* Zone, and is Tournaisian to early Viséan in age.

Occurrence. Specimens figured in this paper are from the type locality, L1288 UQ in the Pond Formation, Mount Morgan, Queensland, and from locality L10024 ANU in the Namoi Formation at Rangari Station, Boggabri district, New South Wales. Specimens in collections at the University of New South Wales are from localities 15-3, 24-7, 8 and 15, 31-1, 38-7 and 39-13, and 16 in the Waverley Formation in the Rouchel district, New South Wales; localities 94-2 and 98-2 in the Ararat Formation at Gresford, New South Wales; localities L23 UNE, 112-1 and possibly 112-4 in the Namoi Formation in the Werrie Syncline, New South Wales; localities F3 and F12 of Yeates (unpublished B.Sc. thesis 1970) in the Namoi and Luton Formations respectively in the Gravesend district, New South Wales; locality L1312 UNE in the Luton Formation, Luton Station near Bingara, New South Wales; and at locality 121-2 in the Pond Formation, Mount Morgan, Queensland.

Material. F56954–F56958 Australian Museum, F15155 (the holotype), F15156 and F15165 University of Queensland.

Subfamily RUGOSOCHONETINAE Muir-Wood, 1962

Genus LEIOCHONETES nov.

Type species. Leiochonetes salisburyensis gen. et sp. nov. from the Flagstaff Sandstone near Brownmore, New South Wales.

Diagnosis. Shell small and moderately to strongly concavo-convex; external surface smooth except for growth lines; hinge spines few in number, and diverging from the hinge at between 90° and 60°; ventral median septum short and separating deeply impressed muscle scars; dorsal interior with a short ridge-like median septum, lateral septa, an alveolus, and well-defined brachial markings; cardinal process with two concave posterior lobes.

Remarks. Smooth chonetaceans are rare in Early Carboniferous rocks, and few of those so far described are closely comparable with *Leiochonetes*. The nearest Australian form, an indeterminate species from the Tournaisian Enga Sandstone in the Bonaparte Gulf Basin, Western Australia (Roberts 1971, pl. 10, figs. 1–10), has a smooth exterior, but is more gently arched and has two spines on either side of the umbo; its interior is unknown. *Tornquistia*? *transversalis* Carter (1967) from the Chappel Limestone of Texas may also belong to the genus.

The Pennsylvanian genus *Eolissochonetes* Hoare (1960) has an external ornament similar to that of *Leiochonetes*. Externally it differs from *Leiochonetes* in having a moderately to weakly developed ventral median sinus, and a larger number of hinge spines. Internally *Eolissochonetes* is characterized by the possession of a longer dorsal median septum, weaker brachial ridges, and a flatter dorsal visceral disc. According to Hoare (1960), *Eolissochonetes* was derived from *Mesolobus* Dunbar and Condra, 1932 and is transitional between that genus and *Lissochonetes* Dunbar and Condra, 1932. The evidence presented by Hoare makes it unlikely that *Eolissochonetes* is genetically related to *Leiochonetes*.

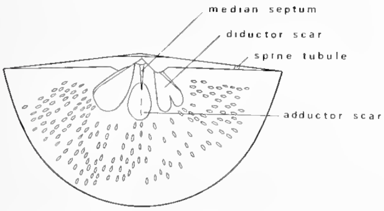
The generic name is derived from the Greek *leios*, smooth, referring to the smooth exterior.

Leiochonetes salisburyensis gen. et sp. nov.

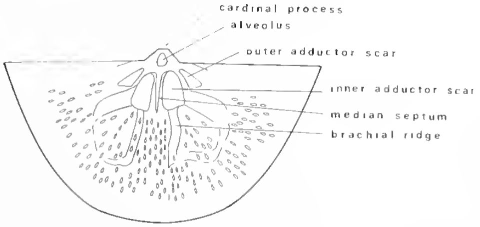
Plate 3, figs. 1–9

1975 Chonetoid gen. et sp. B, Roberts, Table 1.

Diagnosis. Shell transverse and trigonal in outline; a single hinge spine near the postero-lateral extremities projects at between 90° and 60° to the hinge; ventral median septum extending one-fifth the length of the valve, and separating ovoid adductor and lachrymose diductor muscle scars; dorsal median septum extending



TEXT-FIG. 6. Ventral interior of *Leiochonetes salisburyensis* gen. et sp. nov. drawn from a paratype F56936 AM. The anterior margin of the right diductor scar is apparently deformed. Approximately × 4.



TEXT-FIG. 7. Dorsal interior of *Leiochonetes salisburyensis* gen. et sp. nov. drawn from the holotype F56933b AM. Approximately × 4.

one-third the length of the valve; socket ridges almost obsolete; internal surface of the shell bearing fine endospines.

Description. External. Shell moderately to strongly concavo-convex and with alate postero-lateral extremities; greatest width at or immediately in front of the hinge; external surface essentially smooth, lacking radial ornament, but having fine concentric growth lines; faint radial markings on some valves apparently originate within the shell rather than being on the exterior; specimens ranging in size up to 10·5 mm wide and 6 mm long. Pedicle valve highest and most strongly convex at the mid-point; umbo moderately high and projecting a short distance behind the hinge; lateral slopes steep nearest the umbo, but becoming flatter towards the postero-lateral margins. Brachial valve strongly concave, deepest at the mid-point, and then sloping upwards to flat postero-lateral margins.

Internal. Pedicle valve (text-fig. 6). Median septum high and blade-like at the apex, but becoming abruptly lower and ridge-like anteriorly; muscle field deeply impressed, particularly posteriorly; adductor muscle scars ovoid, diductor muscle scars having pointed posterior extremities which curve medially around the posterior of the adductor muscle scars, and expanding anterior portions which extend beyond the front of the adductor muscle scars; postero-lateral margins of the diductor muscle scars bordered by ridges extending laterally from the apex of the valve; teeth not observed; internal surface of the valve bearing small radially arranged endospines. Brachial valve (text-fig. 7). Cardinal process highest medially and with two concave lobes on the posterior face; alveolus deep and circular; median septum low, narrow and ridge-like posteriorly, and broader and higher anteriorly; lateral septa short, divergent and dividing the adductor muscle scars into two pairs; inner adductor scars narrow posteriorly, broader anteriorly, and situated on small platforms; outer adductor muscle scars less well defined and forming triangular depressions on the outer margins of the lateral septa; brachial ridges commencing on the anterior margins of the outer adductor muscle scars, enclosing brachial discs which are high posteriorly, and distally curving towards the front of the inner adductor muscle scars.

Remarks. Leiochonetes salisburyensis gen. et sp. nov. is comparable with two forms: an unnamed species from the Tournaisian Enga Sandstone in the Bonaparte Gulf Basin (p. 27), and *Tornquistia*? *transversalis* Carter (1967, pp. 274–276, pl. 14, figs. 15–20) from the Chappel Limestone of Texas. The relationship with the unnamed form is discussed in the remarks on the genus. *T.*? *transversalis* is distinguished from *L. salisburyensis* by the possession of a high ventral interarea, and a wide delthyrium closed apically by a pseudodeltidium. Although the brachial valve of *transversalis* is unknown, other morphological features, particularly those of the ventral interior, suggest that it should be assigned to *Leiochonetes* rather than *Tornquistia*. The species ranges from the *Gigantoproductus tenuirugosus* Subzone of the *Delepinea aspinosa* Zone into the *Rhipidomella fortimuscula* Zone, and is known only in New South Wales; it is late Viséan in age.

Occurrence. Locality 85-10 (the type locality), Quartpot Creek near Brownmore; locality 90-2, Big Creek, Salisbury; possibly at locality 100-3, Native Dog Creek, west of Bendolba; all in the Flagstaff Sandstone. Locality 114-1 in sediments mapped as Wootton Beds by Mayer (1972), 2 km north of Rawdon Vale.

Material. F56933–F56937, Australian Museum. Holotype F56933b; paratypes F56934, F56935, and F56936.

Genus RUGOSOCHONETES Sokolskaya, 1950

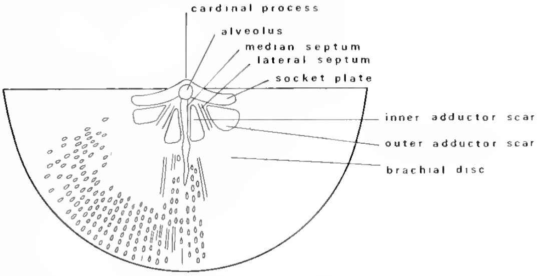
Type species. Orthis hardrensis Phillips, 1841.

Rugosochonetes magnus Maxwell emend.

Plate 4, figs. 21–29

1954 *Rugosochonetes kennedyensis* var. *magnus* Maxwell, pp. 44–45, pl. 5, figs. 9–10.
?1961 *Rugosochonetes kennedyensis* var. *magnus* Maxwell, pl. 19, fig. 1.

Diagnosis. Shell strongly concavo-convex, transverse, with slightly pointed postero-lateral extremities; costellae having a density of 19–20 per 5 mm at 5 mm from the umbo; pedicle valve with a prominent umbo, convex venter, steep lateral and anterior slopes, and one or two erect hinge spines on either side of the umbo; ventral adductor muscle scars ovoid; brachial valve with subparallel socket ridges located anteriorly from the hinge, a deep alveolus, a wide median septum extending to the mid-length of the valve, and robust lateral septa; brachial ridges high distally.



TEXT-FIG. 8. Dorsal interior of *Rugosochonetes magnus* Maxwell drawn from F15288 UQ, a topotype specimen figured by Maxwell (1954, pl. 5, fig. 13). Approximately ×3.

Description. External. Shell approximately 1·5 times wider than long, with the greatest width at or immediately in front of the hinge; costellae increasing by bifurcation and intercalation; micro-ornament of concentric growth lines; specimens range in size up to 12·5 mm wide and 7·5 mm long. Pedicle valve highest at the mid-point; umbo extending behind the hinge but not strongly incurved; postero-lateral extremities convex, slightly auriculate, and lacking radial ornament near the hinge; anterior margin steep and almost trail-like; one or two hinge spines on either side of the umbo emerging at between 70° and 90° to the hinge; ventral interarea low, apsacline laterally to orthocline medially. Brachial valve deepest around the middle or immediately in front of the mid-point of the valve; anterior margin steep and trail-like; postero-lateral margins small, flat, and with weak radial ornament.

Internal. Pedicle valve. Visceral disc deep; median septum extending to approximately the mid-point of the valve; muscle field moderately well impressed; adductor muscle scars giving rise anteriorly to vascular trunks; diductor muscle scars flabellate, narrow posteriorly, wider anteriorly, and deeply impressed along the postero-lateral margins; teeth are robust; internal surface bearing radially arranged rows of fine endospines; the spines are finest near the centre of the valve and become coarser towards the margin. Brachial valve (text-fig. 8). Alveolus very large and deep or infilled with callus; median septum strongest posteriorly, and extending from the front of the alveolus or platform to the middle part of the valve; lateral septa extending up to two-thirds the length of the median septum; inner adductor muscle scars narrow, triangular, and located on low platforms; outer adductor muscle scars lachrymose, pointed postero-laterally, rounded antero-laterally, and deeply impressed; posterior face of cardinal process with two long lobes, the lateral portions being obscured by chilidial plates; brachial markings originate from the anterior margins of the outer adductor muscle scars, and enclose round brachial discs; proximally the markings comprise a smooth shallow depression, but distally, where they have recurved posteriorly, form distinct ridges; endospines coarsest on the trail but also present on the lateral margins of the brachial discs.

Remarks. Rugosochonetes magnus Maxwell was previously recognized as a variety of *R. kennedyensis* (Maxwell, 1954); the latter species is now referred to *Retichonetes*, and *magnus* is interpreted as a species of *Rugosochonetes. R. magnus* and *Retichonetes kennedyensis* are both recorded from eastern Australia in the *Tulcumbella tenuistriata* and *Schellwienella* cf. *burlingtonensis* Zones. *R. kennedyensis* is readily distinguished by its smaller size, semicircular outline, coarse costellae which bear a well-defined concentric ornament, and by the possession of a pedicle valve which is especially convex over the venter, and which has up to eight hinge spines.

Larger rugosochonetoids, mainly from the *Orthotetes australis* and *Delepinea aspinosa* Zones, which were previously identified as *R. kennedyensis* by Roberts (1964*b*, 1965*b*) are now referred to *Rugosochonetes careyi* (Campbell). *R. magnus* is distinguished from *R. careyi* by its smaller size, more prominent ventral umbo, greater curvature of the valves, and the possession of pointed postero-lateral extremities. The pedicle valve of *magnus* is more strongly convex, has a steep trail-like anterior margin, steeper lateral slopes, possesses fewer but more erect hinge spines, and has ovoid rather than linear adductor muscle scars. In the brachial valve the visceral disc is more convex, the socket ridges are more robust and are located further anteriorly than those in *R. careyi*, the alveolus is deeper, the median septum wider and longer, and the lateral septa stronger.

R. gloucesterensis (Cvancara) (Cvancara 1958, pp. 866–868, pl. 111, figs. 1–7), from the *Rhipidomella fortimuscula* Zone, was erroneously placed in synonymy with *Rugosochonetes magnus* by Maxwell (1961, p. 87). *R. gloucesterensis* is larger, more quadrate, has relatively smaller postero-lateral extremities, a flange-like inner margin on the pedicle valve, and a finer external ornament.

McKellar (*in* Kirkegaard *et al.* 1970, p. 148) suggested that the type specimens of *magnus* appeared to lack a dorsal median septum. An examination of a rubber cast of specimen F15288 UQ, the figured topotype in Maxwell (1954, pl. 5, fig. 13), and which is illustrated in text-fig. 8, confirms the existence of a dorsal median septum. *R. magnus* is recorded from the *T. tenuistriata* and *Schellwienella* cf. *burlingtonensis* Zones; it is Tournaisian to early Viséan in age.

Occurrence. Collections at the University of New South Wales contain specimens of *R. magnus* from the following areas in New South Wales: in the Rouchel district from locality 4-1 in the Dangarfield Formation, and localities 15-3, 24-8, 38-7, 39-18, 41-3, 58-3 and 12, 63-5, and 107-1 in the Waverley Formation; at Gresford from locality 72-3 in the Bingleburra Formation; in the Werrie Syncline at localities 112-1, 2, 4,

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EXPLANATION OF PLATE 4

Figs. 1–11. *Rugosochonetes careyi* (Campbell). 1, 2, rubber casts of the exterior of F56946a and F56946b respectively, ×1·5. Locality 88-2. 3, rubber cast of the dorsal interior of F56947, ×2. Locality 88-2. 4, exteriors of two specimens from locality 85-10. F56948, ×1·5. 5, 6, internal mould and rubber cast of the ventral interior of F56949, ×1·5 and ×2 respectively. Locality 17-5. 7, 8, internal mould and rubber cast of the ventral interior of F56950, ×1·5 and ×2 respectively. Locality 17-7. 9–11, rubber cast of three dorsal exteriors from locality 106-15. Note the width of the specimens. F56951, F56952, and F56953 respectively. All ×1·5.

Figs. 12–20. *Retichonetes kennedyensis* (Maxwell). 12, rubber cast of a brachial valve interior. F56954, ×4. 13–15, exteriors of three pedicle valves. F56955, F56956, and F56957 respectively, ×4. 16, 17, exterior and rubber cast of the exterior of F56958a and F56958b respectively, ×4. Figs. 13–17 from locality 10024 ANU. 18, rubber cast of a dorsal valve. F15165 UQ, ×4. 19, rubber cast of the holotype. F15155 UQ, ×4. 20, rubber cast of a dorsal valve. F15156 UQ, ×4. Figs. 18–20 from locality L1288 UQ.

Figs. 21–29. *Rugosochonetes magnus* Maxwell. 21–23, rubber casts of three dorsal interiors. F56959, F56960, and F56961. All ×4. 24, exterior of a dorsal valve. F56962, ×3. 25, internal mould of a pedicle valve. F56963, ×3. 26, rubber cast of a dorsal exterior. F56964, ×3. 27–29, rubber casts of three pedicle valves. F56965, F56966, and F56967 respectively. All ×3. Figs. 21–29 from locality 107-1.

PLATE 4


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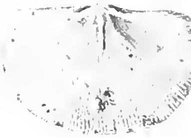
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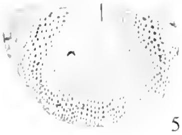
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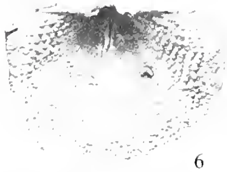
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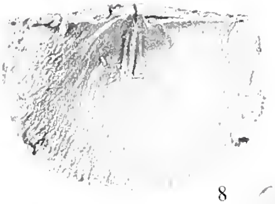
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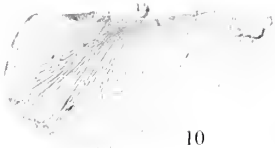
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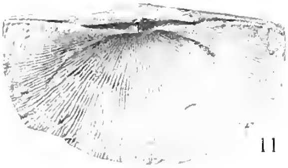
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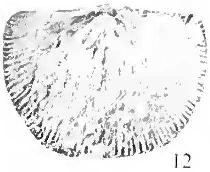
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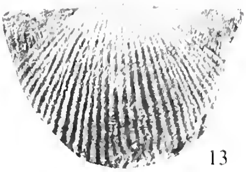
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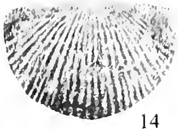
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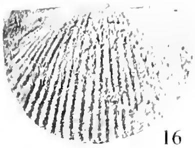
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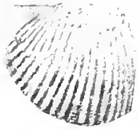
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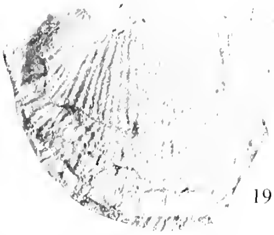
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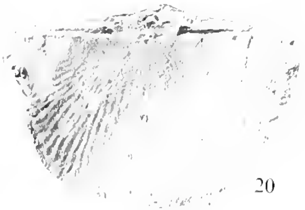
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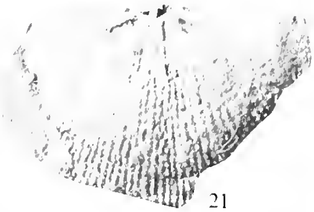
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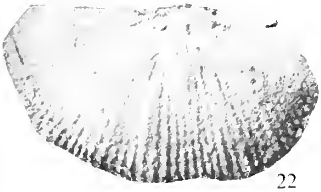
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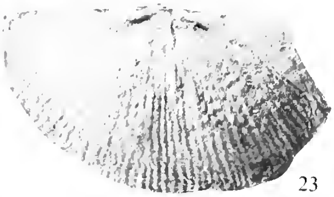
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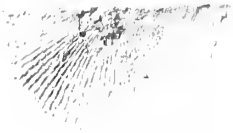
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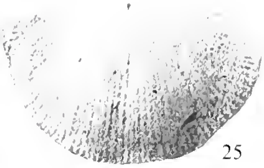
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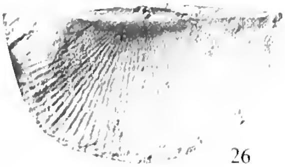
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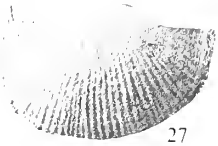
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ROBERTS, Australian chonetaceans

6, 7, 9, and 10 in the Namoi Formation; and from near Gravesend at localities F13 and F14 of Yeates (1970, unpublished B.Sc. thesis) in the Luton Formation. Occurrences of the species in Queensland are documented by Maxwell (1954, 1961), Dear (1968), and McKellar (*in* Kirkegaard *et al.* 1970).

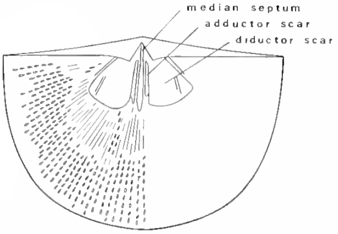
Material. F56959–F56967, Australian Museum.

Rugosochonetes careyi (Campbell)

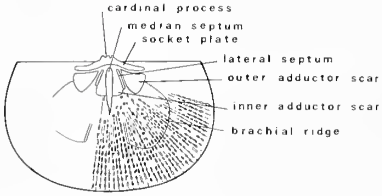
Plate 4, figs. 1–11

1957 *Chonetes careyi* Campbell, pp. 63–65, pl. 12, figs. 21–26.
1964*b* *Rugosochonetes kennedyensis* Maxwell; Roberts, pp. 181–182, pl. 2, figs. 1–7.

Diagnosis. Shell semicircular to rectangular in outline, and gently to moderately concavo-convex; the brachial valve has relatively less curvature than the pedicle valve; density of costellae at 20–22 per 5 mm at 20 mm from the umbo; ventral umbo low, resulting in the pedicle valve having a nearly even curvature from the venter to the lateral margins; ventral median septum extending one-quarter to one-third the length of the valve; ventral adductor muscle scars narrow and linear; cardinal process bilobate posteriorly; alveolus absent, but median septum originating from in front of the cardinal process and extending one-third to one-half the length of the valve; lateral septa short, slender, and divergent.



TEXT-FIG. 9. Ventral interior of *Rugosochonetes careyi* (Campbell) drawn from F56950 AM. Approximately × 2.



TEXT-FIG. 10. Dorsal interior of *Rugosochonetes careyi* (Campbell) drawn from F56947 AM. Approximately × 2.

Description. External. Postero-lateral extremities flat and either pointed or rounded; greatest width at, or a short distance in front of, the hinge; costellae bearing minute spinule and apertures increasing by bifurcation and intercalation; micro-ornament of faint concentric growth lines; the majority of specimens range in size to 18·5 mm wide and 10·5 mm long; some from Chichester are larger, particularly in width, and are up to 24 mm wide and 13·5 mm long. Pedicle valve gently to moderately convex over the venter, and having a low umbo which barely projects behind the hinge; three to six hinge spines on either side of the umbo project at 45° to the hinge; interarea low, varying from apsacline near the lateral margins to orthocline adjacent to the delthyrium; delthyrium triangular and open; anterior margin of some specimens bearing faint median sinus. Brachial valve gently concave, deepest a short distance in front of the umbo, and flat on the postero-lateral margins; some specimens bear a faint fold at the anterior margin.

Internal. Pedicle valve (text-fig. 9). Diductor muscle scars large, flabellate in outline, with moderately well-impressed pointed posterior margins, and shallow subrounded anterior margins; mantle canals originate from the anterior margins of both the adductor and diductor muscle scars, and in some specimens form a ridge extending anteriorly from the median septum; teeth are large, and situated on the inner margins of the delthyrium; endospines arranged in radial rows, finest medially and near the visceral disc, and coarsest on the postero-lateral shoulders. Brachial valve (text-fig. 10). Socket ridges parallel with the hinge; cardinal process bilobate posteriorly, the concave lobes being highest medially and flanked by small chilidial plates;

lateral septa extending half the length of the median septum; inner adductor scars triangular, and situated on low muscle platforms; outer adductor scars larger, lachrymose and slightly impressed; brachial markings extremely faint, originating from the antero-lateral margins of the outer adductor scars, forming an arcuate curve, and at their distal ridge-like extremities abruptly changing direction posteriorly; inner surface of the valve, including the brachial discs, bearing radial rows of endospines.

Variation. Specimens from locality 106-15 (Pl. 4, figs. 9–11) from the Flagstaff Sandstone near Chichester are larger and more transverse than individuals from other localities. Because their remaining characters are consistent with those of *careyi* they are referred to this species and are interpreted as gerontic variants.

Remarks. The description of *Rugosochonetes careyi* was made from relatively poorly preserved topotype specimens from Babbinboon, and from material from the Dungog and Rouchel districts of New South Wales. The type specimens figured by Campbell (1957) were destroyed by fire in 1958. Figured specimens (Pl. 4) are all from the Dungog and Rouchel districts.

R. careyi (Campbell) is morphologically close to *R. gloucesterensis* (Cvancara) (Cvancara 1958, pp. 866–868, pl. 111, figs. 1–7) from the *Rhipidomella fortimuscula* Zone at Barrington, New South Wales. An examination of topotype specimens shows that *gloucesterensis* is more quadrate in outline. The pedicle valve of *gloucesterensis* is characterized by the possession of a wider and deeper visceral disc which restricts the size of the postero-lateral extremities, a flange-like inner margin, more deeply impressed muscle scars, and ovoid rather than linear ventral adductor muscle scars. The external ornament has approximately the same density as that on *Rugosochonetes careyi*, and cannot be used as a distinguishing character (Cvancara 1958, p. 867). A detailed comparison with *R. magnus* Maxwell is given on page 30.

R. careyi is morphologically close to the finely ribbed group of *R. celticus* Muir-Wood, from the Viséan and Namurian of Great Britain. *R. celticus*, as originally defined by Muir-Wood (1962, pp. 68–70, pl. 6, figs. 8–9; pl. 7, figs. 3–14), encompassed a wide range of forms. Brunton (1968, p. 54, pl. 8, figs. 1–9) demonstrated that *celticus* could be divided into three informal groups: a finely ribbed group typified by the holotype; a coarsely ribbed group; and a third group with poorly defined ribs. The fine-ribbed group of *R. celticus* resemble *careyi* in having a small ventral umbo and gentle umbonal shoulders; it differs from most of the specimens referred to *careyi* in being less transverse, particularly posteriorly, and in having a slightly finer costellate ornament, possibly a greater convexity, and a longer dorsal median septum. In addition to having coarser ribs than those of *careyi*, the coarse-ribbed form of *celticus* is typified by ovoid rather than strap-like ventral adductor muscle scars. Brunton (1968, pp. 54–55) regards *R. celticus* as a possible junior synonym of *R. hardrensis* (Phillips), and hence the same distinctions may apply to that species. The characters of *hardrensis* are still poorly understood because of the loss of some of Phillips's specimens, doubt about the type locality, and difficulties in relating specimens still in existence with the original illustrations (Muir-Wood 1962, pp. 66–68). Specimens referred to *R. hardrensis* (Phillips) by Sokolskaya (1950, pl. 3, figs. 1–16) and compared with specimens from Greenhills by Roberts (1964*b*, p. 182) are smaller and more quadrate than *R. careyi*. The transverse specimens of *R. careyi* from locality 106-15 (Pl. 4, figs. 9–11) are close in shape to a Scottish specimen of *Rugosochonetes* sp. compared by Brand (1970, p. 107) with *R. hardrensis*. The Scottish form (Brand 1970, pl. 9, fig. 24) from the Penton Limestone in the Archerbeck Bore has six spines on either side of the umbo.

The species ranges from the *Schellwienella* cf. *burlingtonensis* to the *Gigantoproductus tenuirugosus* Subzone, and is late Tournaisian to late Viséan in age.

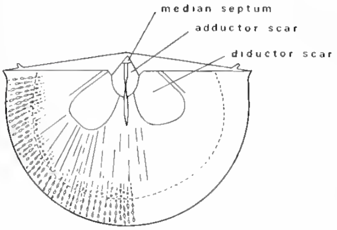
Occurrence. The type locality is L35 UNE (equals 112-14) at Babbinboon in the Werrie Syncline, New South Wales. Stratigraphically the type locality is in a mudstone member of the Merlewood Formation (Roberts 1975), not near the top of the Namoi Formation as indicated by Campbell (1957). In the Rouchel district, New South Wales, the species is present in locality 4-2, Dangarfield Formation, possibly in localities 24-7 and 8, Waverley Formation, and in localities 6-10, 17-5, 7 and 11, 29-1, 2 and 7, 30-13, and 41-1 and 2 in the Woolooma Formation. At Gresford and Dungog the species is present in localities 72-3 and 100-8 in the Bingleburra Formation, localities 16-3, 72-18, and 74-7A in the Bonnington Siltstone, localities 73-8, 90-1 and 2, 100-4 and 13, 104-1 and 106-2, 9 and 15 in the Flagstaff Sandstone, at L404 U Newcastle in the Wootton Beds, and at L359 U Newcastle in the Ararat Formation. A form closely comparable with *R. careyi* is present in the Namoi Formation at localities 112-1, 4, 7 and 10 in the Werrie Syncline, New South Wales.

Rugosochonetes gloucesterensis (Cvancara)

Plate 5, figs. 1–2

1958 *Chonetes gloucesterensis* Cvancara, pp. 866–868, pl. 111, figs. 1–7.

Rugosochonetes gloucesterensis has been fully described by Cvancara (1958). An emended diagnosis is provided to illustrate the distinction between *gloucesterensis* and the morphologically close forms *R. magnus* Maxwell and *R. careyi* (Campbell). Comparisons with *R. magnus* Maxwell and *R. careyi* (Campbell) are given above.



TEXT-FIG. 11. Ventral interior of *Rugosochonetes gloucesterensis* (Cvancara) drawn from F56968b AM. Approximately ×2.

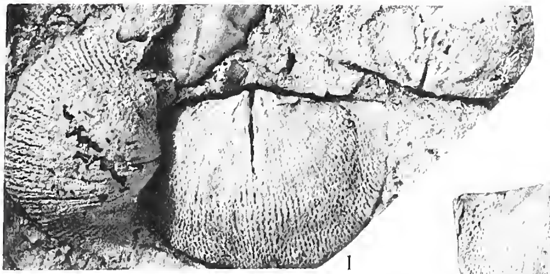
Diagnosis (emend.). Shell quadrate to rectangular in outline, strongly concavo-convex, and with the greatest width anterior to the hinge; postero-lateral margins slightly constricted immediately in front of the hinge; costellae with a density of 19–23 per 5 mm at 5 mm from the umbo; pedicle valve having a broad deep visceral disc, flange-like inner margins, and small postero-lateral extremities; ventral muscle field deeply impressed, and with ovoid adductor muscle scars (text-fig. 11).

EXPLANATION OF PLATE 5

Figs. 1–2. *Rugosochonetes gloucesterensis* (Cvancara). Internal moulds of pedicle valves showing flange-like lateral and anterior margins. F56968a and b respectively, ×2. Figs. 1–2 from locality L422 U Newcastle.

Figs. 3–12. *Megachonetes alatus* sp. nov. 3, rubber cast of pedicle valve interior. Note the tubules through the hinge. F56969, ×2. 4, rubber cast of portion of a brachial valve showing the cardinal process. F56970, ×2. Figs. 3–4 from locality 31-1. 5, rubber cast of pedicle valve exterior. F56971, a paratype, ×1·5. 6, rubber cast of ventral interior. F56972, a paratype, ×1·5. 7–8, internal mould and rubber cast of a pedicle valve. F56973, a paratype, ×1·5. 9, rubber cast of a dorsal interior. F56974, the holotype, ×1·5. Figs. 5–9 from locality 15-3. 10, rubber cast of a dorsal exterior. F56975, ×1. 11, rubber cast of a dorsal interior. F56976, ×2. 12, rubber cast of a ventral interior. F56977, ×1·5. Figs. 10–12 from locality 39-16.

PLATE 5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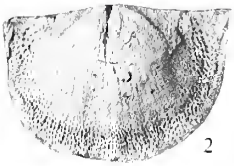
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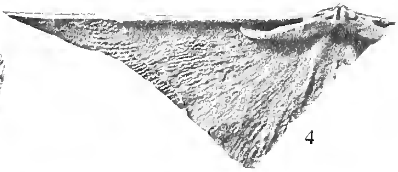
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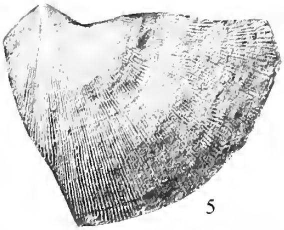
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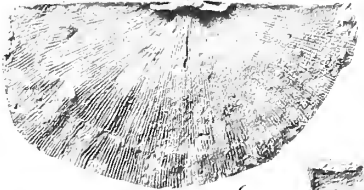
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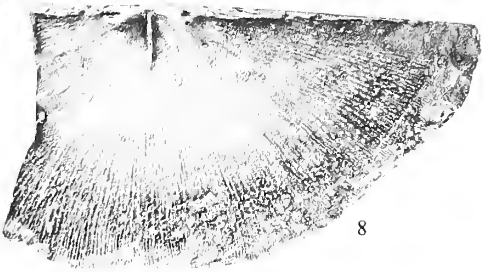
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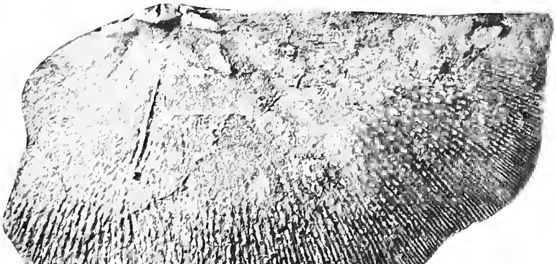
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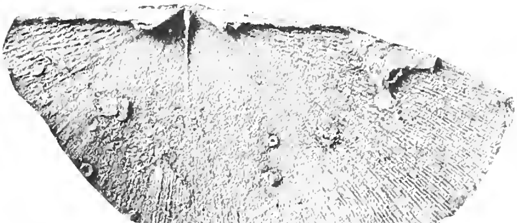
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Occurrence. In New South Wales *R. gloucesterensis* is restricted to the *Rhipidomella fortimuscula* Zone. It is recorded from locality L422 U Newcastle in the Copeland Road Formation at Barrington, and from localities 85-15, 88-3, and 90-6 in an unnamed formation at Salisbury and Brownmore.

Material. F56968, Australian Museum.

Family DAVIESIELLIDAE Sokolskaya, 1960

Subfamily DELEPINEINAE Muir-Wood, 1962

Genus MEGACHONETES Sokolskaya, 1950

Type species. Chonetes compressa Sibly, 1908, equals *C. siblyi* I. Thomas, 1919.

Megachonetes alatus sp. nov.

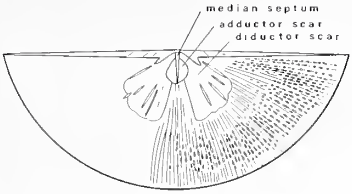
Plate 5, figs. 3–12

Diagnosis. Shell large for the genus, semi-elliptical in outline, approximately twice as wide as long, gently concavo-convex posteriorly, but more strongly incurved anteriorly; costellae with a density of 18–20 per 5 mm at 20 mm from the umbo; ventral median septum extending one-quarter to one-third the length of the valve; ventral adductor muscle scars subovate; socket ridges nearly parallel with the hinge; dorsal median septum extending from the alveolus to between one-third and one-half the length of the valve; lateral septa diverging at 20° from the median septum.

Description. External. Shell transverse, with the lateral margins meeting the hinge at nearly right angles; costellae frequently irregular and wavy, increasing mainly by intercalation and to a lesser extent by bifurcation; specimens range in size to an estimated 85 mm wide and 38 mm long. Pedicle valve gently and evenly convex; umbo low and barely rising above the level of the lateral slopes; ventral interarea apsacline, and bearing a wide delthyrium closed apically by a small arched pseudodeltidium; hinge bearing a row of spine bases spaced approximately 3 mm apart. Brachial valve gently concave to nearly flat on the posterior half of the valve, but becoming increasingly concave anteriorly; dorsal interarea short, catacline, and bearing a convex notothyrial plate over the dorsal exterior of the cardinal process.

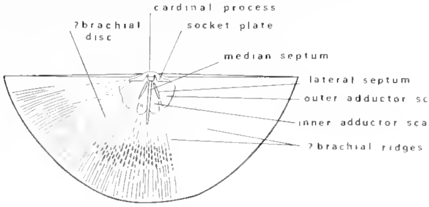
Internal. Pedicle valve (text-fig. 12). Adductor muscle scars slightly impressed, subovate, pointed posteriorly, and bluntly rounded anteriorly; diductor muscle scars less well impressed, bounded postero-laterally by ridges, and flabellate in outline; teeth slender, laterally elongate, and supported by thickened dental plates on the margins of the delthyrium; internal surface of valve ornamented by spinose radially arranged ribs. Brachial valve (text-fig. 13). Socket ridges robust, and enclosing narrow sockets; cardinal process high and bilobed, the posterior face (text-fig. 14) having two elongate concave lobes separated ventrally by a narrow groove; median septum commencing in front of a shallow but almost cavernous depression or alveolus located anteriorly from or beneath the cardinal process; lateral septa slender, commencing in front of the cardinal process, and extending approximately half the length of the median septum; inner adductor muscle scars elongate, pointed posteriorly, expanding anteriorly, and extending two-thirds the length of the median septum; outer adductor muscle scars impressed postero-medially on the margins of the lateral septa and in front of the cardinal process, striated, but obscure anteriorly; internal surface of the valve ornamented by radial ridges which are particularly spinose on the margins of the visceral disc; brachial markings comprising relatively smooth subquadrate discs bordered laterally by low brachial ridges (text-fig. 13); ridges absent along the anterior margins of the brachial discs.

Remarks. Megachonetes alatus may belong to the *papilionaceus* (Phillips) group of species, a group of transverse gently concavo-convex forms. None of the *papilionaceus* group has previously been adequately described, presumably because of poor preservation of the thin shells. From a brief description of the type specimen of *M. papilionaceus* given by Muir-Wood (1962, p. 106) and a figure in Phillips (1836,



TEXT-FIG. 12. Ventral interior of *Megachonetes alatus* sp. nov. drawn from paratype F56973 AM. Approximately ×0·75.

TEXT-FIG. 14. External face of the cardinal process of *Megachonetes alatus* sp. nov.



TEXT-FIG. 13. Dorsal interior of *Megachonetes alatus* sp. nov. drawn from the holotype F56974 AM. Approximately ×0·75. The brachial markings are apparently the first described in a species of *Megachonetes*.

pl. 11, fig. 6) it appears that *M. alatus* is shorter, and has a coarser costellate ornament. Davidson's (1861, pl. 46, figs. 3–6) figures of *M. papilionaceus*, including Phillips's original specimen from Bolland, show that species to be larger, particularly in width, than *M. alatus*. Specimens of the *papilionaceus* group from Scotland figured by Brand (1970, pl. 11, figs. 15–18; pl. 12, fig. 3), resemble this species in the morphology of the dorsal and ventral musculature and septa. *M. alatus* differs from the Scottish form in having a brachial valve which is strongly concave anteriorly, and socket plates which are nearly parallel with the hinge. *M. papilio* (Paeckelmann) from the Viséan of Germany (Paeckelmann 1930, pp. 295–299, pl. 22, figs. 1–3; pl. 23, fig. 5) resembles *M. alatus* in the over-all outline and convexity of the shell, but differs in its larger size and coarser costellate ornament; adult shells of *alatus* have eighteen costellae per 5 mm, and those of *papilio* approximately ten costellae per 5 mm at the anterior margin. One other species of *Megachonetes* has been described from Australia. *M. zimmermanni* (Paeckelmann), described by Roberts (1971, pl. 10, figs. 11–22) from the Burvill Beds in the Bonaparte Gulf Basin, is less transverse, has a stronger ventral umbo, sloping ventral cardinal margins, and is smaller in size. These same distinctions apply to specimens of *M. zimmermanni* described by Paeckelmann (1930, pl. 17, fig. 23; pl. 18, fig. 1) from the Viséan of Germany, and by Sokolskaya (1950, pl. 6, figs. 7–13) from the Viséan of the Moscow Basin. *M. alatus* ranges from the *Schellwienella* cf. *burlingtonensis* Zone into the base of the *Orthotetes australis* Zone, and is late Tournaisian to possibly middle Viséan in age.

Occurrence. M. alatus sp. nov. is present at localities 15-3, 31-1, 39-16, 39-18, and 24-7 in the Waverley Formation, and locality 17-5 and possibly 29-7 in the Woolooma Formation in the Rouchel district; at locality 94-2 in the Ararat Formation near Gresford; at localities 112-4 and 12 in the Namoi Formation in the Werrie Syncline; at locality 113-4 in the Namoi Formation near Boggabri; and at locality F3 of Yeates (1970, unpublished B.Sc. thesis) in the Namoi Formation near Gravesend.

Material. F56969–F56977, Australian Museum. Holotype F56974; paratypes F56971, F56972, and F56973.

Superfamily PRODUCTACEA Gray, 1840
Family LEIOPRODUCTIDAE Muir-Wood and Cooper, 1960
Subfamily PRODUCTININAE Muir-Wood and Cooper, 1960
Genus PRODUCTINA Sutton, 1938

Type species. Productus sampsoni Weller, 1909, by original designation of Sutton 1938.

Productina striata sp. nov.

Plate 6, figs. 10–20

1975 *Productina* sp. A., Roberts, Table 1.

Diagnosis. Shell strongly to moderately concavo-convex, subround in small forms, but elongate and spreading anteriorly in large individuals; ornament of fine to sometimes obsolete costae having a density of 25 per 10 mm at 10 mm from the umbo; pedicle valve rugose to slightly lamellose, with one or two erect spines on the postero-lateral margins, and usually one median spine; ventral diductor muscle scars wide; dorsal median septum extending to about the mid-length of the valve.

Description. External. Pedicle valve with greatest width near the mid-length in small forms, but at about two-thirds the length in large individuals; valve with steep umbonal shoulders, but becoming flatter on the spreading anterior of gerontic specimens; postero-lateral margins ear-like, and flat to slightly convex; hinge slightly shorter than the greatest width; spines large and halteroid, one or two erect spines arising from the umbonal slopes near each ear, and usually one or sometimes two spines arising at a low angle from wide costae on the median part of the valve; costae strap-like, and increasing by bifurcation and intercalation. Brachial valve deepest at about one-third the length of the valve, and with extremely steep umbonal shoulders rising to flat or slightly concave postero-lateral extremities; concentric lamellae frequently irregular, crowded anteriorly and in some cases crossed by rugae; specimens range in size up to 28 mm wide and 26 mm long.

Internal. Pedicle valve. Adductor muscle scars subrectangular, pointed posteriorly, wider and with slightly rounded extremities anteriorly, and bearing faint radial striae; adductor scars on low platforms divided by a narrow furrow containing a median ridge; diductor muscle scars slightly impressed, extending well in front of the adductor muscle scars, broad and rounded anteriorly, tapering posteriorly, and marked by faint radial mantle canals; internal surface bearing fine endospines. Brachial valve. Median septum low; inner adductor scars situated on platforms between the median septum, elongate and pointed posteriorly,

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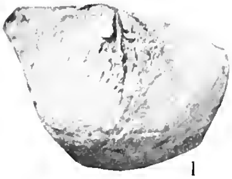
EXPLANATION OF PLATE 6

Figs. 1–9. *Productina macdonaldi* sp. nov. 1–2, rubber casts of two brachial valve interiors. F57000a and F57001a the holotype, ×3. 3–4, internal moulds of the pedicle valve. F57002 and F57001b, both paratypes, ×3. 5–7, rubber casts of pedicle valve exteriors. F57003 a paratype, F57004, and F57000b a paratype, ×3. 8–9, rubber casts of two brachial valve exteriors. F57005 and F57006, a paratype, ×3. All from locality 92-1.

Figs. 10–20. *Productina striata* sp. nov. 10, internal mould of the apical portion of pedicle valve. F57007, ×1·5. 11–13, internal mould and a rubber cast of the brachial valve interior of the holotype. F57008, ×1·5. 14, rubber cast of a pedicle valve exterior. F57009, a paratype, ×1·5. 15–16, rubber casts of two brachial valve exteriors. F57010 and F57011, paratypes, ×1·5. Figs. 10–16 from locality 6-10. 17, rubber cast of a brachial valve interior from locality 6-13. F57012, ×3. 18–19, a rubber cast of a pedicle valve exterior and an internal mould of a pedicle valve. F57013 and F57014 respectively. Both ×1·5 and from locality 89-1. 20, rubber cast of the pedicle valve exterior of F57015, ×1·5, from locality 41-1.

Figs. 21–23. *Productina* cf. *striata* sp. nov. 21, internal mould of a pedicle valve showing narrow diductor muscle scars. F57016, ×1·5. 22, rubber cast of a brachial valve exterior. F57017, ×1·5. 23, rubber cast of a deformed pedicle valve showing an additional spine on the postero-lateral extremities. F57018, ×1·5. Figs. 21–23 from locality L386 U Newcastle.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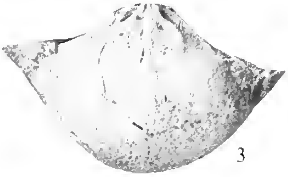
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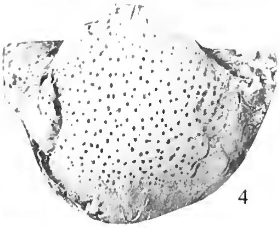
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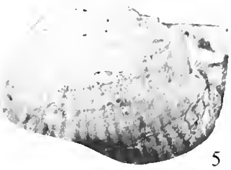
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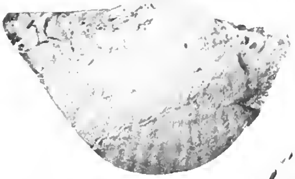
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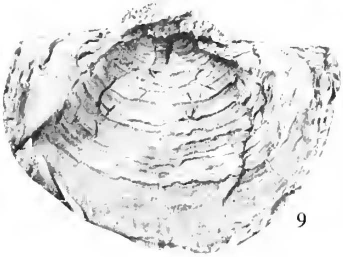
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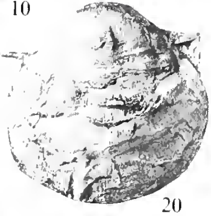
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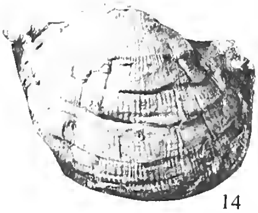
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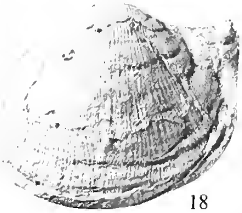
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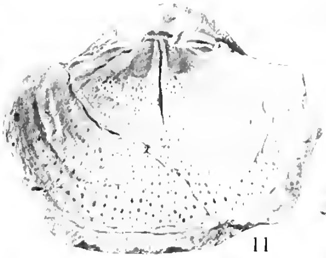
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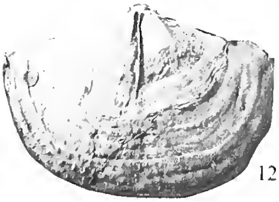
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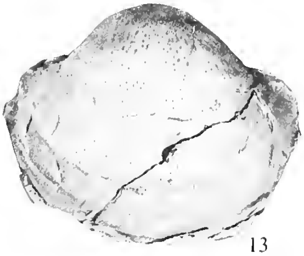
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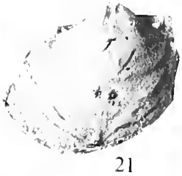
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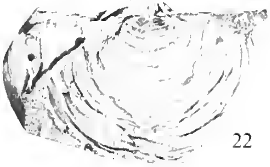
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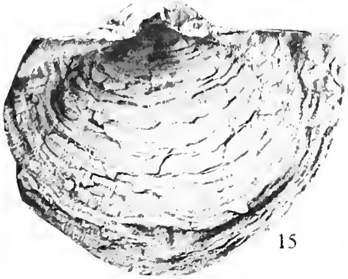
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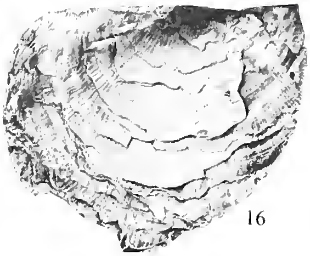
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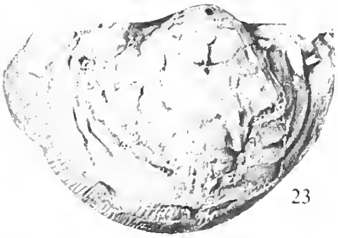
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ROBERTS, Australian productaceans

and expanding anteriorly; outer adductor scars shallowly impressed, and narrowly triangular in outline; cardinal process bilobed, each lobe bearing a deep median furrow on the postero-dorsal surface; lateral ridges short and obsolete; brachial markings faint, comprising low ridges extending in a sinuous curve anteriorly from the front of the inner adductor scars, and curving laterally near the front of the valve; internal surface bearing fine endospines.

Remarks. Morphologically *Productina striata* is close to the cosmopolitan species *P. margaritacea* (Phillips). This species is distinguished from *margaritacea* by its generally more round outline, and by the possession of much finer costae (25 per 10 mm at 10 mm from the umbo compared with 12–16 in the same dimensions on *margaritacea*), and a more rugose pedicle valve. The dorsal median septum of *striata* is more robust than that of specimens of *margaritacea* from Northern Ireland figured by Brunton (1966, pl. 8, fig. 9), but may be weaker than that on a specimen from the Utting Calcarenite in the Bonaparte Gulf Basin (Roberts 1971, pl. 17, figs. 22 and 25). In addition, the ventral diductor muscle scars are wider in *striata* than in *margaritacea*, and *striata* may have one less spine on each umbonal shoulder. Material from the Carboniferous Limestone of Great Britain figured by Davidson (1861, pl. 44, figs. 6–8), including Phillips's type specimen, show *P. margaritacea* to be more lamellose on the pedicle valve and to have much stronger costae and a greater number of postero-lateral spines when compared with *P. striata*. The specimen of *P. margaritacea* illustrated by Sarycheva and Sokolskaya (1952, pl. 15, fig. 106) from the C_1st of the Moscow Basin is less rugose and has coarser costae than *P. striata*. *P. pectinoides* (Phillips) figured by Davidson (1861, pl. 44, fig. 8) resembles *striata* in outline, but has coarser costae and, according to Dr. C. H. C. Brunton (pers. comm.), may lack median and flanking spines on the pedicle valve.

Specimens of *Productina* cf. *striata* from locality L386 at Alison near Dungog (Pl. 4, figs. 21–23) are externally very close to *striata*. They are similar in size, have a comparable density of costae (22–28 per 10 mm at 10 mm from the ventral umbo), and are rugose to lamellose on the pedicle valve. There may be an additional spine on each umbonal shoulder, and a group of five or more spines on the posterior portion of the visceral disc behind the large median spine; the major difference with *striata* is the smaller size of the ventral diductor muscle scars, and the more narrow elongate outline of the diductor muscle scars.

P. globosa Roberts (1963, pp. 12–13, pl. 3, figs. 1–3) which ranges from the *Schellwienella* cf. *burlingtonensis* Zone into the lower part of the *Orthotetes australis* Zone in New South Wales, and is also recorded from Queensland (McKellar 1967), is much smaller than *striata*. *P. globosa* is more strongly concavo-convex, has a coarser costate ornament, a band of six to eight spines around the front of the pedicle valve, obsolete diductor muscle scars, a delicate dorsal median septum, and divergent lateral ridges in the dorsal valve.

Occurrence. P. striata is restricted to the Viséan *Inflatia elegans* Subzone. It is recorded from locality 6-10, the type locality, and localities 6-11 and 13, 35-3, and 41-1 and 2 in the Woolooma Formation in the Rouchel district; locality 89-1 in the Flagstaff Sandstone at Mirannie; localities 100-2, 10 and 12, 106-2 and 16 in the Flagstaff Sandstone in the Salisbury–Brownmore district; and at localities 98-1 and 129-1 in the Flagstaff Sandstone in the Gresford district, New South Wales. In Queensland the species is present at locality K21 GSQ in the Caswell Creek Group at Cannindah. *Productina* cf. *striata* is present at locality L368 U Newcastle at Alison, near Dungog, New South Wales.

Material. F57007–F57015 AM. Holotype F57008; paratypes F57009, F57010, F57011.

Productina macdonaldi sp. nov.

Plate 6, figs. 1–9

1975 *Productina* sp. B., Roberts, Table 1.

Diagnosis. Shell small, globose, and strongly concavo-convex; pedicle valve with 6–7 costae per 3 mm at the anterior margin, and two or three spine bases on each umbonal shoulder, but lacking median spines or a concentric row of spines near the anterior of the valve; ventral adductor muscle scars in two pairs separated by a furrow bearing a median ridge; dorsal costae obsolete to absent; brachial valve having a median septum extending beyond the mid-length of the valve, triangular inner adductor muscle platforms, prominent hook-shaped brachial ridges, and lateral ridges parallel with the hinge.

Description. External. Pedicle valve semicircular to rounded-rectangular in outline, narrow at the umbo, and flaring anteriorly; umbo prominent, with steep umbonal shoulders passing on to flat moderately wide postero-lateral extremities; costae poorly defined on the umbo, stronger anteriorly, increasing by bifurcation, and crossed by several lamellose growth halts. Brachial valve deepest at about one-third of its length, with steep lateral slopes and flat postero-lateral extremities; concentric lamellae closely spaced and short posteriorly, and longer and more widely spaced anteriorly; specimens range in size up to 14 mm long and 10·5 mm wide.

Internal. Pedicle valve. Adductor muscle scars comprising a larger club-shaped inner pair, and a smaller impressed ovoid outer pair inset into the postero-lateral extremities of the inner adductor scars; median ridge arising at the umbo and extending through a median furrow to the anterior margin of the adductor scars; diductor muscle scars less well defined, extending in front of the adductor scars, broad and rounded posteriorly, and tapering posteriorly; internal surface ornamented with small endospines. Brachial valve. Inner adductor muscle scars situated on high muscle platforms; outer adductor muscle scars poorly defined, subquadrate, and slightly impressed; median septum commencing at a position level with the posterior of the inner adductor platforms, narrow between the muscle platforms, and becoming wider and higher anteriorly; cardinal process bilobed and supported by slender lateral ridges; posterior of cardinal process not observed; brachial ridges high, extending from the front of the outer adductor muscle scars and enclosing nearly square pustulose brachial discs (Pl. 6, fig. 2); internal surface of valve bearing small endospines, particularly in front of the muscle field.

Remarks. P. macdonaldi sp. nov. is known only from the upper part of the *Rhipidomella fortimuscula* Zone at Salisbury and Brownmore. Morphologically, it is remarkably close to *P. globosa* Roberts (1963, pp. 12–13, pl. 3, figs. 1–3) which in New South Wales ranges from the *Schellwienella* cf. *burlingtonensis* Zone into the lower part of the *O. australis* Zone. There are no small globose species of *Productina* recorded in either New South Wales or Queensland from the intervening upper part of the *australis* and *Delepinea aspinosa* Zones, and hence *macdonaldi* is considered to be a homeomorph of *globosa.* The differences between the species are slight. *P. globosa* is a little less transverse, does not possess a low ventral median ridge, lacks brachial ridges, which, however, are not invariably present in *macdonaldi*, possesses a row of 6–8 spines around the front of the pedicle valve, and has divergent lateral ridges in the brachial valve. In *macdonaldi* the inner adductor muscle platforms are triangular in shape and higher than those in *globosa*, the dorsal median septum is slightly longer, and the postero-lateral extremities may be a little wider.

P. sampsoni (Weller) from the Lower Mississippian of U.S.A. (Muir-Wood and Cooper 1960, pl. 123, figs. 1–10; Carter 1967, pl. 10, fig. 1) is morphologically close to both *globosa* and *macdonaldi*. When compared with *macdonaldi* the main distinguishing features of *P. sampsoni* are the geniculation at the front of the brachial valve, and a shorter hinge line. Another species from the Lower Mississippian of the U.S.A., *P. lodgepolensis* Rodriguez and Gutschick (1968, pl. 128, figs. 1-9), is characterized by a hinge line of comparable width to that in *macdonaldi*. *P. lodgepolensis* is distinguished by the smaller convexity of the pedicle valve, the possession of coarser dorsal endospines, and the lack of brachial ridges.

Occurrence. Locality 92-1, the type locality, and locality 103-4 in an unnamed formation in the Salisbury-Brownmore district. Late Viséan *R. fortimuscula* Zone.

Material. F57000-F57006 AM. Holotype F57001a; paratypes F57000b, F57001b, F57002, F57003, F57006.

Productina morrisi sp. nov.

Plate 7, figs. 26-31

?1931 *Productus* (*Thomasina*) *pectinoides* Phillips; Paeckelmann, pp. 188-191, pl. 17, figs. 13-16.
1975 *Productina pectinoides* (Phillips); Roberts, Table 1.

Diagnosis. Shell large, transverse, moderately concavo-convex, and with coarse costae; pedicle valve with wide postero-lateral extremities, each bearing a row of three large spines; ventral median spines absent; dorsal median septum extending two-thirds the length of the valve.

Description. External. Shell pentagonal in outline, and widest behind the mid-length; specimens range in size up to 36 mm wide and 26·5 mm long. Pedicle valve most strongly convex at the umbo, and with broad evenly convex lateral slopes; umbo wide, and extending well behind the hinge; hinge slightly less than the greatest width of the valve; costae wide, increasing in number by rare bifurcations, having a density of 10-13 per 10 mm at 10 mm, and 8-10 per 10 mm at 20 mm from the umbo, and crossed by occasional lamellose growth halts. Brachial valve rounded-rectangular in outline, and with flat postero-lateral extremities; gerontic individuals having an elongate trail; concentric lamellae regularly spaced over the

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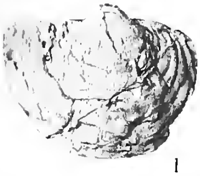
EXPLANATION OF PLATE 7

Figs. 1-18. *Spinorugifera chichesterensis* gen. et sp. nov. 1, internal mould of a pedicle valve. F57019, ×2. 2-3, rubber cast and mould of the interior of a pedicle valve. F57020, ×2. 4-5, rubber cast and mould of the interior of a pedicle valve. F57021, ×2. 6, rubber cast of a pedicle valve interior. F57022, ×2. 7, rubber cast of a pedicle valve exterior. F57023, ×2. 8, rubber cast of a pedicle valve exterior. F57024, ×2. 9-11, rubber casts of the ventral and dorsal exterior and an internal mould of the pedicle valve of F57025a, b, and c, the holotype, ×2. 12-13, rubber casts of the dorsal interior and exterior of F57026, paratype, ×2. 14-15, rubber casts of the dorsal interior and exterior of F57027, paratype, ×2. 16-17, rubber casts of two pedicle valve exteriors. F57028 and F57029 respectively, ×2. 18, rubber cast of a brachial valve exterior. F57030, ×2. Figs. 1-18 from locality 106-15.

Figs. 19-25. *Antiquatonia spinulicosta* sp. nov. 19, rubber cast of a brachial valve interior from locality 24-7. F57031, ×1·5. 20-21, rubber casts of two brachial valves. F57032 and F57036, the holotype, ×1·5 and ×3 respectively. 22, internal mould of pedicle valve. F57033, paratype, ×1. 23, rubber cast of a brachial valve interior. F57034a, paratype, ×1·5. 24-25, internal mould and rubber cast of the exterior of pedicle valve. F57035, ×1. Figs. 20-25 from locality 10026 ANU.

Figs. 26-31. *Productina morrisi* sp. nov. 26, interior of brachial valve. F57037, ×1·5. 27-28, internal mould of the dorsal and ventral interior. F57038a, holotype, ×1·5. 29, rubber cast of a group of shells. F57039, ×1. 30, exterior of pedicle valve. F57040, paratype, ×1. 31, external mould of brachial valve. F57038b, ×1·5. Figs. 26-31 from locality L498 U Newcastle.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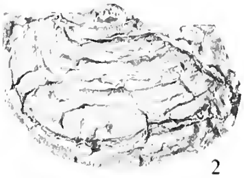
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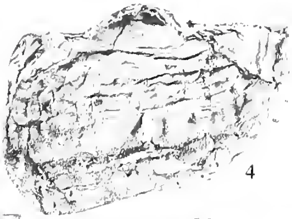
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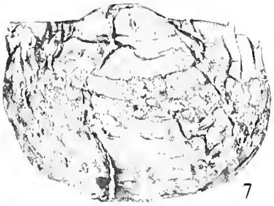
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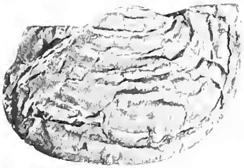
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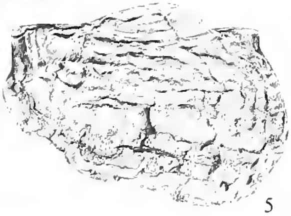
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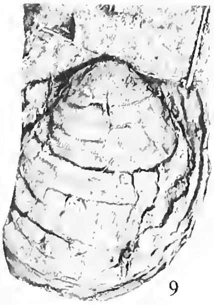
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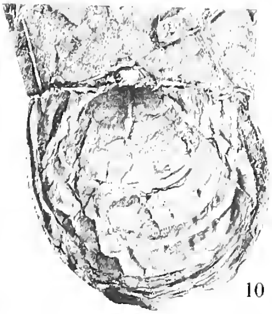
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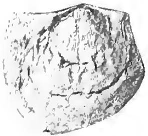
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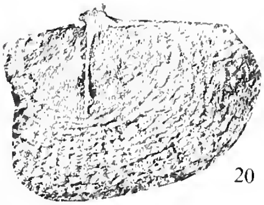
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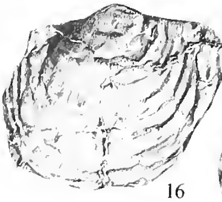
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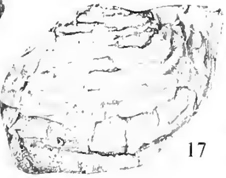
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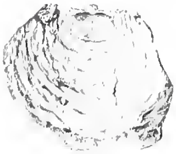
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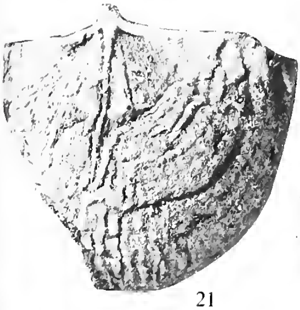
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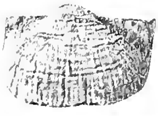
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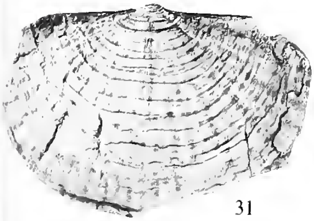
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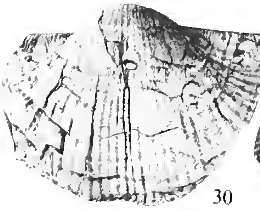
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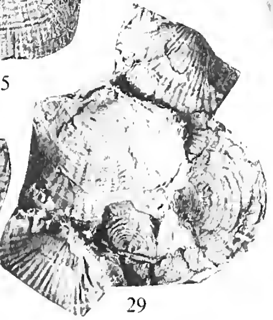
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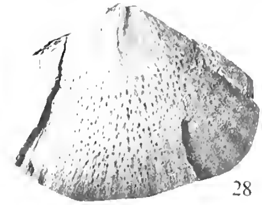
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ROBERTS, Australian productaceans

visceral disc, having a density of 5-9 per 10 mm on the mid-region of the disc; lamellae longer towards the front of the valve, and up to 8 mm in length on the trail of a gerontic specimen.

Internal. Pedicle valve. Adductor muscle scars elongate, tapering posteriorly, wider anteriorly, situated on low muscle platforms, and separated by a deep median furrow; diductor muscle scars immediately adjacent to and extending further anteriorly than the adductor scars, wide and rounded anteriorly, and tapering posteriorly; internal surface of the valve bearing numerous small endospines. Brachial valve. Inner adductor muscle scars triangular, pointed posteriorly and wide anteriorly, and located on high muscle platforms separated by the posterior portion of the median septum; outer adductor muscle scars poorly defined; cardinal process bilobed, but unknown posteriorly; lateral ridges short and divergent; brachial ridges not observed; endospines small, covering most of the internal surface of the valve, but concentrated particularly in the middle of the valve in front of the muscle field.

Remarks. The present material is extremely close to specimens from the Upper Kohlenkalk of Germany identified as *Productus* (*Thomasina*) *pectinoides* Phillips by Paeckelmann (1931); the shells are large, have a similar profile, coarsely costate ornament, large umbo, and configuration of spines on the postero-lateral extremities. *Productina pectinoides* (Phillips) is presently poorly understood, and was placed in synonymy with *P. margaritacea* by Davidson (1861). The type specimen (Phillips 1836, pl. 7, fig. 11; Davidson 1861, pl. 44, fig. 8), however, appears to be circular in outline, and according to Dr. C. H. C. Brunton (pers. comm.) may lack median and flanking spines; it is therefore doubtful whether Paeckelmann's specimens are correctly assigned. Spanish material identified as *P. pectinoides* by Winkler Prins (1968) is small, subcircular in outline, and strongly concavo-convex and is not closely comparable with *P. morrisi*.

P. margaritacea (Phillips), which has a transverse outline and internal features similar to those of this species, differs in having a median spine or spines on the venter, a larger number of spines on the shoulders, and slightly finer costae. Specimens used in this comparison were described by Brunton (1966) from Ireland, and Roberts (1971) from the Bonaparte Gulf Basin, north-western Australia. Phillips's type specimen of *P. margaritacea*, figured by Davidson (1861, pl. 44, fig. 6), appears to have finer costae than specimens figured by Brunton and Roberts.

P. morrisi is the largest of four species of *Productina* recorded from Lower Carboniferous rocks in New South Wales. It is distinguished from *P. striata* sp. nov., the other relatively large species, by its greater size, more rectangular outline, and much coarser costae. In the pedicle valve *morrisi* has wider postero-lateral extremities, each of which bears a row of three spines, has fewer lamellae or rugae, and lacks median spines on the venter. The dorsal median septum of *morrisi* is longer than in *striata*.

Occurrence. P. morrisi is recorded from localities L498 U Newcastle, the type locality, 90-7 and probably 90-9 in an unnamed formation in the Salisbury-Brownmore district, New South Wales. Late Viséan *R. fortimuscula* Zone.

Material. F57037-F57040 AM. Holotype F57038a; paratype F57040.

Family OVERTONIIDAE Muir-Wood and Cooper, 1960
Subfamily OVERTONIINAE Muir-Wood and Cooper, 1960
Genus KROTOVIA Fredericks, 1928 emend. Brunton, 1966

Type species. Productus spinulosus J. Sowerby, 1814.

Krotovia procidua sp. nov.

Plate 9, figs. 24–33

1975 *Krotovia* sp. nov., Roberts, Table 1.

Diagnosis. Shell transverse, and semicircular in outline; ventral ornament of unevenly spaced lamellae with irregular rows of elongate spine bases bearing mainly prostrate spines; dorsal spines in irregular concentric rows, small, erect, and arising immediately from the surface of the valve; dorsal median septum extending one-third the length of the valve; lateral ridges apparently absent.

Description. External. Shell widest in front of the hinge, moderately concavo-convex, and with a thin body cavity; specimens range in size up to 33·5 mm wide and 31·0 mm long. Pedicle valve evenly convex over the venter, with a narrow tapering umbo, steep concave umbonal shoulders, and small, flat postero-lateral extremities; spine bases quincuncially arranged on the anterior of the valve. Brachial valve deepest at the posterior of the visceral disc, and having flat postero-lateral extremities; exterior of valve ornamented by dimples in positions equivalent to spines on the interior of the valve, and irregular spinose lamellae and rugae; rugae forming closely spaced lumpy ridges, strongest on the umbonal shoulders, and in some cases extending across the visceral disc; spines without node-like bases, but arising directly from the surface of the rugae or the lamellae.

Internal. Pedicle valve interior poorly known; diductor muscle scars apparently ovoid in outline, rounded anteriorly, and separated by a low median ridge; adductor muscle scars not observed; internal surface finely spinose. Brachial valve. Median septum low and slender; adductor muscle scars in one pair, lachrymose in outline, pointed posteriorly and rounded anteriorly, and forming elevated muscle platforms; cardinal process bilobed, but unobserved posteriorly; brachial markings absent; internal surface of valve bearing large endospines on concentric ribs, and fine endospines.

Remarks. Specimens from Barrington, New South Wales (Pl. 9, figs. 32–33), are less transverse than those from the type locality at Salisbury. Their spine bases are shorter, but the spines are still arranged in rough concentric rows.

The type species, *Krotovia spinulosa* (Sowerby) from the Lower Carboniferous of Great Britain (Muir-Wood and Cooper 1960, pl. 50, figs. 1–5), differs from *K. procidua* sp. nov. in its smaller size and in details of the external ornament. *K. spinulosa* has quincuncially rather than mainly concentrically arranged spines, lacks lamellose growth halts, and has weaker dorsal rugae. Silicified specimens of *K. spinulosa* described by Brunton (1966, pp. 224–225, pl. 12, figs. 1–18; pl. 13, figs. 1–7) from the D_1 of Northern Ireland have a subcircular outline, are more strongly concavo-convex, and have shorter spine bases on the pedicle valve and weaker rugae on the brachial valve. Internally they have smaller dorsal adductor muscle scars, divergent lateral ridges, and a weaker dorsal median septum. A lamellose form, *K. lamellosa* Brunton (1966, pp. 225–228, pl. 13, figs. 8–16; pl. 14, figs. 1–19) also from the D_1 of Northern Ireland, is more regularly lamellose than *K. procidua*, lacks elongate spine bases, is more circular in outline, and has a smaller size.

The specific name is from the Latin *prociduus*, prostrate, and refers to the prostrate nature of spines on the pedicle valve.

Occurrence. Locality 92-1, the type locality, and locality 90-6 in an unnamed formation at Salisbury; locality L145 UNE in the Copeland Road Formation at Barrington, New South Wales, and locality 119-7 in the Mundubbera Sandstone at Mundubbera, Queensland. Late Viséan *R. fortimuscula* Zone.

Material. F57068–F57075 AM. Holotype F57069; paratypes F57068, F57072b.

Genus PHARCIDODISCUS nov.

Type species. Pharcidodiscus boulderensis gen. et sp. nov. from the Neils Creek Clastics, Mount Morgan, Queensland.

Diagnosis. Shell rounded-rectangular to subquadrate in outline, moderately concavo-convex, auriculate, and with a short dorsal anterior geniculation; ornament rugose posteriorly and costate anteriorly; on the pedicle valve, spines arising from spine ridges on the rugose portion of the valve, from crests of costae on the front of the visceral disc and trail, and also forming a single divergent row at the hinge; brachial valve aspinose; ventral adductor muscle scars divided by a low median ridge; dorsal adductor muscle scars smooth and in two pairs; median septum slender, arising in front of an alveolus in small specimens, but joined by a rod-like callus to the front of the cardinal process in large specimens; cardinal process bilobed internally and with medianly fused lobes posteriorly.

Remarks. Few productaceans are characterized by an ornament which is rugose posteriorly and costate anteriorly. *Semicostella* Muir-Wood and Cooper (1960), which has this type of ornament, resembles *Pharcidodiscus* in having smooth dorsal adductor muscle scars. *Semicostella*, however, has far fewer spines on the costae, less well-defined costae on the brachial valve, a more highly convex pedicle valve which possesses a short trail separated from the visceral disc by a cincture, lateral ridges which extend around the ears to the middle of the valve, a stronger dorsal median septum, prominent brachial markings, and a bilobate posterior face on the cardinal process. The spine ridges in some species of *Rhytiophora* Muir-Wood and Cooper (1960) tend to become elongate and form ridges resembling costae, but this is not a consistent feature of the genus. *Rhytiophora* is distinguished from *Pharcidodiscus* by the possession of long curving lateral ridges, dendritic outer adductor muscle scars in the brachial valve, and a rim-like extension to the trail. *Spinocarinifera* Roberts (1971), from the Tournaisian of the Bonaparte Gulf Basin in north-western Australia, has a spinose costate ornament on the anterior of the shell, but also lacks the strongly rugose posterior ornament.

The generic name is derived from the Greek *pharkidodes*—wrinkled, and *diskos*—disc, and refers to the rugose nature of the visceral disc.

Pharcidodiscus boulderensis gen. et sp. nov.

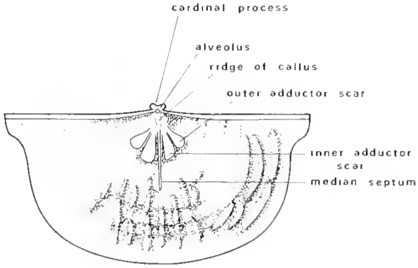
Plate 8, figs. 1–14

1970 *Semicostella*(?) sp., McKellar *et al.*, *in* Kirkegaard *et al.*, p. 149.

Diagnosis. Shell subrectangular to subquadrate, and strongly auriculate; ventral ornament comprising up to fourteen rugae on the posterior of the largest individuals, and irregular spinose costae with a density of 12–14 per 10 mm at 10 mm from the umbo; brachial valve with a similar number of rugae on the visceral disc, and with aspinose costae on the trail.

Description. External. Pedicle valve moderately convex on the visceral disc, evenly rounded across the venter, and with a steep elongate trail; valve highest around the mid-part and widest at the hinge; posterior portion ornamented by spine-bearing rugae, and the trail by irregular spinose costae; rugae high and well defined on the ears, extending as lower ridges across the visceral disc, and bearing erect spines; costae interfingering with the rugae at the posterior of the trail, irregular in width and height, bearing longitudinal rows of erect spines, and giving a strongly ribbed appearance to the trail; spines distributed in a row diverging from the hinge, in concentric rows on the crests of rugae, and in longitudinal rows on the trail; micro-ornament of concentric growth lines. Brachial valve having a moderately concave visceral disc, large flat auricles, and a short trail formed by an anterior geniculation; visceral disc with steep lateral margins, and slightly dimpled by depressions corresponding to spine bases on the pedicle valve; ears and visceral disc strongly rugose, large individuals having up to fourteen rugae; costae interrupting the rugae on the anterior of the visceral disc, and strongly developed on the trail; valve aspinose; specimens ranging in size up to 20 mm wide and 11 mm long.

Internal. Pedicle valve. Muscle field divided by a slender median ridge; muscle scars obscure; elongate radially arranged tubules, connected to the external spines, emerging from hollows in the floor at the posterior of the visceral disc. Brachial valve (text-fig. 15). Inner adductor muscle scars narrow posteriorly, usually widest anteriorly, and located on elevated muscle platforms; outer adductor muscle scars less well defined, and almost completely obscure in small specimens; median septum slender, highest at the anterior, and extending through a trough between the inner adductor muscle scars to the mid-length of the visceral disc; in small specimens the septum arises as a low narrow ridge in front of a circular alveolus; in large specimens a tapering rod-like callus extends from between the base of the cardinal process and the median septum; cardinal process with two convex lobes internally, and medianly fused lobes posteriorly; lateral ridges low, and extending along the hinge; brachial markings poorly defined; floor of valve surrounding the muscle field ornamented with fine radial granules; trail bearing small endospines.



TEXT-FIG. 15. Dorsal interior of *Pharcidodiscus boulderensis* gen. et sp. nov. drawn from F12143 GSQ. Approximately × 2.

Remarks. No other species referable to *Pharcidodiscus* are known. A productacean from slightly lower in the sequence at Mount Morgan, *Spinocarinifera kennedyensis* (Maxwell), is distinguished from *P. boulderensis* by its subovate pedicle valve, more prominent and incurved ventral umbo, smaller ears, spinose brachial valve, fainter rugose ornament on the posterior of both valves, and more regularly developed and finer costae.

Occurrence. P. boulderensis is known only from locality L955 GSQ in the Neils Creek Clastics, west of Boulder Creek, Mount Morgan. Late Tournaisian part of the *Schellwienella* cf. *burlingtonensis* Zone.

Material. F10258, F10259, F10260a, F10262a, F10263, F10268, F10269, F10270, F10271b, F10273b, F12143–F12146 all GSQ. Holotype F10269; paratypes F10260a, F10262a, F10268, F10273b, F12145.

Genus SPINOCARINIFERA Roberts, 1971

Type species. Spinocarinifera adunata Roberts, 1971 from the Tournaisian Burt Range Formation, Bonaparte Gulf Basin, north-western Australia.

Diagnosis. See Roberts (1971, p. 100).

Spinocarinifera kennedyensis (Maxwell)

Plate 8, figs. 15–29

1954 *Avonia kennedyensis* Maxwell, p. 23, pl. 2, figs. 13-16.
1964 *Avonia kennedyensis* Maxwell, *in* Hill and Woods, pl. 6, figs. 11-14.

Diagnosis. Shell longer than wide and moderately concavo-convex; pedicle valve with a slightly flattened venter and an elongate trail; spines subprostrate posteriorly but not forming a strong group at the ears; brachial valve with a short anterior geniculation, and spines arranged in poorly defined concentric rows; dorsal adductor muscle scars divided into two pairs.

Description. External. Pedicle valve subround to subovate in outline, slightly wider at the mid-length than at the hinge, and having a constriction immediately in front of the hinge; umbo prominent, and separated by steep concave umbonal shoulders from small, flat auricles; umbonal regions ornamented by weak rugae and spine ridges; rugae becoming obsolete at about one-quarter the length of the valve, but well defined on the umbonal shoulders; costae discontinuous and crossed by weak rugae on the anterior part of the visceral disc, but continuous and usually evenly spaced on the venter and trail; costae increasing by bifurcation and intercalation, and having a density of 14–16 per 10 mm at 10 mm from the umbo; subprostrate spines originating from spine ridges on the umbo, and erect spines arising from the crests of costae on the venter and on the trail. Brachial valve round to subquadrate in outline, with flat to slightly concave ears; rugae strongest on the ears and on the lateral shoulders but also extending across the posterior of the visceral disc; up to seventeen rugae on the visceral disc of a mature valve; anterior half of the visceral disc and the trail ornamented by well-defined rounded costae bearing ill-defined concentric rows of subcircular erect spines; specimens range in size up to 22 mm long and 18 mm wide.

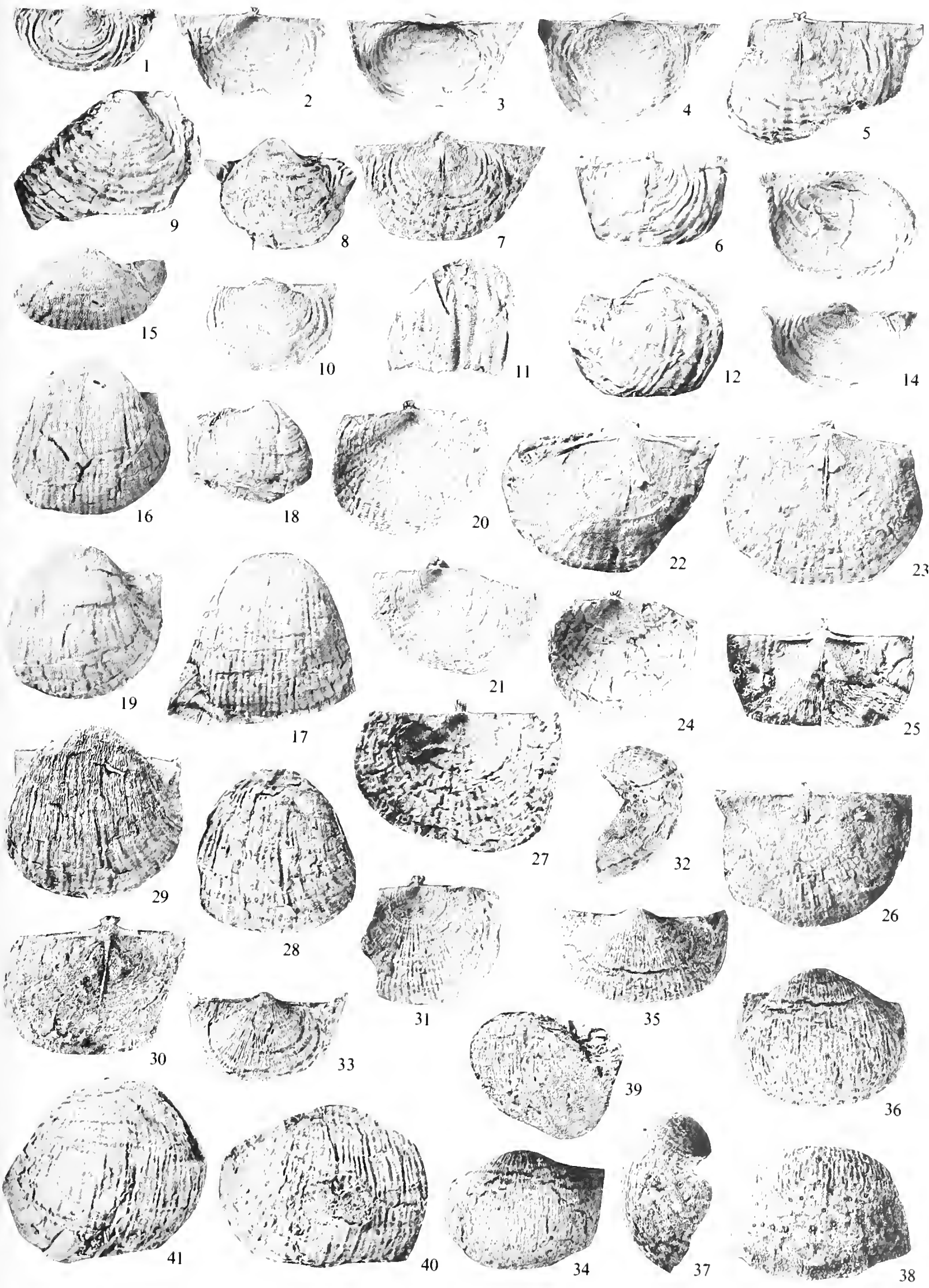
EXPLANATION OF PLATE 8

Figs. 1-14. *Pharcidodiscus boulderensis* gen. et sp. nov. 1, rubber cast of apical portion of pedicle valve. F10268 GSQ, × 1·5 paratype. 2–4, rubber casts of the exteriors of three brachial valves. F10260a GSQ, a paratype, F10259 GSQ, and F10263 GSQ respectively. All × 1·5. 5–7, rubber casts of three brachial valve interiors. F12143 GSQ, F10270 GSQ, and F10269 GSQ, the holotype, × 2, × 1·5, and × 1·5 respectively. 8–10, rubber casts of the exteriors of three pedicle valves. F10258 GSQ, F12144 GSQ, and F10262a GSQ a paratype. All × 1·5. 11–12, rubber casts of the anterior and antero-lateral parts of two pedicle valves. F10271b GSQ and F12145 GSQ, paratype, × 1·5. 13, rubber cast of a brachial valve exterior. F12146 GSQ, × 1·5. 14, rubber cast of a pedicle valve interior. F10273b GSQ, × 1·5, paratype. Figs. 1–14 from locality L955 GSQ.

Figs. 15-29. *Spinocarinifera kennedyensis* (Maxwell). 15–17, posterior and anterior views of the ventral internal mould of F10217a GSQ, and rubber cast of the exterior of F10217b GSQ. All × 1·5. 18, rubber cast of a pedicle valve exterior. F10220 GSQ, × 1·5. 19, internal mould of a pedicle valve. F10226a GSQ, × 1·5. 20–21, rubber casts of two brachial valve exteriors F10223 GSQ and F10219a GSQ, × 1·5. 22–23, rubber casts of two brachial valve interiors. F10219b GSQ and F10235 GSQ, × 2. Figs. 15–23 from locality K91 GSQ. 24, rubber cast of a brachial valve exterior from L244 GSQ. F12147, × 1·5. 25, rubber cast of a brachial valve interior. F67154 UQ, × 1·5. 26, rubber cast of a brachial valve interior. F15154 UQ, the holotype, × 1·5. Figs. 25 and 26 from L1288 UQ. 27, rubber cast of a topotype brachial valve. F57041, × 1·5. 28–29, rubber cast of the exterior, and an internal mould of a topotype pedicle valve. F57042, × 1·5. Figs. 27–29 from locality 121-2 which equals L1288 UQ.

Figs. 30-41. *Antiquatonia spinulicosta* sp. nov. 30, rubber cast of a brachial valve interior. F57043, × 1·5. 31, rubber cast of a brachial valve exterior. F57044, × 1. 32–34, lateral, posterior, and anterior views of the internal mould of a pedicle valve. Note the row of spines down the flanks. F57045, × 1. 35–38, posterior, ventral, anterior, and lateral views of the internal mould of pedicle valve. F57046, × 1. 39–40, rubber casts of the anterior and antero-lateral parts of two pedicle valve exteriors showing the spinose ornament. F57047, × 1, and F57048, × 1·5 respectively. Figs. 30–40 from locality L203 UNE. 41, rubber cast of a pedicle valve exterior. F57034b, × 1·5 from locality 10026 ANU.

PLATE 8



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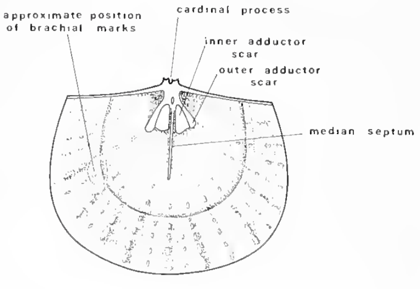
Internal. Pedicle valve. Adductor muscle scars subrectangular, slightly wider anteriorly than posteriorly, bearing longitudinal striations, and separated by a low median ridge; diductor muscle scars flabellate, also radially striated, and slightly less well defined; internal surface of valve bearing fine granular micro-ornament. Brachial valve (text-fig. 16). Inner adductor muscle scars triangular in outline, low and pointed posteriorly, and having a high bulbous anterior extremity; outer adductor scars lower, and also triangular in outline; median septum originating from a broad callus or from in front of a small alveolus at the anterior margin of the cardinal process, and extending to the middle of the visceral disc; lateral ridges variable in strength and parallel with the hinge (one specimen from locality K91 (Pl. 6, fig. 22) has lateral ridges which diverge slightly from the hinge); cardinal process with two convex lobes internally and medianly fused lobes posteriorly; brachial ridges faint, diverging from the antero-lateral margins of the adductor muscle scars at about 40° and enclosing partly smooth subquadrate brachial discs; visceral disc bearing a granular ornament similar to that on the interior of the pedicle valve; anterior part of the visceral disc and the trail with radially arranged endospines.



TEXT-FIG. 16. Dorsal interior of *Spinocarinifera kennedyensis* (Maxwell) drawn from F10235 GSQ. Note the subdivision of the adductor muscle scars. Approximately ×2.

Remarks. S. kennedyensis (Maxwell) has a number of morphological features which separate it from the type species, *S. adunata* Roberts (1971, pp. 101–104, pl. 19, figs. 1–18; pl. 20, figs. 9–16). Externally, *S. kennedyensis* is more elongate, has a less convex pedicle valve, possesses irregular rows of small spines on the brachial valve, and appears to lack a group of large halteroid spines on the postero-lateral extremities. Internally the two species are morphologically close, the only difference being the possession by *kennedyensis* of two pairs of dorsal adductor muscle scars; a specimen of *S. adunata* figured by Roberts (1971, pl. 20, fig. 16) may in fact show a very poorly defined second pair of adductor scars on the lateral margins of well-defined inner adductor muscle scars.

When compared with *S. niger* (Gosselet) from the Etroeungt and early Tournaisian of France (Dehee 1929, pp. 39–41, pl. 4, figs. 1–6), *S. kennedyensis* has the same external differences established in the comparison with the type species. The external ornament of *S. kennedyensis* is close to that of *S.*? *arcuata* (Hall) from the Kinderhook of Missouri and Iowa (Weller 1914, pp. 107–108, pl. 13, figs. 1–12). *S.*? *arcuata*, however, has a more convex pedicle valve, and a more strongly geniculate brachial valve.

Occurrence. Locality 1288 UQ (equals 121-2), the type locality, in the Pond Formation at Mount Morgan, Queensland; locality 956 GSQ in the Pond Formation, Gelobera Range, Mount Morgan; locality K91 GSQ in the uppermost part of the Crana Beds west-north-west of Dakiel, Queensland; locality 244 GSQ from Mount St. Michael in the Star Basin, Queensland; and in locality L1312 UNE in the Luton Formation near Bingara, New South Wales. Tournaisian *Tulcumbella tenuistriata* Zone, and possibly equivalents of the *Spirifer sol* Zone.

Material. F57041–F57042 AM. F10217a and b, F10219a and b, F10220, F10223, F10226a, F10235, F12147 GSQ. F15154, F67154 UQ.

Genus SPINORUGIFERA nov.

Type species. Spinorugifera chichesterensis gen. et sp. nov. from locality 106-1, in the Flagstaff Sandstone, Upper Chichester, New South Wales.

Diagnosis. Shell gently to moderately biconvex, having an evenly curved lateral profile and lacking a well-defined trail; pedicle valve with a short tapering umbo, well-differentiated ears, a small number of posteriorly projecting spines near the hinge, and a triangular muscle field; ventral surface rugose to partly lamellose, the rugae bearing concentric rows of widely spaced erect to suberect spines; brachial valve rugose, usually aspinose and with flat postero-lateral extremities; cardinal process bilobate, supported by short divergent lateral ridges, and bordered anteriorly by an alveolus and a breviseptum; dorsal adductor muscle scars smooth and in two pairs, an elevated inner pair and a slightly impressed outer pair; brachial ridges narrow and hook-shaped.

Remarks. Spinorugifera gen. nov. is similar in many respects to the early Carboniferous genus *Rugauris* Muir-Wood and Cooper (1960), having a rugose ornament which bears concentric rows of spines, and a row of spines on the posterior of the pedicle valve. *Rugauris* is distinguished from *Spinorugifera* by the possession of a geniculate brachial valve, a trilobed cardinal process which is supported anteriorly by the thickened base of the median septum, dendritic dorsal adductor muscle scars, and in the detailed configuration of the external ornament: on the pedicle valve spines are prostrate rather than erect, and they are rare on the visceral disc; and on the brachial valve rugae are narrower and more numerous than those on the pedicle valve, and are replaced by growth lines on the trail.

The Russian genus *Jakutoproductus* Kaschirtsew, 1959 (Abramov 1970, pl. 7, figs. 1–10) also has a spine-bearing rugose ornament, but is distinguished from *Spinorugifera* by the possession of larger spine bases, a narrow but prominent ventral median sinus and corresponding dorsal fold, different musculature in both valves, a dorsal marginal rim in the brachial valve, and brachial ridges which appear to originate nearly horizontally from the dorsal adductor muscle scars.

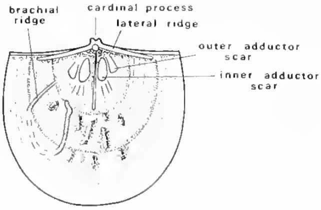
Spinorugifera chichesterensis gen. et sp. nov.

Plate 7, figs. 1–18

1975 Productoid n. gen., Roberts, Table 1.

Diagnosis. Pedicle valve rounded-rectangular to subquadrate in outline, with a low umbo, well-defined umbonal shoulders, and four long curving spines near the hinge; brachial valve moderately to strongly concave, with a breviseptum which extends one-third the length of the valve, and short divergent lateral ridges.

Description. External. Pedicle valve gently to moderately convex, evenly convex in profile and without a well-defined trail; valve constricted immediately in front of the hinge, the greatest width being either at the hinge or at the mid-length; umbo narrow, and extending a short distance behind the hinge line; postero-lateral margins flat to slightly convex, and slightly auriculate; surface of valve with irregular partly lamellose rugae bearing scattered spines, and concentric growth lines; spines on the body of the valve situated mainly on the rugae, arranged in a roughly concentric pattern, widely spaced, erect to suberect, and having slightly elongate bases with diameters of up to approximately 0·2 mm; two long spines on either side of the umbo are slightly larger in diameter than the body spines, and originate normal to the hinge. Brachial valve with an evenly concave visceral disc and broad flat to concave postero-lateral extremities; valve strongly rugose and to a lesser extent lamellose, the rugae extending irregularly across the venter, but being more pronounced and regular on the postero-lateral margins; most specimens aspinose, but one small individual bearing minute suberect spinules arranged in irregular concentric rows; specimens ranging in size up to 17 mm wide and 14 mm long.



TEXT-FIG. 17. Dorsal interior of *Spinorugifera chichesterensis* gen. et sp. nov. drawn from F57027 AM, a paratype. Approximately ×2·5.

Internal. Pedicle valve. Muscle field triangular in outline, but not clearly differentiated into adductor and diductor muscle scars; spine bases opening into the interior of the valve. Brachial valve (text-fig. 17). Cardinal process bilobate, each of the lobes being subdivided by a deep sulcus; median septum narrow, low, and arising from in front of an alveolus; adductor muscle scars smooth; inner adductor muscle scars forming low subovate platforms, and outer adductor muscle scars slightly impressed, tapered posteriorly and expanding anteriorly; brachial ridges arising at a high angle (approximately 40°) from the front of the outer adductor scars, and having high distal extremities in front of the inner adductor scars; internal surface bearing fine radially arranged endospines.

Remarks. S. chichesterensis gen. et sp. nov. is the only known species of the genus. A morphologically similar form referred to *Rugauris*? *brookeri* sp. nov. from the Woolooma Formation at Malumla in the Rouchel district of New South Wales is compared with this species on p. 57.

Occurrence. Locality 106-16, the type locality, in the Flagstaff Sandstone, Upper Chichester, New South Wales. Viséan *Inflatia elegans* Subzone.

Material. F57019–F57030 AM. Holotype F57025a–c; paratypes F57026, F57027.

EXPLANATION OF PLATE 9

Figs. 1–12. *Rugauris*? *brookeri* sp. nov. 1–2, internal moulds of two pedicle valves. F57049, the holotype, and F57050, ×1·5. 3–4, rubber casts of the exterior of two pedicle valves. F57051a, a paratype, and F57052, ×1·5. 5, internal mould of F57051b, the counterpart of fig. 3, ×1·5. 6, rubber cast of a pedicle valve exterior. F57051c, ×1·5. 7–9, rubber casts of three brachial valve exteriors. F57053, a paratype, F57054, and F57055 a paratype, ×1·5. The spines on fig. 9 come from the pedicle valve. 10, internal mould of a distorted pedicle valve. F57056, ×1·5. 11, rubber cast of a pedicle valve interior. F57057, ×1·5. Note the tubules on the interior of the valve. 12, rubber cast of a brachial valve interior. F57058, ×1·5. Figs. 1–12 from locality 29-1.

Figs. 13–23. *Scoloconcha geniculata* sp. nov. 13–14, rubber casts of the exterior and interior of a pedicle valve. Note the spine apertures on the interior of the valve. F57059, ×3. 15, rubber cast of a pedicle valve exterior. F57060, ×3. 16–17, rubber casts of a specimen showing the apical parts of the pedicle valve and the brachial valve interior and exterior. F57061a and b, ×3. 18, rubber cast of a brachial valve interior. F57062, ×3. Figs. 13–18 from locality 85-10. 19, rubber cast of a brachial valve interior. F57063, the holotype. 20, rubber cast of a brachial valve exterior. F57064, a paratype, ×3. Figs. 19–20 from locality 17-8. 21, rubber cast of a pedicle valve exterior from locality 16-3. F57065, ×3. 22, rubber cast of a brachial valve exterior from locality 17-7. F57066, ×3. 23, rubber cast of a pedicle valve exterior from locality 74-7A. F57067, ×3.

Figs. 24–33. *Krotovia procidua* sp. nov. 24, rubber cast of a distorted brachial valve interior. F57068, a paratype, ×1·5. 25–26, rubber casts of the dorsal interior and exterior of the holotype. F57069, ×1. 27, internal mould showing the apicle portion of the pedicle valve and the anterior of the brachial valve. F57070, ×1. 28, distorted internal mould of the pedicle valve. F57071, ×1. 29–30, rubber casts of the exterior of two brachial valves. F57072a and F57073, ×1·5. 31, rubber cast of the exterior of a pedicle valve. F57072b, a paratype, ×1. Figs. 24–31 from locality 92-1. 32, rubber cast of a pedicle valve exterior showing slightly more erect spines. F57074, ×1·5. 33, internal mould of a pedicle valve. F57075, ×1·5. Figs. 32 and 33 from locality L145 UNE.

PLATE 9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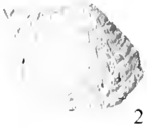
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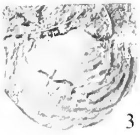
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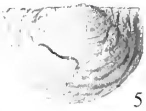
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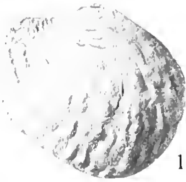
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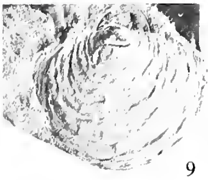
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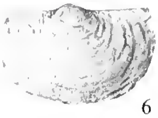
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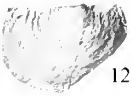
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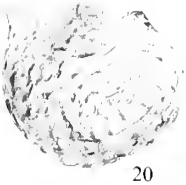
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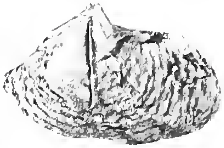
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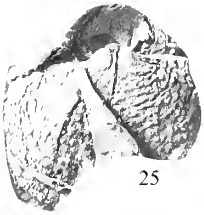
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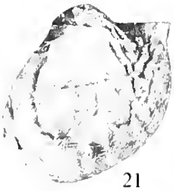
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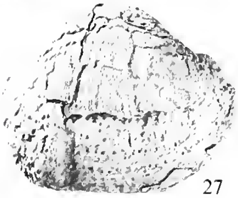
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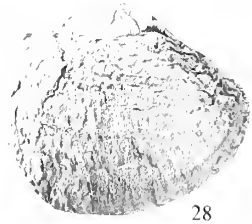
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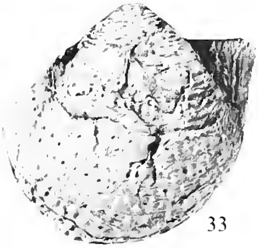
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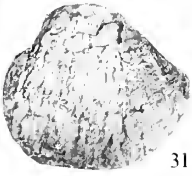
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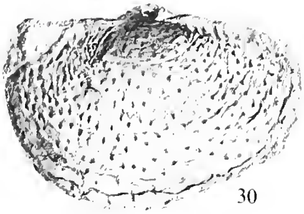
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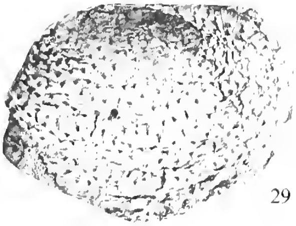
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ROBERTS, Australian productaceans

Genus STEGACANTHIA Muir-Wood and Cooper, 1960

Type species. Stegacanthia bowsheri Muir-Wood and Cooper, 1960 from the Lake Valley Formation, New Mexico.

Diagnosis. See Muir-Wood and Cooper (1960, p. 198).

Stegacanthia leviatha sp. nov.

Plate 10, figs. 1-8

Diagnosis. Shell extremely large, semi-ovate in outline, and with a finely spinose external ornament; pedicle valve having a narrow median sinus; brachial valve with a low median fold and a short trail; lateral ridges thickened at the cardinal process; median septum extending two-thirds the length of the valve; front of visceral disc and trail bearing coarse endospines.

Description. External. Pedicle valve strongly convex posteriorly, having a swollen umbo, steep umbonal shoulders, and convex ears; median sinus commencing on the umbo and forming a narrow furrow along the length of the valve; concentric lamellae usually bearing single rows of prostrate spines, but on some, spine bases emerging from the posterior of a lamella alternating with bases arising from near the front of the lamella; spines near the hinge erect and divergent; approximately fifteen spine bases present along 10 mm of a lamella near the anterior margin. Brachial valve. Large specimens having a short rim-like trail produced by a small anterior geniculation; fold narrow, commencing in front of a small umbonal concavity, and extending on to the trail; concentric ornament of low rugae on posteromedian parts of the valve, but elsewhere lamellose; concentric lamellae crowded on the trail, more widely spaced on the visceral disc, ornamented by closely spaced growth lines, and bearing single rows of long prostrate spines; spines much denser on the trail than on the visceral disc with up to 40 spines per 10 mm on the trail of a large specimen compared with 12-15 per 10 mm at 20 mm from the umbo; small erect spines forming one or possibly two rows near the hinge; specimens ranging in size up to 86 mm wide and 64 mm long.

Internal. Pedicle valve. Diductor muscle scars elongate, pointed posteriorly, rounded anteriorly, and situated on high platforms separated by a low median ridge; adductor muscle scars large, flabellate, strongly striated, and impressed into the shell. Brachial valve. Adductor muscle scars obscurely subdivided into a dendritic posterior pair and smooth anterior pair; posterior scars subround to elongate, impressed, in large specimens diverging laterally from buttresses in front of the cardinal process and flanking the anterior scars; anterior muscle scars trigonal to subround, usually forming elevated platforms, but occasionally lower and nearly level with the floor of the valve; median septum buttressing the base of the cardinal process, wide rounded and high posteriorly, and narrow near the front of the muscle field; cardinal process with two elongate internal lobes separated by a deep furrow; posterior face of process with a wedge-shaped median ridge at the junction between the two deeply concave lobes; lateral ridges straight and parallel with the hinge in small specimens, but in large individuals laterally diverging from the hinge; brachial ridges originating horizontally from the front of the muscle field; brachial discs large, smooth, and subround; fine pits present on thickened areas of the shell on the postero-lateral margins of the muscle field of large specimens; the remainder of the visceral disc and the trail bearing prostrate endospines.

EXPLANATION OF PLATE 10

Figs. 1-8. *Stegacanthia leviatha* sp. nov. 1, rubber cast of a brachial valve interior. F10461b GSQ, holotype, × 1. 2-3, rubber casts of the interior and exterior of a brachial valve. F10464b GSQ and F10464a GSQ, × 1. 4, rubber cast of the apical portion of a brachial valve. F12148 GSQ, × 1. 5, rubber cast of a brachial valve interior. F10462b GSQ, paratype, × 1. 6, rubber cast of the exterior of a pedicle valve. F10465 GSQ, paratype, × 1. 7, rubber cast of a brachial valve exterior. F10462a GSQ, paratype, × 1. Figs. 1-7 from locality L988 GSQ. 8, internal mould of a pedicle valve. F30198 UQ from locality L2187 UQ, × 1.

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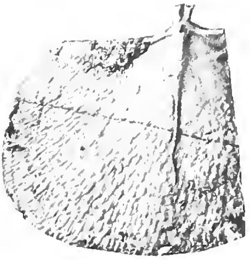

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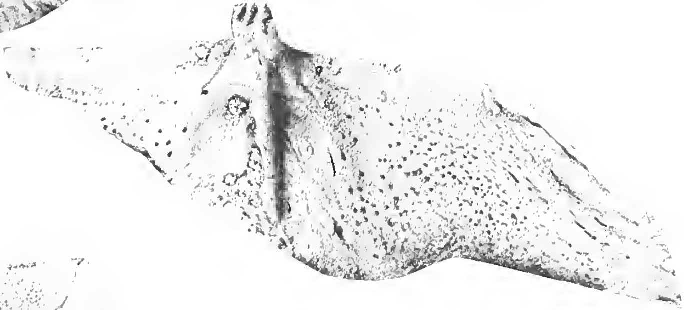

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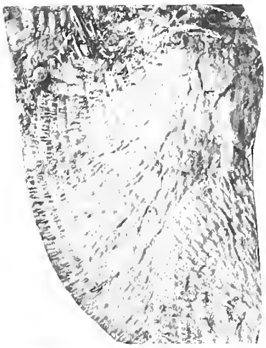

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ROBERTS, Australian productaceans

Remarks. Specimens of *Stegacanthia larga* (Cvancara) (1958, pp. 864–865, pl. 110, figs. 14–19) from Barrington, New South Wales, are morphologically comparable to some of the smaller specimens of *S. leviatha*: features which are close include the finely spinose external ornament, the fold and sinus, the cardinal process, lateral ridges, median septum, and the outline of the dorsal muscle field. When compared with *S. larga*, *S. leviatha* is much larger, more transverse, and has a short dorsal anterior geniculation. In the interior of the brachial valve the muscle field is larger but not entirely set on high platforms as in *S. larga*, the lateral ridges are divergent from the hinge line, and there are very coarse endospines around the front of the visceral disc and on the trail. In Queensland *S. larga* is present in the Baywulla Formation at locality K63 GSQ near Monto, and in the Lion Creek Limestone near the Stanwell–Dalma road.

S. strigis Roberts (1971, pp. 118–120, pl. 27, figs. 1–9) from the Utting Calcarenite and Burvill Beds of the Bonaparte Gulf Basin resembles *S. leviatha* in size and in the possession of a fold and sinus. *S. strigis* is distinguished by the possession of a coarser spinose ornament, a more dorsally recurved cardinal process, slightly more divergent lateral ridges, and a shorter dorsal median septum; large individuals of *S. strigis* lack the massive thickening around the dorsal muscle field and cardinal process, but this may be of ontogenetic rather than of specific significance. *S. sibirica sibirica* (Sarycheva) from the late Tournaisian and early Viséan of the Kuznetsk Basin, Siberia (Sarycheva *et al.* 1963, pl. 18, figs. 1–3), is smaller, and has a weaker median sinus. The internal morphology of the Russian subspecies has not been illustrated, but a closely related form *S. s. artyshtensis* (Sarycheva) figured by Sarycheva *et al.* (1963, pl. 17, fig. 4, and fig. 59) has a dorsally recurved cardinal process.

Occurrence. Locality 988 GSQ, the type locality (equals L2187 UQ), in the Baywulla Formation at 43169275, Major Mitchell Creek, Monto 1:100000 Sheet, Kalpowar, Queensland. Late Viséan to Early Namurian *Marginirugus barringtonensis* Zone.

Material. F10461b, F10462a and b, F10464a and b, F10465, F12148 GSQ. F30198 UQ. Holotype F10461b; paratypes F10462a and b, F10465.

Genus RUGAURIS Muir-Wood and Cooper, 1960

Type species. Rugauris paucispina Muir-Wood and Cooper, 1960 from the Lower Kinderhook oolitic limestone, Iowa.

Rugauris? *brookeri* sp. nov.

Plate 9, figs. 1–12

1975 *Rugauris* sp., Roberts, Table 1.

Diagnosis. Pedicle valve subrectangular to subquadrate in outline, and having small ears; hinge slightly less than the greatest width of the valve; spines near the hinge medianly coiled; ten rugae on the exterior of mature individuals; brachial valve aspinose; rugae branching on the umbonal shoulders and up to eighteen in number on the visceral disc.

Description. External. Shell of average size for the genus, moderately concavo-convex, widest at the mid-length; individuals ranging in size up to 20 mm wide and 16 mm long. Pedicle valve with an evenly rounded venter, highest at about one-third the length of the valve, and with flat ears; umbo low, tapered, and weakly incurved; rugae strongest on the umbonal shoulders, extending across the venter, and up to ten in number on large individuals; spine ridges originating on or between the rugae, arranged in concentric rows, and subtending prostrate spines; spine ridges short on the posterior and median parts of the valve, but longer anteriorly; a single row of about twelve erect spines originating from larger spine bases near the hinge, and curving behind the umbo; a group of larger suberect spines also present on the postero-lateral extremities. Brachial valve with flat auriculate postero-lateral extremities; in large individuals a slight anterior geniculation produces a short trail; exterior of valve bearing depressions between the rugae in positions corresponding to the spine ridges on the pedicle valve; rugae strongest on the postero-lateral margins, continuous across the visceral disc, slightly irregular, and becoming bunched on the trail; from ten to twelve rugae present along the hinge of large individuals, but branching on the umbonal shoulders and increasing in number to eighteen on the visceral disc.

Internal. Pedicle valve. Adductor muscle scars subtriangular to subovate in outline, and separated by a faint median ridge; diductor muscle scars not observed; internal surface bearing impressions of the external rugae, and very fine endospines; posterior half of the visceral disc bearing elongate radially oriented hollow tubules connected with the external spines; other spines having subcircular openings into the interior of the valve. Interior of brachial valve unknown.

Remarks. The present material is tentatively referred to *Rugauris* because of similarities in shape and external ornament. The features of the brachial valve interior, which are particularly distinctive in *Rugauris*, are unknown and it is possible that this form belongs to another genus. When compared with *R.*? *brookeri* sp. nov., *R. paucispina* Muir-Wood and Cooper (1960), the type species, has larger ears, a relatively wider hinge, a more abrupt geniculation at the front of the brachial valve, and a spinose dorsal exterior.

Spinorugifera chichesterensis gen. et sp. nov. from the Flagstaff Sandstone at Upper Chichester, New South Wales, is a spiney rugose productacean with features similar to those of *R.*? *brookeri* sp. nov. It is difficult to make a complete comparison between the two forms because the brachial valve interior of *R.*? *brookeri* is unknown, but it is clear that they belong to different species and genera: *S. chichesterensis* is characterized by the possession of a broader and higher ventral umbo, steeper umbonal shoulders, and the absence of an anterior geniculation on the brachial valve; externally, the spines are erect rather than prostrate, and arise from bases which are larger in diameter but shorter than the spine ridges of *R.*? *brookeri*, and there is a greater number of rugae, some of which are lamellose.

Occurrence. Locality 29-1 (the type locality) in the Woolooma Formation at Malumla, Rouchel district, New South Wales. Viséan *Orthotetes australis* Zone.

Material. F57049–F57058 AM. Holotype F57049; paratypes F57051a, F57053, F57055.

Family MARGINIFERIDAE Stehli, 1954
Subfamily MARGINIFERINAE Stehli, 1954
Genus EOMARGINIFERA Muir-Wood, 1930

Type species. Productus longispinus J. Sowerby, 1814.

Remarks. Brunton (1966) amended the concept of *Eomarginifera* by the recognition of a subgenus, *Eomarginiferina*, which is distinguished by its globose profile, three symmetrically arranged spines on the body of the pedicle valve, and the absence of hinge spines; an anterior fold is present on many specimens. The present material resembles the type species of *Eomarginiferina*, *E. trispina* Brunton, in having a similar profile and pronounced ears, but it is distinguished by the possession of a greater number of body spines and spines near the hinge on the pedicle valve, and the absence of a ventral anterior fold.

Eomarginifera (*Eomarginifera*) *megalotis* sp. nov.

Plate 11, figs. 13–26

1960 *Dictyoclostus paradoxus* Campbell; Maxwell, pp. 4–5, pl. 1, figs. 8–12.
1964 *Eomarginifera paradoxa* (Campbell); Hill and Woods, pl. 6, figs. 22–27.
1975 *Eomarginifera* sp., Roberts, Table 1.

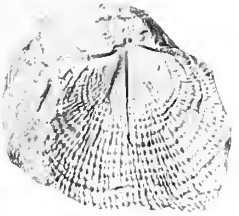
Diagnosis. Shell with prominent well-differentiated auricles and a narrow ventral umbo; costellae having a density of 10–12 per 5 mm at 10 mm from the umbo; brachial valve with a sharp anterior geniculation; marginal ridge extending across the ears to the mid-part of the lateral margins; median septum narrow, commencing well in front of the cardinal process and extending to the mid-point of the valve.

Description. External. Shell slightly smaller than average for the genus, semicircular in outline, and widest at the hinge; specimens ranging in size to 19·5 mm wide and 15·5 mm long. Pedicle valve with well-differentiated flat auricles; umbo small and gently incurved; costellae increasing by bifurcation and intercalation, and frequently bearing small spine bases behind points of bifurcation; costellae on the trail more regular than those on the visceral disc; rugae low, crossing the visceral disc, producing a faintly reticulate ornament, and numbering thirteen or fourteen on a large individual; five large halteroid spines, more than 20 mm long, extending in a row around the lateral slopes and the trail; two smaller erect spines along the hinge on each of the postero-lateral extremities, and smaller probably low-angle spines arising from costae on the visceral disc. Brachial valve. Visceral disc flat to gently convex; ears separated by a strong ridge from nearly vertical lateral slopes; anterior margin of valve geniculate and produced into a curved trail; rugae extending across the visceral disc but absent from the ears and trail.

EXPLANATION OF PLATE 11

Figs. 1–12. *Marginicinctus reticulatus* sp. nov. 1–3, a mould and rubber cast of the dorsal interior, and a rubber cast of the ventral exterior of the holotype. F57076a and b, ×1. 4–5, internal mould and rubber cast of the exterior of a pedicle valve. F57077, ×1. Figs. 1–5 from locality 88-3. 6, rubber cast of a pedicle valve exterior showing the prominent cincture and flange. F57078, ×1. 7, coiled spines at the apex of a pedicle valve. F57079, ×2. 8, rubber cast of a brachial valve exterior and coiled spines from the pedicle valve. Note the prominent flange. F57080, ×1. 9, external mould of a brachial valve showing a partly preserved flange. F57081, ×1. Figs. 6–9 from locality L466 U Newcastle. 10, rubber cast of a brachial valve interior from locality 85-8. F57082, ×1·5. 11, rubber cast of a pedicle valve exterior from locality L577 U Newcastle. F57083, ×1·5. 12, rubber cast of a brachial valve interior from locality 89-1. F57113, ×1·5.

Figs. 13–26. *Eomarginifera megalotis* sp. nov. 13, rubber cast of a brachial valve interior. F57084, ×2. 14, mould of a dorsal interior. F57085, the holotype, ×2. 15, internal mould of a pedicle valve. F57086, paratype, ×2. 16, rubber cast of a pedicle valve exterior showing the configuration of spines. F57087, paratype, ×2. 17–18, anterior and dorsal views of an external mould of the brachial valve showing the sharply geniculate trail and large ears. F57088, a paratype, ×2. 19–20, ventral and lateral views of an internal mould of the pedicle valve. Note the large spine bases. F57089, ×2. 21–22, rubber casts of the exteriors of a pedicle and a brachial valve. F57090 and F57091, both paratypes, ×2. 23–24, rubber casts of two pedicle valve exteriors. F57092, and F57093 a paratype, ×2. Figs. 13–24 from locality 92-1. 25–26, rubber cast of the dorsal interior, and internal mould of the ventral interior of a specimen from locality K31 GSQ. The strength of the muscle scars and brachial ridges suggest the specimen is gerontic. F10453a GSQ.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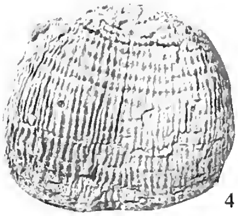
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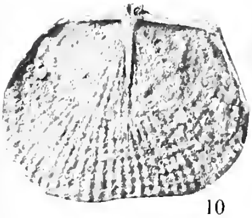
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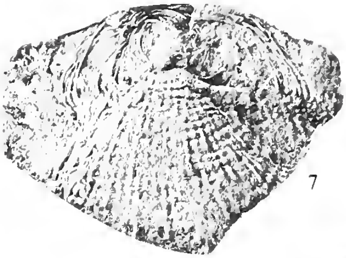
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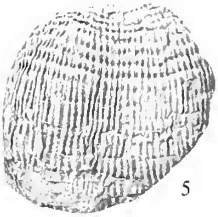
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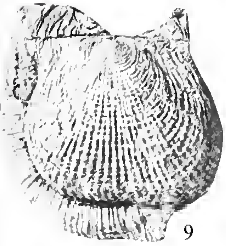
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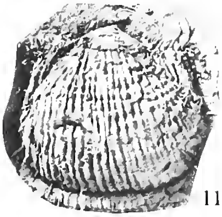
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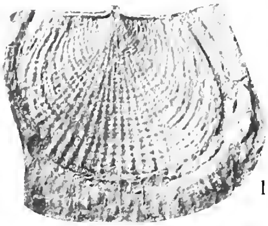
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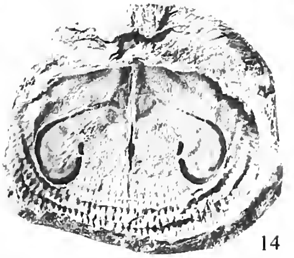
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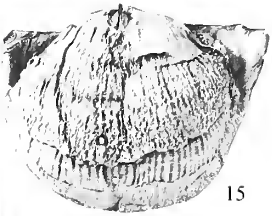
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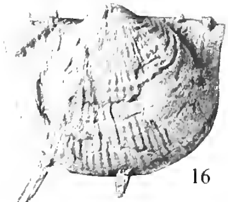
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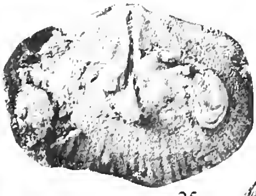
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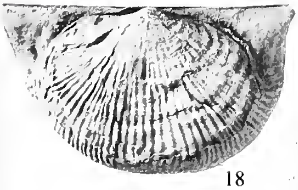
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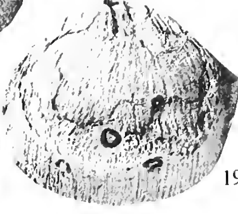
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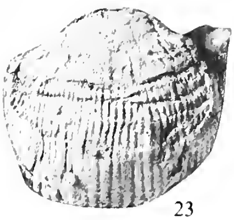
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ROBERTS, Australian productaceans

Internal. Pedicle valve. Adductor muscle scars narrow, rectangular, situated on high muscle platforms, and separated by a narrow median ridge; diductor muscle scars large, flabellate, and bearing longitudinal grooves and ridges; internal surface bearing small pustulose endospines, and openings of the large halteroid spines; ears separated from the visceral region by ridge-like swellings. Brachial valve. Cardinal process bilobed internally, and bordered anteriorly by two elongate ridges, possibly muscle tracks, on either side of a median furrow; posterior face of process not observed; inner adductor muscle scars smooth, subround to subquadrate, and located on platforms immediately in front of the elongate ridges; outer adductor muscle scars weakly dendritic, slightly impressed, and subround in outline; median septum slender, and arising from the trough between the anterior adductor scars; brachial ridges originating at a low angle from the front of the outer adductor muscle scars, and having discontinuous distal terminations; endospines small and situated on radial ribs.

Remarks. A number of specimens from locality K31 in the Dakiel Formation, Queensland, have strongly sculptured internal features and appear to be gerontic individuals; these are exemplified by the specimen illustrated in Plate 11, figs. 25–26. In the pedicle valve the adductor muscle scars are deeply impressed and strongly dendritic posteriorly, and form a high platform anteriorly. The diductor muscle scars are flabellate, smooth and pointed posteriorly, and wide and longitudinally ribbed anteriorly. The dorsal adductor muscle field is located well in front of the cardinal process, the inner adductor muscle scars being located at the anterior of ridge-like muscle tracks. The median septum is short, commences at approximately one-third the length of the valve between the inner adductor scars, and rises to a short high spine-like septum. Brachial ridges originate at low angles from the outer adductor muscle scars and enclose elevated ovoid brachial discs.

E. paradoxa (Campbell) (Campbell 1957, pp. 60–62, pl. 13, figs. 9–17) has an external ornament similar to that of *E. megalotis*. It is distinguished from *megalotis* by the possession of a shorter hinge, smaller ears, and a wider ventral umbo. Internally, the median septum forms a broad rounded ridge immediately in front of the cardinal process, the septum has a knob-like termination, and the brachial ridges are weaker. *E. tenuimontis* Roberts (1965*b*, pp. 61–63, pl. 10, figs. 6–10) is larger, has smaller ears, coarser costellae, fewer rugae, a small fold and sinus, and a more concave dorsal visceral disc. Internally *tenuimontis* is distinguished from *megalotis* by its coarsely striated diductor muscle scars in the pedicle valve, stronger median septum which forms a broad ridge near the front of the cardinal process, and the possession of an anterior knob on the median septum, and larger and strongly dendritic outer dorsal adductor muscle scars.

The type species, *E. longispina* (Sowerby), described by Muir-Wood (1928, pp. 156–163, pl. 11, figs. 1–4) from the Viséan and early Namurian of Great Britain, has finer costae, and fewer and weaker rugae over the visceral disc. *E. frechi* Paeckelmann (1931, pp. 339–341, pl. 41, figs. 7–10) appears to be morphologically close to *E. megalotis*, having wide ears which are well differentiated from the body of the shell, a comparable lateral profile, and a similar density of costellae. The internal features of *E. frechi* are undescribed. *E. frechi* is recorded from the Oberen Kohlenkalk at Altwasser and Hansdorf, Germany. *E. kaschirica* Ivanov, from the C_2 of the Moscow Basin, illustrated by Sarycheva and Sokolskaya (1952, pl. 45, fig. 235), resembles *E. megalotis* in the shape of the pedicle valve; the valve has a similar outline and convexity, well-defined auricles, and a comparable costellate ornament. Other details of *E. kaschirica* are not illustrated.

Occurrence. Localities 92-1, the type locality, 90-5, 90-6, and possibly 103-3 in an unnamed formation at Salisbury, New South Wales. In Queensland the species is identified at locality K31 GSQ, Dakiel Formation, locality L1920 UQ, Baywulla Station; and from a locality 5·5 km south-east of Bancroft. Late Viséan *Rhipidomella fortimuscula* Zone.

Material. F57084–F57093 AM, F10453a GSQ. Holotype F57085; paratypes F57086–F57088, F57090, F57091, F57093.

Subfamily COSTISPINIFERINAE Muir-Wood and Cooper, 1960

Genus INFLATIA Muir-Wood and Cooper, 1960

Type species. Productus inflatus McChesney, 1860.

Inflatia engeli sp. nov.

Plate 12, figs. 11–28

1964 *Antiquatonia* sp., Hill and Woods, pl. 7, figs. 18–21.
1967 *Inflatia*(?) *elegans* Roberts; McKellar, p. 13.
1975 *Inflatia* sp., Roberts, Table 1.

Diagnosis. Shell widest medially, having small auricles, and with a reticulate ornament on the visceral disc; costae having a density of 16–18 per 10 mm at 10 mm from the umbo; pedicle valve with irregularly developed spines on the flanks and on the trail, and lacking a median sinus; ventral adductor muscle scars in two pairs, a narrow elongate inner pair situated on platforms, and an impressed lachrymose outer pair; posterior of dorsal median septum grooved by an antron.

Description. External. Ventral umbo low, and extending only a short distance behind the hinge; ornament reticulate on the visceral disc, but regularly costate on the flanks and trail; costae increasing by bifurcation, and on the trail occasionally unifying behind spine bases; density of costae 16–18 per 10 mm at 10 mm from the umbo, and 10–12 per 10 mm on the front of the trail of large individuals; rugae extending from the hinge line across the entire visceral disc, and numbering up to 14; large spines irregularly developed on the flanks and on the trail; some specimens with one large spine base on each of the postero-lateral margins, and one or two spines on the trail; others with a concentric row of up to 6 spines on the trail. Brachial valve with a strongly incurved elongate trail; specimens from the type locality range in size up to 34 mm wide and 32 mm long.

Internal. Pedicle valve. Apex of valve filled with callus and bearing a strong median ridge at the posterior extremity of the adductor muscle field; inner adductor scars narrow, elongate, elevated on a muscle platform, and separated by a median furrow; outer adductor scars impressed, lachrymose in outline, and bearing longitudinal furrows; diductor muscle scars weakly impressed anteriorly, large, flabellate, either smooth or concentrically striated posteriorly, and radially striated anteriorly; internal surface finely spinose; ginglymus narrow. Brachial valve. Ginglymus pronounced, and modified by thickening around the lateral ridges on the flanks of the cardinal process; cardinal process bilobed, the posterior face having medianly fused lobes forming a slender wedge-shaped median projection between deep furrows; inner face with rounded tubercular lobes separated by a furrow extending posteriorly on to the median projection; tubercle-like lobes absent in juveniles; lateral ridges extending to the middle of the hinge; median septum extremely broad posteriorly, grooved by an antron, tapering abruptly at the adductor muscle field, and extending slightly beyond the mid-length; inner adductor muscle scars elevated, elongate, rounded at either end and irregularly sculptured; outer adductor scars subround in outline and strongly dendritic; brachial ridges extending at a high angle (30°) from the antero-lateral margins of the outer adductor scars to beyond the end of the median septum, weak proximally, but much higher and discontinuous distally; brachial discs mainly smooth, grooved posteriorly, highest anteriorly, and club-shaped; internal surface of valve pitted and spinose; small and presumably juvenile specimens lacking lateral ridges, and having a deep circular alveolus at the front of the cardinal process; median septum low, narrow elongate, and commencing in front of the cardinal process; muscle field obscure.

Remarks. Specimens from locality K31 in the Dakiel Formation on the western limb of the Yarrol Syncline, Queensland, are identified as *Inflatia engeli* sp. nov.; McKellar (1967) previously referred this form to *I*.(?) *elegans* Roberts. The Queensland specimens (Pl. 12, figs. 22–28) are slightly larger than those from Barrington, but have the same density of costae and rugae, and an irregular distribution of spines on the pedicle valve. A single large brachial valve from locality K31 has a number of features differing from those of the Barrington specimens; the adductor muscle field is larger and impressed into a substantially thickened shell; the grooved posterior shaft of the median septum is longer and extends nearly to the front of the muscle field, and the blade-like anterior portion has a swollen distal extremity; two depressions which resemble muscle scars are located immediately behind the tip of the septum and are impressed into elevated antero-median parts of the brachial apparatus; the brachial ridges originate from the front of the muscle field and initially curve posteriorly before enclosing club-shaped brachial discs; median portions of the brachial markings, as well as the brachial discs themselves form smooth elevated platforms; the unusual angle of origin of the brachial ridges from the front of the muscle field appears to have been caused by the forward movement of the adductor muscle field; the posterior margin of the valve has ridge-like thickening of either side of the cardinal process, and the valve has a marginal groove around the postero-lateral shoulders. In the pedicle valve the Queensland forms are thickened apically, have a wide well-defined ginglymus, and lack a median ridge behind the adductor muscle field; differentiation of the adductor muscle scars into two pairs is not as apparent as in the specimens from Barrington.

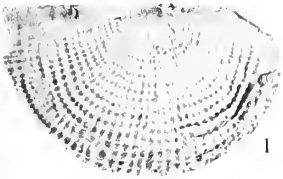
I. elegans Roberts (1964*a*, pp. 202–204, pl. 2, figs. 1–18), from the lower part of the *Delepinea aspinosa* Zone, has an over-all appearance close to that of this species.

EXPLANATION OF PLATE 12

Figs. 1–10. *Marginatia patersonensis* Roberts. 1–2, rubber casts of the ventral exterior and interior. F57094a and b, locality L361 U Newcastle, ×1·5. 3, rubber cast of a brachial valve exterior, F57095, locality 74-7A, ×1. 4, rubber cast of a pedicle valve exterior. F57096, locality L361 U Newcastle, ×1. 5, rubber cast of a brachial valve interior. F57097, locality 29-6, ×1. 6, rubber cast of a pedicle valve exterior. F57098, locality L361 U Newcastle, ×1. 7, rubber cast showing a dorsal view of F57099a from locality 72-18. The spines arise from the pedicle valve, ×1. 8, internal mould of a pedicle valve. F57100, locality L361 U Newcastle, ×1. 9, rubber cast of a brachial valve interior showing brachial markings. F57101, locality 17-9, ×1. 10, rubber cast of a brachial valve exterior. F57102 from locality L361 U Newcastle, ×1.

Figs. 11–28. *Inflatia engeli* sp. nov. 11–12, ventral and anterior views of a rubber cast. F57103, a paratype, ×1. 13, rubber cast of a brachial valve interior, F57104, a holotype, ×1. 14, rubber cast of the apical portion of the brachial valve exterior. F57105, a paratype, ×1. 15, rubber cast of the apical portion of a brachial valve. F57106, ×2. 16, rubber cast of an 'immature' brachial valve interior. F57107, ×1. 17, rubber cast of the trail of a pedicle valve. F57108, ×1. 18, rubber cast of the apical portion of a pedicle valve. F57109, a paratype, ×1. 19, dorsal view of a rubber cast of F57110, a paratype, ×1. 20–21, dorsal and anterior views of the external mould of a brachial valve. F57111, a paratype, ×1. Figs. 11–21 from locality L442 U Newcastle. 22–24, posterior, ventral, and lateral views of an internal mould of the pedicle valve. F8631a GSQ, ×1. 25–26, ventral and anterior views of a rubber cast of a pedicle valve. F8631b GSQ, ×1. 27, apical portion of an internal mould of a pedicle valve. Note the ginglymus. F12071, ×1. 28, rubber cast of a 'gerontic' brachial valve interior. F8630 GSQ, ×1. Figs. 22–28 from locality K31 GSQ.

PLATE 12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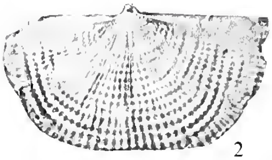
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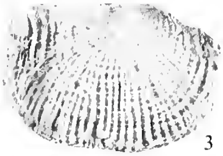
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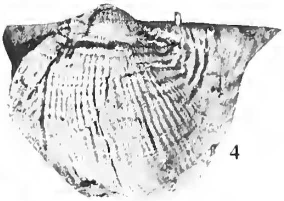
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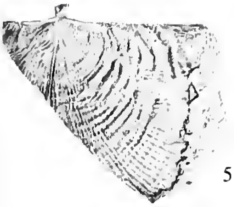
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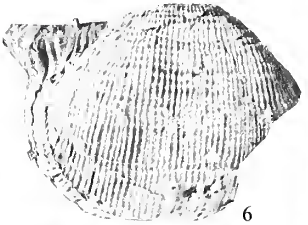
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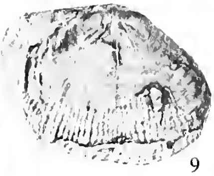
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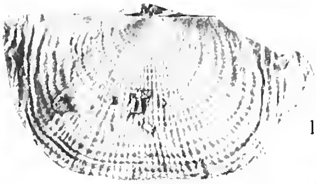
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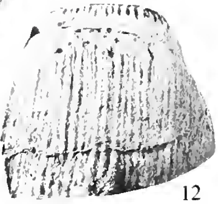
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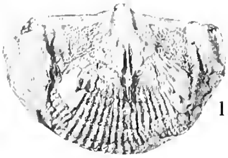
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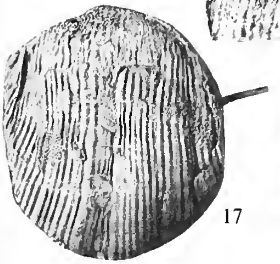
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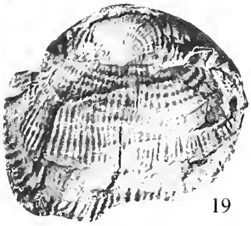
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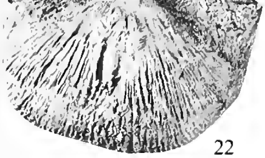
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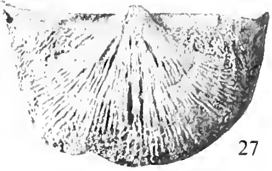
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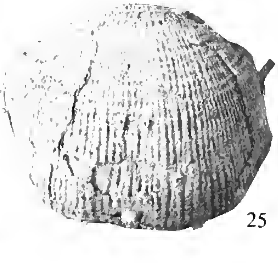
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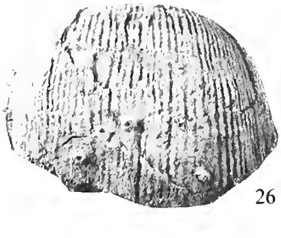
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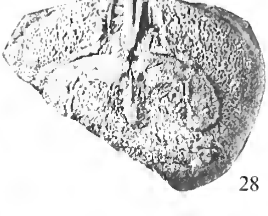
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ROBERTS, Australian productaceans

I. elegans is differentiated from *I. engeli* by possession of spines on either side of the hinge, finer costae, fewer rugae, a single pair of platform-like ventral adductor muscle scars, and brachial ridges which consistently originate horizontally from the muscle field; the internal surfaces of both valves bear weaker ribbing than those of *I. engeli*. *I. inflatia* (McChesney), the type species, differs from this species in being slightly narrower and more elongate, and in having a median fold and sinus, a wider hinge line with a row of spines on either side of the umbo, brachial ridges which originate nearly horizontally from the muscle field, and a coarsely spinose trail on the interior of the brachial valve; the posterior part of the dorsal median septum is smooth rather than grooved. *I. inflatia* is from the Chester Series of U.S.A., and has been figured by Muir-Wood and Cooper (1960, pl. 55, figs. 1–14). Two species of *Inflatia* have been described from central Kazakstan by Litvinovich (1969), but neither are morphologically close to *I. engeli*: *I. patria* Litvinovich from rocks of Viséan age (Litvinovich *et al.* 1969, pl. 52, figs. 1–3) is more elongate and possesses a ventral median sinus; and the Namurian species *I. uschkarensis* Litvinovich (ibid., pl. 53, figs. 1–3) is larger, wider at the ears, and has a ventral median sinus.

Occurrence. L442 U Newcastle, the type locality, in the Copeland Road Formation at Barrington, New South Wales; locality 114-1 in the Wootton Beds at Rawdon Vale, New South Wales; and localities K4 and K31 GSQ in the Dakiel Formation near Monto, Queensland. Late Viséan *Rhipidomella fortimuscula* Zone.

Material. F57103–F57111 AM. F10271, F8630, F8631 GSQ. Holotype F57104; paratypes F57103, F57105, F57109, F57110, F57111.

Genus SCOLOCONCHA Gordon, 1966

Type species. Productus indianensis Hall, 1858 from the Salem Limestone, Indiana.

Remarks. Gordon (1966) suggested that the marginiferid cardinal process and the morphology of the marginal ridge of *Scoloconcha* indicated an affinity with the Marginiferidae and especially the Costispiniferinae. In the present material there are no specimens showing the posterior face of the cardinal process, and hence a comment cannot be made on that criterion. Other features, however, such as the external ornament and the morphology of the dorsal interior suggest an affinity with *Krotovia* Fredericks, 1938 and hence with the Overtoniidae. Genera in the latter family are characterized by the possession of a sessile bilobate cardinal process.

In North America the genus *Scoloconcha* appears to range throughout the Meramecian and Chester Series (Gordon 1966; Nelson 1961), although there is a report of a form resembling the type species in the Chappel Limestone of Texas (Girty 1926). Carter (1967), however, in his revision of the latter fauna could not find any specimens assigned by Girty to *Productus* cf. *indianensis*. In Australia the single species assigned to the genus, *S. geniculata* sp. nov., is middle to late Viséan in age.

Scoloconcha geniculata sp. nov.

Plate 9, figs. 13–23

1975 *Scoloconcha* sp., Roberts, Table 1.

Diagnosis. Shell large for the genus, and usually with well-defined auriculations;

pedicle valve bearing quincuncially arranged spine ridges, and having faint rugae on the umbonal shoulders; ventral muscle field with small subovate adductor muscle scars and obsolete diductor muscle scars; brachial valve geniculate, having a moderately concave visceral disc and an external ornament of irregular elevations and depressions and small erect spines; dorsal interior with a strong marginal ridge, and elevated adductor muscle platforms.

Description. External. Pedicle valve semicircular in outline, strongly convex, evenly rounded across the venter, and widest at the mid-length; umbo narrow, incurved, and with steep lateral shoulders; postero-lateral margins flat, well differentiated from the body of the valve, and frequently auriculate; spine ridges prominent, widely spaced, and quincuncially arranged; ridges short and bearing small spines posteriorly, but longer and with larger spine bases 0·15 mm in diameter anteriorly; spine bases also on postero-lateral margins; rugae present on the umbonal shoulders, but weak and almost completely absent from the body of the valve; micro-ornament of concentric growth lines. Brachial valve. Visceral disc bordered anteriorly by an abrupt geniculation, postero-lateral margins flat and slightly auriculate; most of the valve, particularly the visceral disc and to a lesser extent the trail, ornamented by dimples; rugae present on the ears but obscure on the visceral disc; small erect spines, 0·15 mm in diameter on the visceral disc, trail and ears; specimens range in size up to 9 mm wide and 7·5 mm long.

Internal. Pedicle valve. Adductor muscle scars small, subovate, and separated by a narrow median furrow; diductor muscle scars poorly defined, and probably also subovate in outline; marginal rim present on the inner margins of the ears; fine endospines sparsely distributed immediately in front of the muscle field but concentrated in subconcentric rows on the trail; large hollow tubules, in depressions in the floor of the valve corresponding to the external spine ridges, connected externally with the spines. Brachial valve. Median septum arising from a callus at the front of the cardinal process, located mainly in a trough between the adductor muscle platforms, but extending to between one-third and nearly one-half the length of the valve; adductor muscle scars in a single pair, smooth, subrectangular to subtriangular, and widest and highest anteriorly; cardinal process with two small lobes internally, but unknown posteriorly; lateral ridges supporting the sides of the cardinal process, diverging from the hinge and forming a prominent marginal ridge extending, on some specimens, more than half the length of the visceral disc; brachial ridges poorly defined, originating from the vicinity of the adductor muscle scars, enclosing subovate brachial discs, and always with high distal extremities; internal surface of the valve ornamented by fine radially arranged endospines.

Remarks. S. geniculata sp. nov. is closest morphologically to the type species, *S. indianensis* (Hall), from the Salem Limestone, Indiana, described by Gordon (1966, pp. 583–584, pl. 70, figs. 22–27). *S. indianensis* is slightly smaller, has less well-defined ears, and may have slightly fewer spines on the pedicle valve; the brachial valve interior has a more convex visceral disc, a weaker marginal ridge, and a less-pronounced geniculation. The external face of the cardinal process has not been observed in *S. geniculata* and cannot be compared with the marginiferid process on *S. indianensis*. *Pustula laevicula* Moore (1928, p. 269, pl. 11, figs. 13–14) from the Lower Burlington Limestone and possibly the Sedalia Limestone, Missouri, has a weaker ventral umbo, smaller ears, and fewer and less-prominent spine bases. The brachial valve of *P. laevicula* is unknown. *P. globosa* Mather (1915, pp. 167–168, pl. 10, figs. 7–9) from the Morrow Group of Arkansas and Oklahoma, U.S.A., has a comparable spherical shape and curvature on the pedicle valve. It is distinguished from *S. geniculata* by its smaller ears and fewer spines.

'*Avonia*' *ratingensis* Paeckelmann (1931, pp. 92–94, pl. 4, figs. 15–17) from the Upper Kohlenkalk of Ratingen, Germany, has a similar ornament on the posterior of the pedicle valve, but has longer spine ridges anteriorly. *S. geniculata* has a stronger and more incurved ventral umbo. *P. minima* Tolmachoff figured by Besnosova *et al.*

(1962, pl. 13, figs. 12–13) may belong to *Scoloconcha*. When compared with *S. geniculata* it is slightly larger, and has longer spine ridges. Specimens from Eastern Kazakhstan referred to *A. karpinskiana* (Janishevsky) by Sarycheva (1968, pl. 5, figs. 5–8) also appear to belong to *Scoloconcha*. The exterior of the shell bears random spine bases which are more elongate than those of *S. geniculata*, the brachial valve interior has comparable musculature and a slender median septum, but the lateral ridges do not recurve and form a marginal ridge around the postero-lateral parts of the visceral disc. The name of this species is derived from the Latin *geniculatus*, like the bent knee, and refers to the geniculate brachial valve.

Occurrence. Locality 17-8, the type locality in the Woolooma Formation, Rouchel district, New South Wales. Other localities in the Rouchel district include 17-6, 7 and 9, 27-1, 29-7, 30-13, 41-1, and 66-22, all in the Woolooma Formation. In the Gresford–Dungog district *S. geniculata* is present at localities 16-1, 2 and 3, 72-18, 74-7A, and 79-10 in the Bonnington Siltstone, and L53 UNE in the Flagstaff Sandstone. At Salisbury, at localities 85-10, 90-2, 100-1 and 2 in the Flagstaff Sandstone, and localities 90-5 and 103-2 in an unnamed unit. In the Werrie Syncline the species is present at locality 112-15 in a marine intercalation in the Merlewood Formation. The species is Viséan in age, ranging from the *Orthotetes australis* into the *Rhipidomella fortimuscula* Zone.

Material. F57059–F57067 AM. Holotype F57063; paratype F57064.

Family BUXTONIIDAE Muir-Wood and Cooper, 1960
Subfamily BUXTONIINAE Muir-Wood and Cooper, 1960
Genus MARGINICINCTUS Sutton, 1938

Type species. *Marginicinctus marginicinctus* (Prout) from the St. Louis Limestone of Missouri.

Diagnosis. See Muir-Wood and Cooper (1960, p. 264).

Marginicinctus reticulatus sp. nov.

Plate 11, figs. 1–11

1957 *Dictyoclostus* sp., Campbell, p. 62, pl. 13, figs. 18–19.
1975 *Marginicinctus* sp., Roberts, Table 1.

Diagnosis. Shell slightly larger than average for the genus, rugose over the visceral discs of both valves, the rugae producing a reticulate ornament particularly on the brachial valve; costae spinose but not particularly swollen at the spine bases; spines near the hinge in six rows, each with about twenty spines on either side of the umbo; brachial valve interior lacking prostrate endospines.

Description. External. Shell subquadrate to subrectangular in outline, and bearing a flange around the lateral and anterior margins; specimens ranging in size up to 36 mm wide and 26 mm long. Pedicle valve with a shallow median sinus originating a short distance in front of the umbo, and extending to the cincture; trail modified distally by a cincture extending anteriorly from the lateral extremities of the hinge, and bearing a recurved flange; costae increasing by bifurcation and intercalation, and bearing numerous elongate spine bases; costae on the visceral disc crossed by rugae and having a knobbly appearance; rugae absent from in front of the visceral disc, and costae pass regularly from the trail through the cincture and on to the flange; costae on the flange bearing occasional spine bases; density of costae 11–14 per 10 mm at 20 mm from the umbo; hinge spines coiled postero-medially behind the umbo. Brachial valve. Fold low, broad, and originating a short distance in front of the umbo; visceral disc reticulate, rugae frequently increasing by splitting; costae on the trail regular, and usually crossing on to the flange; spines more numerous than on the pedicle valve, and tending to project dorsally instead of anteriorly or antero-laterally.

Internal. Pedicle valve with an obscure muscle field, and an internal surface which is ribbed and bears endospines towards the front of the trail. Brachial valve. Cardinal process bilobed internally, having peg-like lobes separated by a deep median groove; posterior face of process with a narrow trigonal ridge between fused lobes; lateral ridges slender, and parallel with the hinge; median septum wide and rounded posteriorly, narrow anteriorly, and extending slightly beyond half the length of the valve; in small individuals septum linked to the front of the cardinal process by two ridges separated by a slit-like antron, but in larger specimens the antron is infilled with shell material and the septum arises from either in front of or from the anterior margin of the cardinal process; adductor muscle field narrow, pointed and slightly dendritic posteriorly, expanding anteriorly, and terminating in smooth slightly elevated platforms; brachial ridges slender, arising from the antero-lateral margins of the muscle field but becoming obsolete laterally; internal surface bearing many endospines on radially arranged ribs.

Remarks. Marginicinctus reticulatus sp. nov. is morphologically close to specimens of *M. projectus* (Muir-Wood) from the Viséan of Eire, illustrated by Muir-Wood and Cooper (1960, pl. 76, figs. 12–16). The brachial valve of *projectus* has a reticulate appearance similar to that of *reticulatus*; Muir-Wood (1928, p. 103) also records *M. projectus* from Derbyshire, England. The type species, *M. marginicinctus* (Prout) from the St. Louis Limestone, Missouri, differs from *reticulatus* by its smaller size, and the possession of a slightly narrower flange, weaker rugae particularly on the pedicle valve, costae which enlarge at spine bases, and long prostrate spines on the interior of the brachial valve. There is no available information on the distribution of the hinge spines in either *M. projectus* or *M. marginicinctus*. Specimens identified as *Productus redesdalensis* Muir-Wood by Monakhova (1959, pl. 4, figs. 1–3) from the early Viséan of Uglia, Kazakhstan, have a cincture and flange and probably should be placed in *Marginicinctus*. The latter specimens resemble *M. reticulatus* in the form of ornament on the brachial valve, but appear to have a less rugose pedicle valve. Neither of the forms referred to *P. redesdalensis* by Muir-Wood (1928, pp. 61–64, pl. 2, figs. 9–11) or Sarycheva and Sokolskaya (1952, pl. 37, fig. 185) belong to *Marginicinctus*.

Occurrence. The type locality is 88-3 in an unnamed formation at Brownmore. Other localities include 85-8, 86-1, 5 and 6, 88-1, 90-1, 2 and 5, 100-3 and 13, 103-1, 106-5, and L466 and L414 U Newcastle in the Flagstaff Sandstone in the Salisbury–Brownmore district; localities 89-1 and 2 in the Flagstaff Sandstone at Mirannie; possibly at locality 73-8, Flagstaff Sandstone at Gresford; localities 85-15, 88-3, and 106-12 in an unnamed unit above the Flagstaff Sandstone at Salisbury and Brownmore; localities 114-1 and possibly 2 in the Wootton Beds at Rawdon Vale; locality L442 U Newcastle in the Copeland Road Formation at Barrington; locality L457 Flagstaff Sandstone, and L577 (both U Newcastle), Wootton Beds east of Dungog; locality 112–14, Watts, Babbinboon in a marine intercalation in the Merlewood Formation; and locality L246 UNE in the Caroda Formation at Caroda. In Queensland the species is recorded at localities K4 and K31 GSQ in the Dakiel Formation near Monto. Late Viséan *Delepinea aspinosa* and *Rhipidomella fortimuscula* Zones.

Material. F57076–F57083 and F57113 AM. Holotype F57076.

Genus MARGINATIA Muir-Wood and Cooper, 1960

Type species. Productus fernglenensis Weller, 1909 from the Fern Glen Formation, Missouri.

Marginatia patersonensis Roberts

Plate 12, figs. 1–10

1965*b Marginatia patersonensis* Roberts, pp. 63–65, pl. 10, figs. 1–5.

Remarks. Material collected since the original description of this species has clarified a number of morphological features. Amongst these is the earlier suggestion that *M. patersonensis* differed from the type material by the possession of non-dendritic dorsal adductor muscle scars. This is the case in most specimens, but large and presumably gerontic specimens have dendritic muscle scars. Details of additions and emendations to the concept of the species are given below:

1. Spines near the hinge are fine in small individuals, but grow to a large diameter in gerontic forms. The row of spines on the front of the trail is irregular and may contain up to about ten long halteroid spines; the spines are at least 30 mm in length.
2. Musculature of the pedicle valve. Ventral muscle scars are poorly defined in small- to medium-sized specimens, but in large forms are impressed into the shell. Adductor muscle scars are elongate, strongly dendritic, and are separated from one another by a median groove. Diductor muscle scars are large, triangular to flabellate in outline, relatively smooth, and ornamented by an indistinct concentric ornament posteriorly, and by irregular discontinuous radial grooves and ridges anteriorly. In smaller specimens the adductor muscle scars are mainly smooth, and the diductor muscle scars are marked by regular grooves and ridges.
3. Dorsal adductor muscle scars of small- to medium-sized individuals consist of two pairs: a smooth slightly elevated inner pair which are triangular to semicircular, and an outer pair which are pointed posteriorly, inflated anteriorly, and are partly dendritic. In large and presumably mature specimens the adductor muscle scars are strongly dendritic and it is difficult to differentiate inner and outer pairs.
4. Brachial ridges originate at the postero-lateral margins of the outer adductor scars and diverge at 20° from horizontal.

Specimens of *M. patersonensis* now at hand suggest an even closer similarity with *M. burlingtonensis* (Hall) than originally suggested by Roberts (1965*b*). The new specimens are in many cases larger than the type specimens and exhibit adult characters which were absent in the type material. *M. patersonensis* differs from *M. burlingtonensis*, figured by Weller (1914, pl. 9, figs. 1–10) from the Burlington Limestone of U.S.A., only in the possession of a row of spines along the hinge and a slightly larger number of body spines. *M. monachovae* Litvinovich (Litvinovich *et al.* 1969, pl. 31, figs. 4–6) from the early Viséan of Zakahstan resembles this species in having auriculate postero-lateral extremities and large body spines. The Russian species differs from *M. patersonensis* in having coarser costae and in lacking a row of spines along the ventral hinge.

Occurrence. The type locality is L233 UNE in the Bonnington Siltstone at Trevallyn in the Gresford–Dungog district. Other localities in this district include 74-7A (=L270 UNE), 72-18, L86 UNE, L215 UNE, L217 UNE, L50 UNE, L204 UNE, L206 UNE, L208 UNE, L496 U Newcastle, L573 U Newcastle in the Bonnington Siltstone, and localities 88-2 and L53 UNE in Flagstaff Sandstone. The species is also present at locality L361 U Newcastle at Clarencetown; in the Rouchel district, New South Wales, at localities 1-22 and 23 in the Dangarfield Formation; possibly from locality 63-5 in the Waverley Formation, and from localities 6-10, ?11 and 13, 17-5, 6, 7, 8, 9 and 11, 29-2, 6 and 7, 30-9 and 13, and 41-1 and 2 in the Woolooma Formation. In northern New South Wales the species is present at locality L1537 UNE in the Namoi Formation near Bingara. Viséan *Pustula gracilis* Subzone to the *Inflatia elegans* Subzone.

Material. F57094–F57102 AM.

Family DICTYOCLOSTIDAE Stehli, 1954
Subfamily DICTYOCLOSTINAE Stehli, 1954
Genus ANTIQUATONIA Miloradovich, 1954

Type species. Productus antiquatus J. Sowerby, 1821.

Remarks. Specimens from throughout New South Wales and Queensland referred to *Antiquatonia spinulicosta* sp. nov. have a number of morphological features which differ from those of the type species. Externally, the arrangement of major spine rows and the ornament are close to those of the type species, but the body spines are more dense. The ears of *A. spinulicosta* are smaller, and the greatest width of the shell is at the mid-length rather than at the hinge. Internally, particularly in the brachial valve, there are a greater number of features inconsistent with those of *A. antiquata.* In this material the lateral ridges are parallel with the hinge rather than divergent, the median septum is slightly shorter than that of the type species, and the adductor muscle scars are smooth rather than dendritic.

Antiquatonia spinulicosta sp. nov.

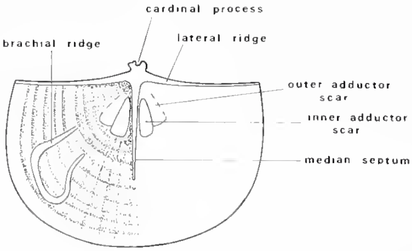
Plate 7, figs. 19–25; Plate 8, figs. 30–41

1964 *Antiquatonia* sp. Hill and Woods, pl. 7, figs. 15–17.
1975 *Antiquatonia* sp. Roberts, Table 1.

Diagnosis. Shell small for the genus, rounded-rectangular in outline, and widest at the mid-length; pedicle valve with a short trail, and small auricles; costae bearing a large number of prostrate spines posteriorly and erect spines anteriorly; seven larger spines in a curving row on the flanks, and three to four spines on the ears; ventral adductor muscle scars apparently non-dendritic; brachial valve having a short trail; dorsal median septum extending half the length of the valve; lateral ridges parallel with the hinge; dorsal adductor muscle scars smooth.

Description. External. Shell moderately concavo- or plano-convex, with a strongly arched pedicle valve and a geniculate brachial valve; specimens ranging in size up to 30 mm wide and 17 mm long. Pedicle valve particularly convex at the umbo and having a curving trail and steep flanks; postero-lateral margins small, flattened, and auriculate, and well differentiated from concave umbonal shoulders; umbo narrow apically, and projecting a short distance behind the hinge; venter flat or bearing an obsolete median sinus; costae increasing by intercalation, and tending to become obsolete at the front and on the extremities of the flanks of large valves; density of costae 14–16 per 10 mm at 10 mm from the umbo; rugae confined to the posterior half or one-third of the valve, extending from the hinge line across the venter, and producing a slightly reticulate ornament; seven large erect spines arranged in a curving row extending from the groove between the ears and the umbonal shoulders down the flanks, the diameter of spine bases increasing towards the extremities; a second row or group of three to four spines of similar shape and size present on the ears; spines arising from costae on the body of the valve smaller in diameter, those on the anterior half being prostrate and originating from elongate bases, and those on the front of the valve erect, having circular bases and being distributed either randomly or in irregular concentric rows. Brachial valve. Visceral disc having flat or gently convex postero-lateral extremities, and in some instances bearing a low median fold; costae with a small number of minute spine bases particularly near the area of geniculation; rugae low and rounded, continuous across the visceral disc, and producing a faintly reticulate pattern.

Internal. Pedicle valve having a short ginglymus along the hinge; adductor muscle scars elongate, ovoid in outline, faintly impressed posteriorly, and slightly elevated anteriorly; diductor muscle scars large, nearly twice the length of the adductor muscle scars, triangular in outline, and ornamented by longitudinal grooves and ridges; internal surface of valve bearing fine spinules. Brachial valve (text-fig. 18). Median septum wide posteriorly, becoming narrower anteriorly; lateral ridges robust, especially on the flanks of the cardinal process, and faceted posteriorly to articulate with the ginglymus on the pedicle valve; cardinal process bilobed internally, with two rounded protuberances on the ventral face, and posteriorly having a prominent wedge-shaped median ridge at the junction between the two deeply sulcate lobes; inner adductor scars smooth, pointed posteriorly, and expanding anteriorly into wider elevated platforms; outer adductor scars less well defined, subrectangular in outline and in some cases also elevated anteriorly; brachial ridges rarely preserved, originating from the postero-lateral margins of the outer adductor scars at angles between 10° and 30°, and enclosing club-shaped brachial discs; internal surface of valve bearing fine spinules immediately in front of the muscle field and coarser spines on the trail.



TEXT-FIG. 18. Dorsal interior of *Antiquatonia spinulicosta* sp. nov. incorporating details from F57031 AM and F57043. Approximately × 3.

Remarks. A. insculpta (Muir-Wood) from the D_2 of Great Britain (Muir-Wood 1928, pp. 89–92, pl. 3, figs. 10–12) is one of the few species resembling *A. spinulicosta*. *A. insculpta* has a similar rounded-rectangular outline and external ornament, particularly the density of the costae and the rugose nature of the visceral disc. It differs from this species in being slightly larger in size, and in having wider ears, a longer and more incurved trail, and a more pronounced fold and sinus. From Muir-Wood's illustrations, it appears that *A. insculpta* has fewer spines arising from the costae. Her description of an imperfectly preserved brachial valve indicates that the lateral ridges diverge from the hinge whereas those in *A. spinulicosta* are parallel with the hinge. Specimens identified as *A. insculpta* from the C_1^{tr} and C_1^{st} (late Viséan) of U.S.S.R. by Sarycheva (1949) are distinguished from *A. spinulicosta* by these same features, but they also have a more coarsely costate ornament, fewer and larger spines scattered over the body of the shell, extremely wide ears, and a longer dorsal median septum.

A. spinulicosta resembles *P. sedaliensis* Weller (1914, pp. 108–110, pl. 14, figs. 1–7), from the Chouteau Limestone of Missouri, in over-all shape and in the reticulate nature of the ornament at the posterior of the shell. The arrangement of spines differs, with *P. sedaliensis* having a row of cardinal spines as well as scattered spines on the anterior and on the lateral slopes. *A. spinulicosta* has a large number of spines arising from costae as well as a row of spines down the flanks, and a group of spines on the ears. The interior of *P. sedaliensis* is undescribed. *Dictyoclostus agmenis* Hyde (1953, pp. 236–239, pl. 10, figs. 6–35) from the Logan and Cuyahoga Formations of Ohio, similarly resembles *A. spinulicosta* in the shape and ornament of the shell. *D. agmenis* has rows of spines on the postero-lateral parts of the pedicle valve, but lacks the large number of spines arising from the costae, typical of *A. spinulicosta*.

Occurrence. Locality 10026 ANU, the type locality, in the Namoi Formation in the Boggabri district. Other localities include 72-3, 98-4, 100-6, 7 and 8 in the Bingleburra Formation, and localities L203 UNE and 98-2 in the Ararat Formation in the Gresford district; locality 1-27 in the Dangarfield Formation, and localities 24-7 and 15, 39-16 and 18, 15-3, 31-1, and 41-3 in the Waverley Formation in the Rouchel district; localities 112-1, 2, 4, 6, 7, 8, 9, and 10, L14 UNE, ?L7 UNE, L18 UNE, L23 UNE, L26 UNE, and L30 UNE in the Namoi Formation, Babbinboon district at the northern end of the Werrie Syncline; locality 113-1 (= locality L10024 ANU) in the Namoi Formation in the Boggabri district; and localities F3 of Yeates (1970, unpublished B.Sc. thesis) in the Namoi Formation and possibly F13 of Yeates in the

Luton Formation near Gravesend. Dear (1968) recorded the species in the upper part of the Cania Formation in the Yarrol Trough, Queensland. Late Tournaisian to early Viséan *Schellwienella* cf. *burlintonensis* Zone.

Material. F57031–F57036 AM and F57043–F57048 AM. Holotype F57036; paratype F57033.

Genus RETICULATIA Muir-Wood and Cooper, 1960

Type species. Productus huecoensis King, 1931 from the Early Permian Hueco Limestone, Texas.

Diagnosis. See Muir-Wood and Cooper (1960, p. 284).

Reticulatia cinctifera sp. nov.

Plate 13, figs. 1–15

1964 *Reticulatia* sp. Hill and Woods, pl. 8, figs. 5–8.

Diagnosis. Shell transverse, subovate in outline, and with the exception of the trail bearing a weak reticulate ornament; a single row of divergent halteroid spines near the hinge, but the remainder of the shell aspinose; pedicle valve with a narrow trough-shaped median sinus; brachial discs club-shaped; external face of cardinal process with short strongly incurved lateral lobes, and a large V-shaped lophidium.

Description. External. Pedicle valve widest at or just in front of the hinge line, highest at about one-third of its length, slightly flattened on the venter, and strongly convex at the umbo and at the trail; ginglymus well developed; median sinus narrow, maintaining a constant width anteriorly, and extending from just behind the umbo to the front of the trail; seven large halteroid spines inclined at 40° to the hinge in a single row on either side of the umbo; rugae highest on the postero-lateral margins, extending across the venter, best developed on the posterior two-thirds of the valve, and rare on the trail; costae narrow, increasing by bifurcation and intercalation, and having a density of 13–15 per 10 mm at 20 mm from the umbo, and 10–12 per 10 mm at the front of the trail. Brachial valve flat to moderately concave on the visceral disc, with a prominent geniculation producing a short steep trail; ears wide and flat; median fold low, narrow, and usually affecting the front of the visceral disc and the trail; ornament strongly reticulate on the visceral disc, but rugae absent from the trail; costae increasing mainly by bifurcation; specimens ranging in size up to 61 mm wide and 54·55 mm long.

Internal. Pedicle valve. Muscle field deeply impressed; adductor muscle scars in two pairs, a narrow dendritic posterior pair which is elevated anteriorly, and a smooth lanceolate anterior pair which has an internal longitudinal line of subdivision and forms platforms above the remainder of the muscle field; diductor muscle scars large, smooth or with a faint concentric ornament at the posterior, and with deep radial striae on the flabellate anterior; cincture extending as a ridge along the hinge, cutting across the ears and traversing the anterior just behind the front of the trail; one specimen having a cincture comprised of two ridges and a separating furrow; internal surface of valve between the umbo and the cincture bearing fine randomly oriented or radially arranged pits. Brachial valve. Outer adductor muscle scars strongly dendritic, impressed, and subrectangular in outline; inner adductor scars subovate in outline, possibly longitudinally subdivided into two portions, and situated on high platforms; septum originating as a wide ridge from the callus in front of the cardinal process, narrow through the muscle field, becoming higher at the front, and extending two-thirds the length of the valve; cardinal process supported by a thick callus, bearing two highly convex lobes divided by a narrow groove internally, and on the posterior face having a sulcate wedge-shaped median ridge at the junction of the concave lobes; dorsal portion of the process protected by a V-shaped lophidium; lateral ridges nearly parallel with the hinge, but cutting across the ears and forming a marginal rim around the geniculation at the posterior of the trail; brachial ridges arising from the front of the muscle field, extending normal to the median septum, enclosing smooth elevated club-shaped brachial discs, and returning to the front of the septum; visceral disc between the marginal rim and the brachial markings and muscle scars bearing randomly oriented pits; the front of the visceral disc having radially arranged ribs bearing fine endospines; trail and ears smooth.

Remarks. R. cinctifera sp. nov. is extremely close morphologically to specimens referred to *P.* (*Dictyoclostus*) aff. *americanus* Dunbar and Condra by Demanet (1943, pl. 2, figs. 4–7) and to *Tolmatchoffia demaneti* by Böger and Fiebig (1963, pp. 133–136, pl. 16, fig. 12; pl. 17, figs. 1–6). The specimens from Belgium, described by Demanet, have the same shape, a cincture in the ventral valve, a single row of spines near the hinge of the pedicle valve, and a comparable reticulate ornament; they come from the base of the Westphalian C (Wn3a). The German material figured by Böger and Fiebig is slightly less transverse, has more erect spines on the pedicle valve, and may have a slightly smaller ventral umbo; it also comes from the Westphalian C.

When compared with the type species, *R. huecoensis* (King) illustrated by Muir-Wood and Cooper (1960, pl. 104, figs. 1–5; pl. 105, figs. 1–8), *R. cinctifera* is more transverse and has a less well-developed reticulate ornament on the visceral disc; spines are present only along the hinge line and are absent from the furrow bordering the ears, the trail, and the visceral disc. In the brachial valve interior the posterior adductor muscle scars in *R. cinctifera* are smaller, the brachial markings are club-shaped, the lateral lobes on the external face of the cardinal process are shorter, and the lophidium is larger than those of the type species. Specimens of *R. americana* (Dunbar and Condra) from the Pennsylvanian of Oklahoma, Kansas, and Texas, which according to Branson (1964) are not synonymous with the type species as alleged by Muir-Wood and Cooper (1960), have a more quadrate shape, a more strongly reticulate ornament, and coarser costae when compared with *R. cinctifera.*

R. rugatia Sturgeon and Hoare (1968, pp. 49–50, pl. 14, figs. 10–16) from the lower part of the Allegheny Group of Ohio is more subquadrate, has smaller ears, and slightly stronger rugae when compared with this species. Specimens of *R. tiawahensis* (Hoare) from the Desmoinsian Tiawah Limestone of Missouri (Hoare 1960, pp. 224–226, pl. 32, figs. 5–9; Hoare 1961, pp. 51–52, pl. 6, figs. 4–8) have a comparable weakly reticulate ornament, but are broader and have much wider ears when compared with *R. cinctifera. R. tiawahensis* appears to lack a cincture, has wider and more strongly dendritic ventral adductor muscle scars, and more strongly dendritic dorsal adductor muscle scars. Specimens tentatively referred to *Reticulatia* have been reported from the Desmoinesian (Moscovian) ?*Reticulatia* Zone and equivalents in the Yukon Territory of Canada by Bamber and Waterhouse (1971). These differ from *R. cinctifera* in having large spine bases on the trail, and, in most cases, larger ears. The material

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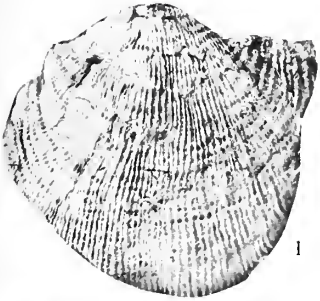
EXPLANATION OF PLATE 13

Figs. 1–15. *Reticulatia cinctifera* sp. nov. 1, rubber cast of a pedicle valve exterior. F10472b GSQ, ×1. 2–3, rubber casts of two brachial valve exteriors. F10472a GSQ and F8612b GSQ, both paratypes, ×1. 4–5, posterior and ventral views of a rubber cast of the brachial valve interior. F10468 GSQ, holotype, ×2 and ×1 respectively. 6, rubber cast of portion of a brachial valve interior. F10469 GSQ, ×1. 7–8, rubber cast of the interior and internal mould of two pedicle valves showing the musculature, mantle canals, and the cincture. F30186 UQ and F30190 UQ from locality L2181 UQ. Both ×1. 9–11, rubber casts of the exteriors of three pedicle valves. Note the single row of hinge spines and the absence of body spines. F8612a GSQ, a paratype, F10470a GSQ, and F10473b. All ×1. 12–13, rubber cast of the apical portion of the ventral interior, and internal mould of the pedicle valve. Note the prominent cincture. F8611 GSQ, a paratype, ×1. 14, rubber cast of the apical part of the dorsal interior. F12149 GSQ, ×1·5. 15, rubber cast of a brachial valve exterior. F8610 GSQ, a paratype, ×1. All specimens except Figs. 7–8 from locality K33 GSQ.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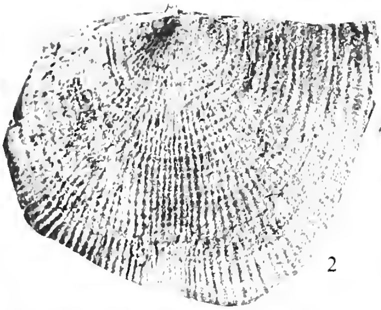
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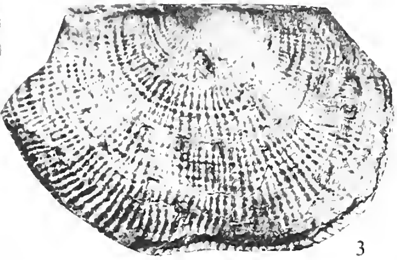
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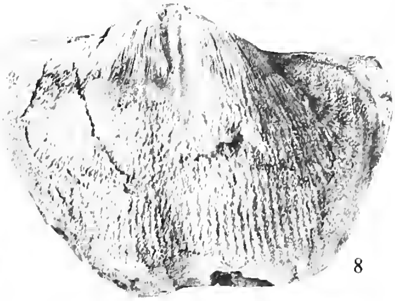
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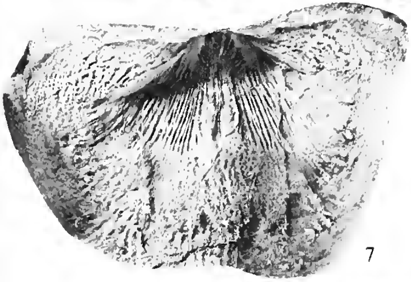
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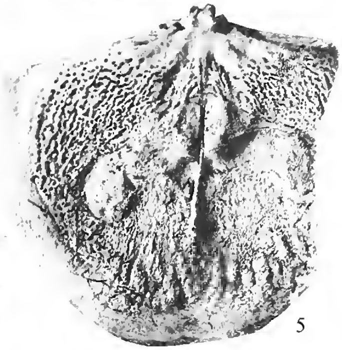
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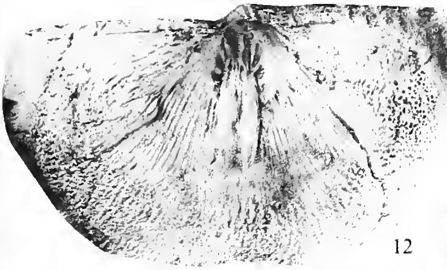
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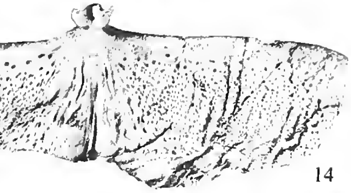
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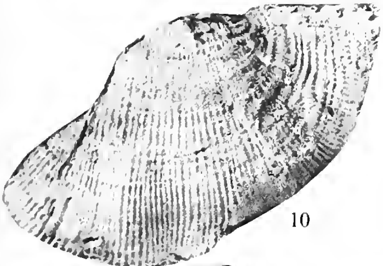
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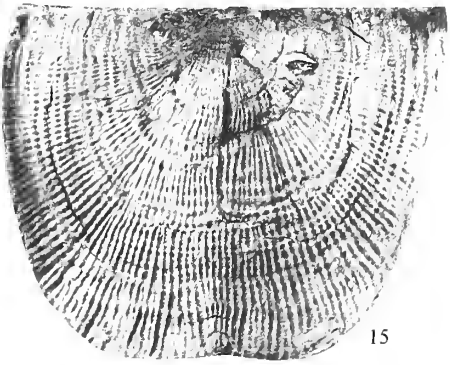
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ROBERTS, Australian productaceans

is insufficiently complete for a more detailed comparison. Three species of *Reticulatia R. huecoensis* (King), *R. moelleri* (Stuckenberg), and *R.* cf. *uralica* (Tschernyschew) described by Winkler Prins (1968) from the Late Carboniferous of the Cantabrian Mountains, Spain, bear spines on the body of the shell and have a more strongly reticulate ornament when compared with *R. cinctifera*.

Occurrence. Locality K33 GSQ, the type locality, in the Branch Creek Formation, Major Mitchell Creek, Kalpowar, Queensland; and locality 2181 UQ, from the same position as locality K33. *R. cinctifera* does not occur at the same locality as *Marginirugus barringtonensis* Campbell, as inferred by Hill and Woods (1964, p. 16), but is found at a separate location near the junction of Major Mitchell and Splinter Creeks. Dear (unpublished Ph.D. thesis 1963) reports this species from the Branch Creek Formation near Yarrol, and from equivalents of the Branch Creek Formation in the vicinity of 'Craigilee' on the Fitzroy River, 65 km west of Rockhampton.

In New South Wales the species is present at locality 126-4 at Yagon Gibber, and locality 47 of Crane (unpublished M.Sc. thesis 1975) in rocks of Late Carboniferous age at 442995 Bulahdelah 1:63360 Sheet. Similar material is found at Forster at 580193, Tuncurry 1:63360 Sheet in a stratigraphic position apparently only several metres above the *M. barringtonensis* Zone (Suters 1972, unpublished M.Sc. thesis). Namurian to Westphalian *Levipustula levis* Zone.

Material. F8610–F8612, F10468–F10470, F10472, F10473, F12149 GSQ. F30186, F30190 UQ. Holotype F10468; paratypes F8610–F8612a, F10472a and b.

LOCALITIES OF FIGURED SPECIMENS

Locality Number	Grid Reference	
University of New South Wales		
6-10	085243	Woolooma
6-13	087240	Woolooma
15-3	207283	Woolooma
16-3	570863	Dungog
17-5	138292	Woolooma
17-7	137289	Woolooma
17-8	135289	Woolooma
17-9	133290	Woolooma
24-7	157341	Woolooma
29-1	205269	Woolooma
29-6	203275	Woolooma
31-1	197288	Woolooma
39-16	177298	Woolooma
41-1	096246	Woolooma
72-18	634949	Dungog
74-7A	575865	Dungog
85-8	655080	Dungog
85-10	659081	Dungog
86-2	637097	Dungog
88-2	596057	Dungog
88-3	615071	Dungog
89-1	427972	Camberwell
90-2	586175	Gloucester
92-1	612124	Gloucester
106-15	640187	Gloucester
107-1	071252	Woolooma
121-2	267752	Mount Morgan
126-4	541858	Bulahdelah
University of Newcastle		
L361	813750	Paterson
L386	797385	Dungog
L422	900317	Gloucester
L437	903973	Dungog
L442	916372	Gloucester
L466	643095	Dungog
L498	632203	Gloucester
L577	885010	Dungog
University of New England		
L145	905362	Gloucester
L203	583912	Dungog
Australian National University		
L10024	411012	Willuri
L10026	408108	Willuri
University of Queensland		
L1288	267753	Mount Morgan
L2181	262667	Monto
L2187	257677	Monto
Geological Survey of Queensland		
K31	262556	Monto
K33	262667	Monto
K91	212597	Monto
L955	256798	Mount Morgan
L988	257677	Monto

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A EURYHALINE OYSTER FROM THE MIDDLE JURASSIC AND THE ORIGIN OF THE TRUE OYSTERS

by J. D. HUDSON *and* T. J. PALMER

ABSTRACT. *Ostrea hebridica* Forbes, 1851 is shown by its morphology to belong to the family Ostreidae, sub-family Ostreinae. Its facies distribution shows that it was euryhaline, as are many members of the Ostreinae but none of the Gryphaeidae, to which all non-plicated Jurassic oysters have previously been referred. *O. hebridica* is closely allied to *O. acuminata* J. Sowerby, the type of *Praeexogyra* Charles and Maubeuge, to which genus it is transferred. Previously it has been placed in *Liostrea* Douvillé. The type species of *Liostrea*, *L. hisingeri* of the Lower Lias, although a gryphaeid, shows some features transitional to the ostreid condition. Consequently the euryhaline oysters (Ostreinae) are diphyletic.

OYSTERS are among the most successful of bivalves, and indeed of invertebrates, in brackish-marine environments of the present day. They have a fossil record in such environments extending at least back to the Cretaceous. In addition, oysters have occurred in fully marine environments since the Triassic. The brackish-water oysters of the present day belong to the family Ostreidae, sub-family Ostreinae of Stenzel (1971); they can be regarded as the 'true oysters'. They are not strongly coiled, nor plicated; characteristically they show high variability of shell shape, much of which is directly phenotypic and arises from their attached mode of life and gregarious habit. They have not received as much attention from palaeontologists as coiled or plicated oyster genera such as *Gryphaea*, *Exogyra*, or *Lopha*; they are not as attractive for studies in functional morphology; they are not good guide fossils in stratigraphy and their apparently chaotic variability has discouraged statistical studies such as those carried out on *Gryphaea* (e.g. Gould 1973). Nevertheless, it is of interest to inquire when the oysters attained euryhalinity, and how this may be reflected in phylogeny—subjects recently discussed by Stenzel (1971).

In Stenzel's classification the sub-family Ostreinae arises in the Cretaceous; the only sub-family of the Ostreidae present in the Jurassic is the Lophinae. These are plicate oysters of tropical origin and distribution and are apparently always stenohaline. The species that we discuss can clearly not be referred to this group. All other Jurassic oysters, including the genera *Liostrea* and *Praeexogyra*, in which *Ostrea hebridica* might be placed, are placed by Stenzel in the family Gryphaeidae. Stenzel considers that all Gryphaeidae were strictly euhaline and stenohaline.

The criteria by which Stenzel distinguishes Ostreidae from Gryphaeidae are primarily concerned with different aspects of the adductor muscle scar, and with shell structure. Those which are potentially applicable to fossils are summarized in text-fig. 1.

In recent years *O. hebridica* Forbes has generally been referred to the genus *Liostrea*. It was Stenzel's conclusion (1971, p. 1103) that *Liostrea* should, on the morphological criteria discussed above, be placed in the Gryphaeidae, and should

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therefore presumably be stenohaline, that led us to look closely at *O. hebridica*. We had reason to think this species was euryhaline (Hudson 1963*a*, *b*). For the present, we shall refer *O. hebridica* to *Ostrea sensu lato*.

MORPHOLOGY OF *OSTREA HEBRIDICA*

The most obvious characteristic of *O. hebridica* is its great variability. The shape variation is well shown in the plates published by Arkell (1934) as part of his excellent description of the species; see also our Plate 14. Arkell also discussed the synonymy of *O. hebridica*, and we accept his conclusion that *O. sowerbyi* Morris and Lycett, 1853 and *O. subrugulosa* Morris and Lycett, 1853 are both junior synonyms of *O. hebridica* Forbes, 1851.

We have applied Stenzel's criteria to *O. hebridica* by considering several large populations independently, in order to take into account variation within and between populations (Table 1). Our observations have established that the species has the following characteristics:

1. The shape of the muscle scar is nearly always crescentic or reniform; occasionally, particularly in thin-shelled individuals, it may be orbicular, although this may be a preservational feature (Pl. 15, fig. 5).
2. The muscle scar is usually positioned nearer to the ventral margin of the valve than to the umbo; occasionally it is more or less central (Pl. 15, fig. 4).
3. The ventral margin of the muscle scar in the left valve is almost invariably not raised.
4. Radial posterior grooves have not been seen on any specimen examined: a shallow sulcus, however, is seen on some specimens from the Fuller's Earth of Langton Herring, Dorset.
5. In the left valve, a shallow to very deep umbonal cavity is present (Pl. 15, fig. 3).
6. Chambers are often present between the shell layers (Pl. 15, fig. 2).
7. A conspicuous outer shell layer (ostracum) of prismatic calcite is present in most specimens (Pl. 15, fig. 1).
8. The attachment area is frequently very large.

All these features are typical of the Ostreidae and suggest that *O. hebridica* should be placed in that family.

EXPLANATION OF PLATE 14

Shape variation in populations of *Praeexogyra hebridica* from the Bathonian (Middle Jurassic) of Britain.

Figs. 1–4. Lower Ostrea Beds, Duntulm, Trotternish, Isle of Skye (1, 40497; 2, 40495; 3, 45524; 4, 45522), ×1·4.

Figs. 5–8. Forest Marble Formation, Wood Eaton Quarry, near Oxford (5, 70511; 6, 70512; 7, 70513; 8, 70514), ×1·2.

Figs. 9–12. Fuller's Earth Clay, Langton Herring, Dorset (9, 38042; 10, 38022; 11, 38059; 12, 38020), ×1·8.

All specimens in the collection of the Geology Department, University of Leicester.

PLATE 14


1


2


3


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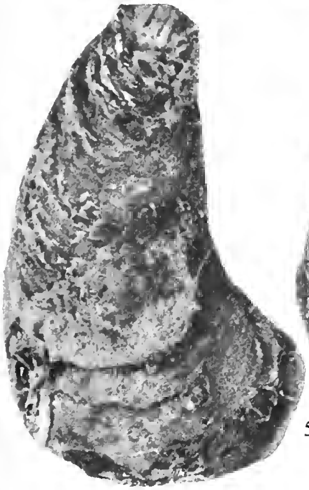
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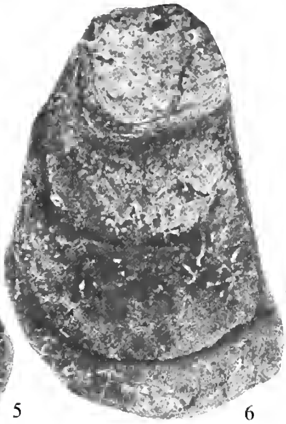
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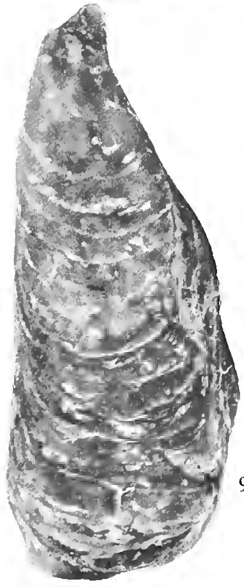
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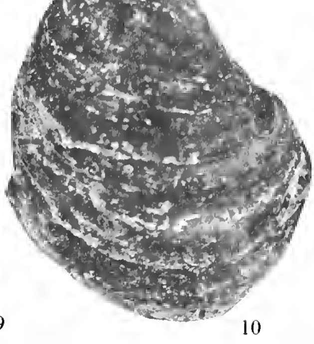
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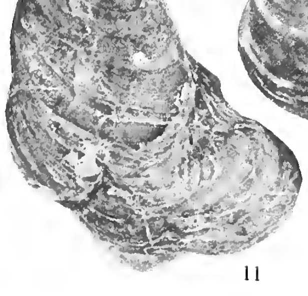
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HUDSON and PALMER, Jurassic euryhaline oyster

OCCURRENCE AND ECOLOGY OF *OSTREA HEBRIDICA*

O. hebridica is widespread in the Bathonian of the British Isles from the Inner Hebrides (Skye is the type locality) to the Dorset coast (Arkell 1934). It often occurs in rock-forming abundance, making up more or less monotypic shell-beds. Individuals are frequently attached to one another. Although the original relief of an oyster 'reef' is rarely preserved in the British Jurassic, it seems very likely that low reefs comparable to those of *Crassostrea* in Texas today (Stenzel 1971, pp. N1045–1048) were present.

In the Inner Hebrides, *O. hebridica* occurs principally in the Lower Ostrea Beds of the Great Estuarine Series (Hudson 1962, 1963*a*, *b*; Tan and Hudson 1974). Shape variation is illustrated in Plate 14, figs. 1–4. Elongate forms are common but not as extreme nor as dominant as those in the Fuller's Earth at Langton Herring, Dorset (Arkell 1934; see below); lunate forms similar to the type of *O. sowerbyi* (see Morris and Lycett 1853, Table 1, fig. 3, 3*a*) are also common. Only one definite example of variety *subrugulosa*, with ribs on the left valve (Arkell 1934), has been found (Pl. 15, fig. 6).

In the Lower Ostrea Beds, virtually monotypic shell-limestones and shelly shales are frequent. In other beds interbedded with these, particularly silts and micritic limestones, *O. hebridica* occurs with a variety of other shallow-marine bivalves (*Modiolus*, *Myopholas*, *Corbula*, *Placunopsis*, *Cuspidaria*, etc.). These more diverse assemblages, in which oysters are less dominant and fossils do not compose most of the rock as they do in the shell-beds, may represent soft-bottom assemblages from the sea-floor between patches of densely attached oysters; indeed, in true shales the oysters are almost absent. Other occasional associates of *O. hebridica* in these beds include the brachiopod *Kallirhynchia*, regular echinoids (indeterminate plates and spines), and encrusting tubes of serpulid worms.

The Lower Ostrea Beds cannot, however, be regarded as fully marine. They include, interbedded with the oyster-bearing beds, siltstones with *Unio*, *Viviparus*, *Neomiodon*, and *Euestheria* (but without oysters). No truly stenohaline forms occur even with the oysters: no corals, no cephalopods, no ectoprocts, no brachiopods apart from

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EXPLANATION OF PLATE 15

Morphological characteristics of *Praeexogyra hebridica*.

Fig. 1. Well-developed prismatic outer shell layer on right valve of specimen from Waterstein, Isle of Skye (70515). Photomicrograph from thin section, × 95.

Fig. 2. Chambers (now filled with sparry calcite) in left valve of specimen from the Isle of Eigg (J 49718). Photomicrograph from thin section, × 10.

Fig. 3. Umbonal cavity (arrowed) in left valve of specimen with conjoined valves. Langton Herring, Dorset (70516), × 3.

Fig. 4. Interior of right valve, showing ventral position of muscle-scar (arrowed). Wood Eaton, Oxon. (70517), × 1·4.

Fig. 5. Interior of right valve, showing reniform adductor muscle scar. Wood Eaton, Oxon. (70518), × 1·3.

Fig. 6. var. *subrugulosa* from Waterstein, Isle of Skye (J 49341), showing characteristic radial riblets on exterior of left valve, × 1·2.

Specimen numbers prefixed J from the Sedgwick Museum, Cambridge; others from the Geology Department, University of Leicester.

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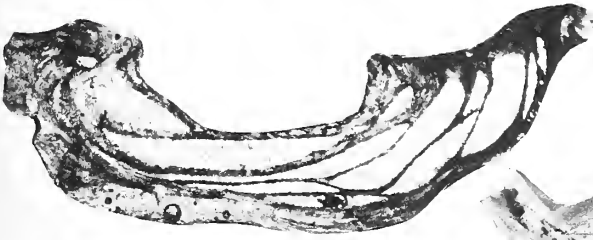

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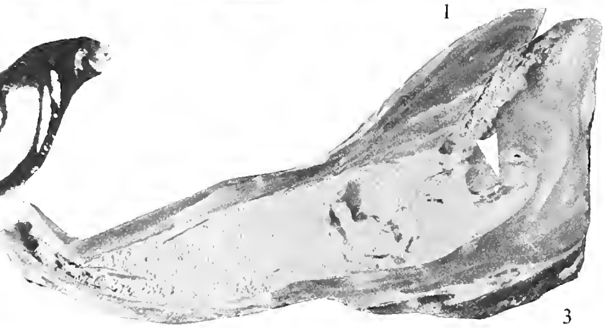

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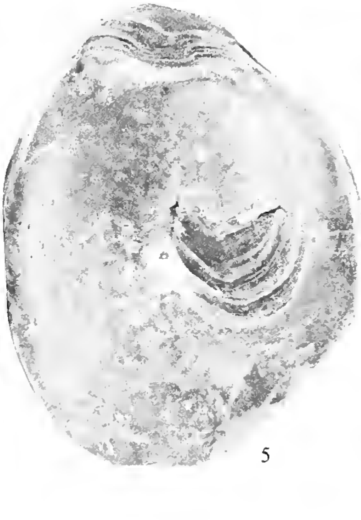

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HUDSON and PALMER, Jurassic euryhaline oyster

TABLE 1. Variation among populations of *Ostrea hebridica* Forbes, compared to diagnostic criteria for the families Gryphaeidae and Ostreidae. Representative suites of populations examined are in the collections of the Geology Department, University of Leicester, the Sedgwick Museum, Cambridge, and the Oxford University Museum.

Criteria used for oyster classification in the Treatise (Stenzel 1971)	Gryphaeidae	Ostreidae	Populations of *O. hebridica* Forbes examined by us						
			Great Estuarine Series, Isle of Skye	Upper Estuarine Series, East Midlands	Hampen Marly Formation, Oxon.	Great Oolite Limestone, Olney, Bedfordshire	Forest Marble Formation, Wood Eaton, Oxon.	Sharp's Hill Formation, Oxon. and Gloucestershire	Upper Fuller's Earth Clay, Langton Herring, Dorset
Shape of adductor muscle scar	Orbicular	Crescentic or reniform	Crescentic or reniform	Orbicular, crescentic, or reniform	Crescentic or reniform	Crescentic	Crescentic	Reniform	Orbicular to reniform
Position of adductor muscle scar	Nearer hinge than opposite margin	Nearly central, or nearer opposite margin than hinge	Nearer opposite margin	Nearer opposite margin	Central, to nearer opposite margin	Nearer opposite margin	Nearer opposite margin	Central, to nearer opposite margin	Central, to nearer opposite margin
Elevation of ventral portion of adductor muscle scar in L.V.	Raised	Not raised	Not raised	Not raised	Not raised	Sometimes raised	Not raised	Not raised	Not raised
Development of radial posterior groove on exterior of L.V.	Often present	Absent	Absent	Absent	Absent	Absent	Absent	Absent	May be present
Development of umbonal cavity in L.V.	Absent or very shallow	Shallow to deep	Present	Present	Shallow	Shallow to deep	Shallow	Present	Deep
Development of lenticular chambers within shell of L.V.	Absent, except in Exogyrinae	Commonly present	Present in some	Present	Present	Present	Present	Present in some	None seen
Development of prismatic calcite outer shell layer in R.V.	Thin or absent	Thin to conspicuous	Conspicuous	Conspicuous	Conspicuous	Conspicuous	Conspicuous in some specimens	Conspicuous	Present
Salinity tolerance	Euhaline and stenohaline	Sometimes euryhaline	Euryhaline	Probably euryhaline	Probably euryhaline; not fully marine	?Marine	Euryhaline	?Marine	Marine

Kallirhynchia. The bivalve fauna is very low in diversity. In all these features, the faunas contrast with those of the limestones of the contemporary Great Oolite Group of southern England. An inference of a generally brackish-water environment (Hudson 1963*a*, *b*) can still be supported. Additional evidence from algal limestones (Hudson 1970) and isotopic studies (Tan and Hudson 1974) indicates hypersalinities at times during deposition of the Lower Ostrea Beds, including some of the oyster-bearing strata. Such alternations of conditions are readily understandable in a setting of semi-enclosed lagoons, as in the recent habitat of *Crassostrea virginica* in Texas (e.g. Stenzel 1971, pp. N1038–1039).

In Central England, *O. hebridica* occurs commonly at two levels within the Great Oolite Group. The lower includes the Upper Estuarine Series of the East Midlands and its approximate lateral equivalent in Oxfordshire and Gloucestershire, the Hampen Marly Formation. The upper level includes the Blisworth Clay of the East Midlands, and its lateral equivalent, which extends over the rest of southern England, the Forest Marble Formation.

In the Upper Estuarine Series, *O. hebridica* is extremely common in clays and limestones, interbedded on a scale of a few centimetres with carbonaceous clays that overlie rootlet-beds. The rootlets penetrate the oyster-bearing clays (Aslin, *in* Sylvester-Bradley and Ford 1968). The associated faunas are, in general, more marine in aspect than those in the Hebrides but, again, fully stenohaline groups are absent. A coastal lagoon environment close to the shore of the Anglo-Belgian landmass, frequently invaded by swamp vegetation, seems indicated. The Hampen Marly Formation of Oxfordshire and Gloucestershire seems to represent the seaward edge of this lagoonal environment. *O. hebridica* commonly forms oyster reefs up to 2 m in thickness (Richardson 1933), and these reefs are interbedded with marls and marly limestones. Nevertheless, the fauna associated with the oysters is principally molluscan, and of low diversity. Stenohaline forms are rare. Passing south-westwards towards the Bath region, however, the Hampen Marly Formation passes into more fully marine limestones in which known stenohaline forms are more common. Significantly, the oyster reefs die out in this region and *O. hebridica*, although still occurring, never approaches the abundance typical of the landward region to the north-east.

In the Blisworth Clay the association of *O. hebridica* with rootlets is again seen. An interesting feature of this region is the occurrence of populations in which the variety *subrugulosa* is common, and locally dominant. The *O. hebridica*/rootlet association also persists across north Oxfordshire, where the Blisworth Clay passes laterally into the Forest Marble Formation. Palmer and Jenkyns (1975) have recently argued, from both faunal and sedimentary evidence, that there was extensive development of brackish lagoons in this region.

Rolled and abraded specimens of *O. hebridica* continue to occur abundantly in the limestones of the Forest Marble Formation over the whole of southern England. Since they are virtually never found in life position, it is difficult to infer their life preferences. They occur with a wide variety of fully marine species, but features suggestive of emergence (mud flakes) and river drainage from land (lignite) are also common.

O. hebridica also occurs relatively rarely in the limestone unit which separates the two stratigraphic levels referred to above. In the White Limestone Formation of Oxfordshire and Gloucestershire the oyster occurs with marine species in micritic sediments representing marine lagoons with poor water circulation. In the laterally equivalent Great Oolite Limestone of the Midlands the occurrence is similar, and the variety *subrugulosa* is common locally. *Subrugulosa*, therefore, seems to be geographically, rather than stratigraphically, restricted in occurrence.

In the Fuller's Earth Clay of Langton Herring on the Dorset coast is one of the best-known occurrences of *O. hebridica* (described by Arkell 1934, 1947). The surrounding bed is a marine clay, although the oyster bed itself is almost monotypic. The bed varies in thickness from 1 to 4 m over a distance of 1·6 km; the same horizon may, however, be present at Watton Cliff, Bridport, 20 km away (Arkell 1947, pp. 16–17). The population is dominated by the variety *elongata* Dutertre (see Arkell 1934) and is somewhat distinct from the others we have studied (Table 1). Growth rugae tend to be more regularly developed. The oysters are heavily encrusted with adherent Foraminifera, a feature only infrequently observed on those from the Great Estuarine Series or the Great Oolite. This probably indicates a higher and more stable salinity, and the elongation may be explained as a phenotypic response to a muddy bottom. It is proposed that this occurrence represents an offshore, sub-tidal marine environment, while the other populations we studied came from more or less enclosed marginal bays and lagoons.

There is therefore strong evidence that *O. hebridica* was a euryhaline species. This is in contrast to Stenzel's view of the ecological preferences of the Gryphaeidae as 'strictly euhaline and stenohaline' (Stenzel 1971, p. N1097). Furthermore, *O. hebridica* individuals frequently grew attached one to another and formed oyster reefs. Again, this is contrary to Stenzel's view of the Gryphaeidae (p. N1097). We feel that these characteristics, taken together with the strong morphological evidence considered above, necessitate placing *O. hebridica* in the Ostreidae. If accepted, the conclusions so far drawn establish our main point, that euryhaline Ostreidae existed in the Middle Jurassic. There are, however, some taxonomic and phylogenetic consequences that need exploring.

GENERIC AFFINITY OF *OSTREA HEBRIDICA*

O. hebridica (as *O. sowerbyi* Morris and Lycett; see above) was one of the original species included in the genus *Liostrea* Douvillé, 1904 by its founder. According to the 'form genus' concept discussed, and deplored, by Stenzel (1971, pp. N1066–1067), *Liostrea* has been widely used since as a name for almost all 'flat' and not strongly ribbed oysters from the Jurassic, including *O. hebridica*. If, however, one is to attempt to disentangle the phylogeny, it is necessary to inquire whether these oysters are a single stock and, as a first step, to examine the type species of *Liostrea*. This is *O. sublamellosa* Dunker, 1846. According to Stenzel (1971) the following species are synonymous: *O. hisingeri* Nilsson, 1832; *O. irregularis* Munster, 1833; *O. anomala* Terquem, 1855; *O. liassica* Strickland, 1876; ?*O. bristovi* Richardson (ex. Etheridge MS.), 1905. Thus the correct name for the type species is *L. hisingeri*. It is widespread in the Lias and Rhaetic of Europe, and its characteristics caused Stenzel (1971, p. N1103) to place the genus firmly in the Gryphaeinae. We discuss *L. hisingeri* below.

Charles and Maubeuge (1953) included *O. sowerbyi* and *O. subrugulosa* in *Praeexogyra*, their new sub-genus of the cupped oyster *Catinula*. They were evidently unaware of Arkell's (1934) demonstration that *O. sowerbyi* and *O. subrugulosa* are synonyms of *O. hebridica*. Furthermore, they placed *O. sowerbyi* and *O. subrugulosa* as members of different lineages in their phylogeny. The type species of *Praeexogyra* is *O. acuminata* J. Sowerby, and our concept of the taxon must be based on that species. *Praeexogyra* was raised to generic rank in Stenzel (1971), and placed in the Gryphaeidae.

All authors are agreed that *O. acuminata* and *O. hebridica* are closely related. When the species occur together, as in the Sharp's Hill Beds and Stonefield Slate (Great Oolite Group) of the Cotswolds (Arkell 1934), they are far from easy to separate. Arkell denied their intergradation, but Sylvester-Bradley (pers. comm.) and the present authors are inclined to uphold it. However, this is unimportant in the present context, because Arkell (1934, p. 31) clearly thought that *O. acuminata* gave rise to *O. hebridica*, but at an earlier horizon; *O. acuminata* characterizes the Upper Bajocian in Eastern France, but ranges into the lower parts of the Bathonian, which is the type horizon. Pugaczewska (1971, pl. XI) figures examples of *O. acuminata* from Poland, some of which approach *O. hebridica* in shape. If one accepts that *Praeexogyra* has generic status, then *O. hebridica* must belong to it. We accept this generic status, but believe on the evidence presented in this paper that *Praeexogyra* Charles and Maubeuge, 1953 should be transferred to the family Ostreidae, sub-family Ostreinae.

MORPHOLOGY OF *LIOSTREA HISINGERI*

O. hebridica, however, remains very similar in general morphology, including range of shape variation, to the type species of *Liostrea*, *L. hisingeri* of the Lower Lias. It is, in fact, much more similar to 'typical' *L. hisingeri* in shape than it is to 'typical' *O. acuminata*. Is it possible that all three species are closely related, or that *L. hisingeri* was an Ostreid, not a Gryphaeid? Were these Liassic oysters euryhaline?

Stenzel (1971, p. N1103) claims that 'orbicular muscle adductor imprint, radial posterior sulcus on left valve, lack of chomata, and absence of umbonal cavity place the genus (*Liostrea*) firmly in the Gryphaeinae'. However, our examination of collections from the Lower Lias at various British localities suggest that its morphological characteristics are somewhat more variable and equivocal (cf. text-fig. 1).

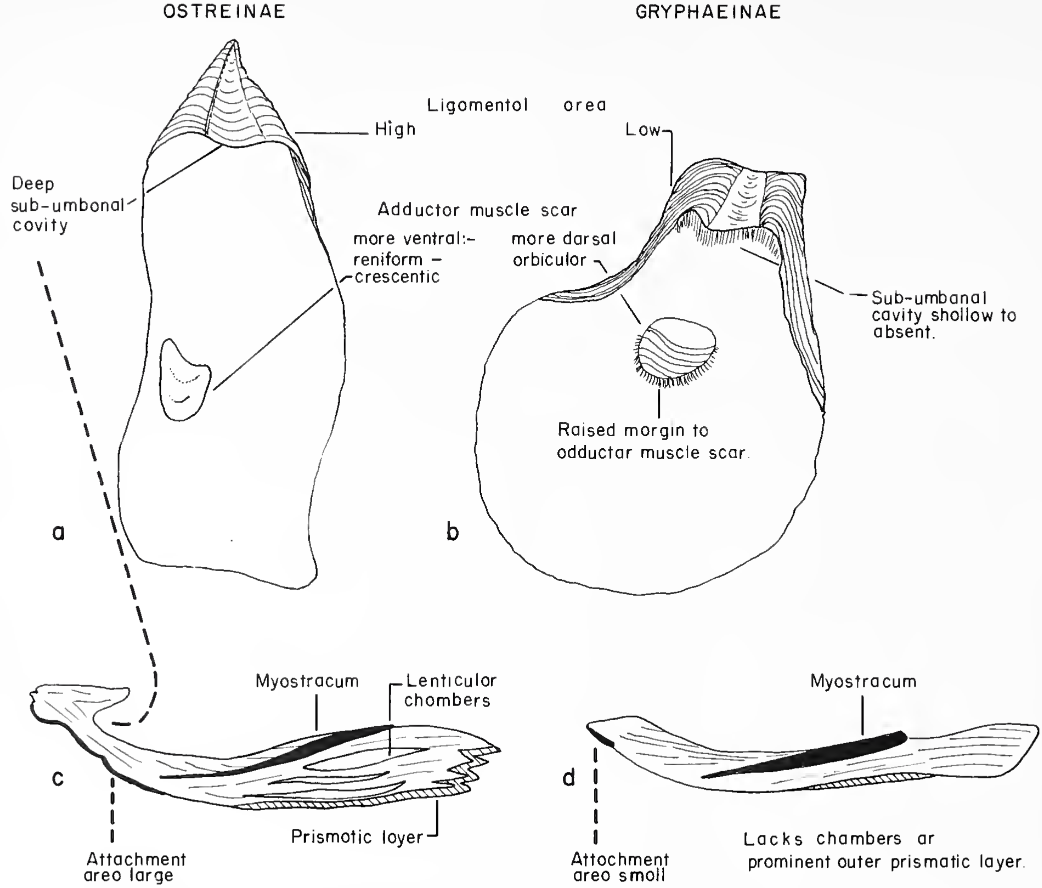
Shape and position of muscle scars. Mainly orbicular; ventral portion of scar in left valve sometimes raised; usually positioned nearer hinge than opposite margin, but position varies.

Radial posterior groove. Not present on any of the material seen by the authors, although present in the material of *L. sublamellosa* seen in Paris by Stenzel.

Umbonal cavity in left valve. Small or absent.

Shell structure. Some chambers; thin prismatic layer sometimes seen.

The general shape and ecological occurrence (reviewed below) of *L. hisingeri* are consistent with Ostreid affinity, as are, more equivocally, the occasional presence of chambers and a prismatic shell layer. On the other hand, the muscle scars, absence



TEXT-FIG. 1. Distinguishing shell-features of left valves of generalized members of the Ostreinae (*a*, *c*) and Gryphaeinae (*b*, *d*), reconstructed from data in Stenzel (1971). *a*, *b*, shell interiors; *c*, *d*, dorso-ventral sections.

of umbonal cavity, and occasional presence of a radial posterior groove point to Gryphaeid affinity.

Stenzel (1971, p. N1096) gives particular weight to shell structure in classification. It is therefore unfortunate from our point of view that Siewert's (1972) recent study of oyster-shell structure includes neither *L. hisingeri* nor *O. hebridica*. It is clear from his list of species that Siewert has a broad concept of the genus *Liostrea* including species referred to *Deltoideum* and to *Praeexogyra* by Stenzel. Our own observations suggest that *L. hisingeri* is more Gryphaeid, *O. hebridica* more Ostreid, in shell structure, but both are variable and the situation is not clear cut.

We discuss aspects of the ecology of *L. hisingeri* below but, basing our taxonomic conclusions on morphological evidence, it seems safest at present to keep *O. hebridica* generically separate from *L. hisingeri*. The unwelcome conclusion is thus that the correct name for *O. hebridica* is currently *Praeexogyra hebridica* (Forbes, 1851). The two species are consequently in different families of the superfamily Ostreacea.

ECOLOGY OF *LIOSTREA HISINGERI*

Our conclusion that *L. hisingeri* may be morphologically intermediate between Gryphaeidae and Ostreidae suggests that its ecological preferences, particularly as regards salinity tolerances, should be investigated. We have not made detailed studies of the conditions of deposition of the beds concerned, but some information is available in the older literature summarized by Arkell (1933) and in works by Hallam (e.g. Hallam 1971).

L. hisingeri is common in the Rhaetic Beds of Dorset, Somerset, and Gloucestershire, principally associated with *Dimyodon intusstriatus*, *Modiolus langportensis*, *Lima valoniensis*, *Cardinia* sp., and *Protocardia* sp. These bivalves may occur in great abundance, whereas known stenohaline groups such as corals, ectoprocts, brachiopods, cephalopods, and echinoderms are either absent or occur only locally. Indicators of shallow water or near-by land, such as mammal, insect, and plant remains, algal limestones (Hamilton 1961), and desiccation cracks, are also found.

A similar situation is seen in the 'pre-*planorbis* beds' of the Lias of South-West England, Yorkshire, Northern Ireland, and Western Scotland. Again, *Liostrea hisingeri* and a small number of other bivalve species occur to the exclusion of stenohaline forms. Such low diversity/high abundance faunas are characteristic of reduced or highly variable salinity, and strongly suggest that *L. hisingeri* was a successful euryhaline species which thrived in the marginal environments associated with the Rhaetic–Liassic transgression in England. As the transgression continued, stenohaline *Gryphaea* almost completely replaced *L. hisingeri*; the typical *Gryphaea* beds of the Lias are also replete with ammonites, belemnites, and echinoderms. A similar picture of the ecology of *L. hisingeri* in the Lias of western Portugal is drawn by Hallam (1971).

EVOLUTION OF EURYHALINITY IN THE OYSTERS

We here present a discussion of the acquisition of euryhalinity in the oyster stock that led to the modern Ostreinae, and thus of the phylogeny of Mesozoic oysters. This is necessarily speculative, because we have not made the required detailed studies of all the oyster species potentially involved; in particular, the bewildering variety of flat oysters in the Lower Lias require further study. The belief that they all belong to one species may well not be correct, and their relationship with the contemporaneous *Gryphaea* species is still far from clear. What we present is one plausible interpretation of the evidence we have discussed.

We believe that *Praeexogyra hebridica* was a fully developed ostreid, and that the group of *L. hisingeri* includes its ancestors. Thus this evolution also represents the evolution of the Ostreidae from the Gryphaeidae. This process began in the Upper Trias/Lower Lias of north-west Europe, and was complete by the Middle Jurassic.

It is possible that many of the ostreid characters shown by *L. hisingeri*, and more strongly by *P. hebridica*, can be explained as adaptations to the marginal marine, highly variable conditions in which these species lived. These include not only the salinity changes which we have stressed so far, but also fluctuations in temperature, current activity, turbidity (associated with river discharge and storms), and temporary subaerial exposure; none of these are experienced to the same extent, if at all, by fully subtidal animals. These effects combine to exert strong selection pressure for 'opportunism', to allow the next generation to be produced quickly before drastic environmental change should wipe out the population, and for various devices to protect the animal from environmental fluctuations.

Changes from a primitive gryphaeid to an ostreid could have helped in the following ways:

1. The young oysters remained attached longer, or throughout life, developing a larger attachment area and becoming less susceptible to current activity. Thus they had no need of the coiled and thickened left valves characteristic of *Gryphaea*. (Whether this represents an evolution of *Liostrea* from *Gryphaea*, as Stenzel believes, or divergent evolution from a common ancestor, is at present uncertain.)

2. The greater importance of cemented attachment meant that suitable attachment sites were more important; thus the reef-forming habit, in which spat-fall and growth were encouraged by a stable framework of adults and dead individuals, developed. The reef-forming habit also allows synchrony of gamete release, as seen in some Recent Ostreinae, which maximizes the chance of fertilization.

3. The oysters developed means of sealing themselves more efficiently from a temporarily unfavourable environment. This included the development of a fringe of flexible conchiolin scales around the edge of the right valve (Stenzel 1971, p. N977). In Recent oysters these scales merge at their proximal ends with the calcite prisms of the outer shell layer, which is well developed in such species. By analogy, fossil Ostreidae, with better-developed prismatic layers than the Gryphaeidae, were more efficient at sealing themselves. The presence of well-developed conchiolin scales in *P. hebridica* may also be inferred from the fact that the margin of the right valve frequently lies inside that of the left valve (Douvillé 1920).

Development of a highly mobile pallial curtain, as described in Recent ostreids by Yonge (1936) and Nelson (1938) may also have occurred at this stage under a similar selection pressure. We cannot, however, make inferences about this property from hard parts alone.

4. The longer time spent with both valves closed produced greater demands on the catch muscle. As Stenzel (1971, p. N1058) points out, ventral shift of the muscle would improve the leverage (and see 6 below). It would also improve the efficiency of the quick muscle, which would be particularly important in a near-shore environment with more suspended inorganic matter, leading to the necessity for frequent expulsion of pseudo-faeces. These points have also been stressed by Yonge (1936) and Nelson (1938).

5. The change in cross-section shape of the adductor muscle to crescentic or reniform increases its surface area/volume ratio. With the heart tucked well into the dorsal concavity of the muscle, improved oxygenation in response to the increased demands on both components of this organ would be a likely result.

6. In Recent non-incubatory Ostreidae, the presence of an umbonal cavity correlates with presence of a promyal passage (Stenzel 1971, p. N1127). This suggests that *P. hebridica* also contained this structure. Nelson (1938) saw the evolutionary development of the promyal passage, resulting in more efficient removal of sediment

from the exhalant chamber, as being a specific adaptation to living in more turbid water, such as is found in marginal marine conditions. Such an opinion supports those which we have stated above. However, living Gryphaeidae all have a promyal passage, and Stenzel considers it a characteristic of the family. This being so, we prefer to regard the presence of the promyal passage in *P. hebridica* (and in Recent non-incubatory ostreids) as being a characteristic inherited from gryphaeid ancestors (discussed further below). We think it is less likely to be one of the specific adaptations developed in response to pressures associated with marginal marine environments, as are the other characteristics discussed above.

PHYLOGENY OF OYSTERS

Our conclusion, although based on a detailed study of only one species, has consequences for the phylogeny of Mesozoic oysters proposed by Stenzel (1971). According to his views, oysters are diphyletic: *Lopha* arises in the Triassic in the Tethyan realm and *Gryphaea* in the Boreal realm; *Liostrea* is an early offshoot of *Gryphaea*; all Ostreidae are descended from *Lopha*; the Ostreinae (true oysters) do not arise until the Cretaceous; *Liostrea* and other non-coiled genera of the Gryphaeidae die out at the end of the Jurassic.

In the phylogeny published by Siewert (1972), *Liostrea* (including *Praeexogyra*) also dies out at the end of the Jurassic. Thus, in both these phylogenies, the origin of the modern 'flat' oysters coincides with the extinction of the morphologically similar 'flat' oysters of the Jurassic, but the two groups are supposedly not related. In Pugaczewska (1971, fig. 3), *Liostrea* (including *Praeexogyra*) is shown persisting to the end of the Cretaceous, but again the modern oysters are derived from *Lopha* (= *Alectryonia*) during the Cretaceous.

Our finding that the *Praeexogyra* belongs to the Ostreidae thus means that the Ostreidae (*sensu* Stenzel) are diphyletic. It also raises the possibility that some, at least, of the Cretaceous to Recent true oysters (Ostreinae) may be descended from the Gryphaeidae *via Liostrea* and *Praeexogyra*, and not from *Lopha* as hitherto believed. This proposal can only be tested by a close examination of the Cretaceous oysters, which we have not attempted. However, a likely descendant of *P. hebridica* is *O. distorta* Sowerby of the middle Purbeck Beds of southern England, now generally dated as basal Cretaceous. Its morphology is poorly known, but in general shape and inferred ecology it is similar to *P. hebridica*. The Lower Cretaceous species, referred to *Ostrea* and figured by Pugaczewska (1975, Pl. XIV) from Poland, are also at least as similar to Jurassic *Liostrea* and *Praeexogyra* as to later *Ostrea*, and could be Gryphaeid descendants.

An independent speculative argument about which modern oysters may be derived from Gryphaeidae, and which from Lophinae, may be stated as follows. Hudson (1963*b*, p. 332) pointed out that *P. hebridica* is closer in morphology and inferred ecology to *Crassostrea* than to *Ostrea*, among living oysters. *Crassostrea* has a promyal passage, is non-incubatory, and is predominantly estuarine in distribution; *Ostrea* lacks a promyal passage, is incubatory, and is more stenohaline. As discussed above, the left valves of many *P. hebridica* exhibit a deep umbonal cavity. According to Stenzel (1971, pp. N1127, 1138) this correlates with the presence of a promyal passage in living members of the Ostreidae. The few living Gryphaeidae (Pycnodonteinae) also have a promyal passage, as does *Crassostrea*, but *Ostrea* and *Lopha* lack this feature. It is possible that Stenzel's informal group of genera centred on *Crassostrea* comprises Gryphaeid descendants, and that genera like *Ostrea* are descendants of *Lopha*.

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GLOBOROTALIA CRASSULA (FORAMINIFERIDA): BLOW'S INTERPRETATION CONSIDERED BIOMETRICALLY

by G. H. SCOTT

ABSTRACT. Analysis of gross shell and substructure dimensions indicates that components both on the spiral and axial aspects of the shell contribute to population discrimination although size differences, possibly of little taxonomic value, obscure the analysis. Harmonic amplitudes based on Fourier approximations to spiral and axial profiles of specimens and normalized to equate for size differences provide data that are more comprehensible in relation to Blow's revision (1969). Subspecies recognized by him exhibit closely similar spiral profiles and this was probably an important unifying feature in his concept of *Globorotalia crassula*. In contrast, axial profiles are divergent. *G. crassula conomiozea* (*sensu* Blow) and possibly also *G. c. crassula* exhibit strong three-fold symmetry due to ventral inflation of chambers whereas in *G. c. viola* shells are biconvex rather than conical, and exhibit four-fold symmetry. Axial shape may broadly correlate with latitude.

W. H. BLOW's great synthesis (1969) of planktonic foraminiferal systematics and Neogene stratigraphy is founded on refined, qualitative, observations of the morphology of individuals, particularly those of type status. To those who consider that classification concerns populations and that variation intrinsic in biological populations should be quantified to be adequately analysed, Blow's work is a challenge in methodology. Can the subtle differences in shape of shells, apprehended by direct perception and used by him to discriminate between taxa, be captured quantitatively? As an example, two representations of population variation in *G. crassula* are considered. One uses gross measurements of the shell and its major structures. The other uses parameters of curves fitted to profiles of the shell. How do they relate to Blow's revision (1969) of the species? *G. crassula* was selected for study because two samples identified by Blow were available. Moreover, his treatment of *G. crassula* is representative of his approach to infraspecific variation. The study is exploratory to identify unifying and discriminating characters. The small number of samples and specimens available precludes evaluation of the subspecies recognized by Blow. His nomenclature is followed.

USAGE

Cushman *et al.* (1930) proposed *G. crassula* to remedy the confusion caused by Brady (1884) when he referred Recent specimens to *Pulvinulina crassa* (d'Orbigny). Their solution was not invariably followed by others (e.g. Barker 1960) and the identity of their new taxon (type locality Humboldt County, California, Pliocene) created further problems. New Zealand workers, for example, followed Finlay and Marwick (1940) and applied the name to *G. crassaformis* (Galloway and Wissler). When the confusion was realized, *G. crassula* became a *nomen dubium*. It was not listed in the local fauna by Jenkins (1967). There is a fuller account of usage in Glaçon *et al.* 1973. The obscurity of the species continued until Blow's study (1969).

[Palaeontology, Vol. 19, Part 1, 1976, pp. 95-105, pl. 16.]

Whereas Cushman and Stewart knew little of the phylogeny and distribution of their species, Blow placed it in historical and geographic contexts. Three variants of *G. crassula* were delineated. Blow called them 'morphotypes' (1969, p. 361) but treated them formally as subspecies. He discussed phylogeny and stratigraphic ranges and considered that the earliest morphotype (*G. c. conomiozea* Kennett) arose from *G. crassaformis* in Zone N.17. It has chambers that are vaulted ventrally, as in *G. truncatulinoides* (d'Orbigny), giving the shell a conical axial profile. The later morphotypes appeared successively in Zone N.18. *G. crassula crassula* was typical of cool-water environments while *G. c. viola* n. sp. occurred in tropical assemblages. They were distinguished by tightness of coiling and appression of chambers but Blow considered that they were closer to each other than to *G. c. conomiozea*. Because *G. c. crassula* seemed more vaulted ventrally, it was considered to be the closer, morphologically, to the ancestral *G. c. conomiozea*. Blow considered that the pattern of evolution was towards flatter, less conical shells.

MATERIAL

1. F100020, Cuba, locality 1583 in Palmer (1948). Type locality of Canimar fauna. Specimen submitted to Dr. W. H. Blow who wrote (14 February 1972) that 'it is referable to *G.* (*G.*) *crassula viola*'. Plate 16, figs. 1–5; twenty-three specimens.

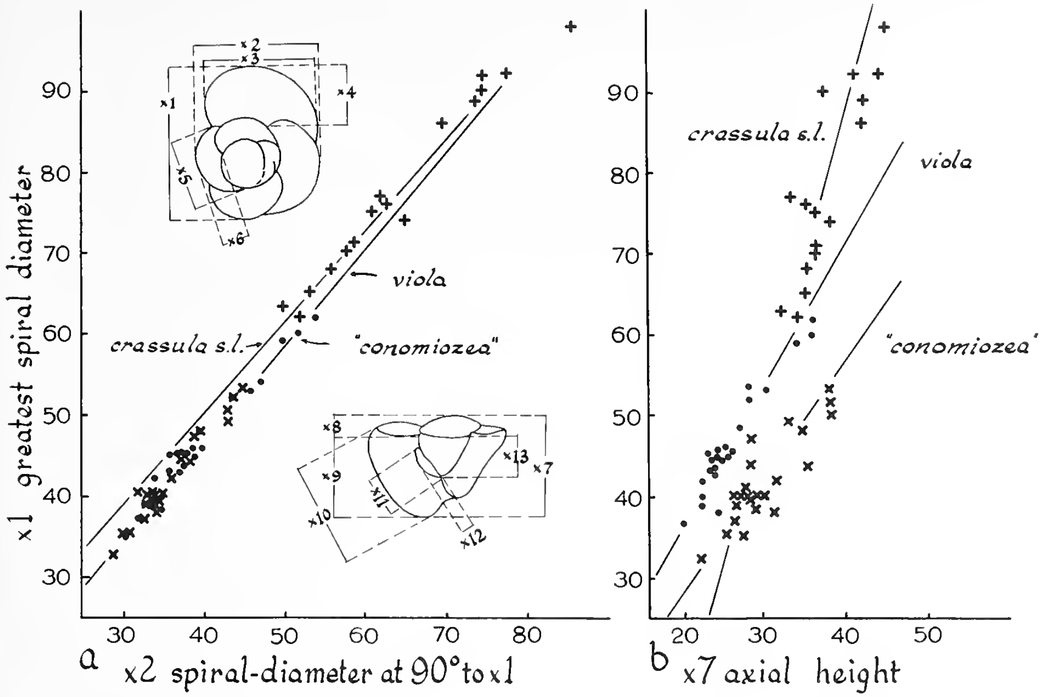
2. S154120, South-western Caribbean Sea, Site 154 Deep-Sea Drilling Project (Edgar *et al.* 1973), core 2, section 6, 120–123 cm, 'early Pliocene'. Material identified and loaned by Dr. W. A. Berggren who noted (21 February 1973) that 'I include the typical *crassula viola* of Blow and forms similar to his re-illustrated holotype of *crassula*. I cannot consistently separate these forms and think that they are all part of a single variable group.' Referred to here as *G. crassula s.l.* Plate 16, figs. 6–10; sixteen specimens.

3. S55/f937, New Zealand, Leader River, Mangapanian Stage (about Pliocene–Pleistocene boundary). Specimen and micrograph identified as *G. c. conomiozea* by Dr. W. H. Blow (14 February 1972). Considered hereafter as *G. c.* '*conomiozea*' because Blow appears to have misidentified *G. conomiozea* Kennett (Scott, in press). Plate 16, figs. 11–15; twenty-three specimens.

The material includes all intact shells from the residues. Data, raw and statistical, are in the author's files at the New Zealand Geological Survey.

ANALYSIS WITH SELECTED VARIATES

Text-fig. 1 shows the location of variates that represent the dimensions of the shell ($x1$, $x2$, $x7$), spiral profiles of the last-formed (nth) and ($n-3$)th chambers ($x3$, $x4$, $x5$, $x6$), ventral surfaces of the same chambers ($x9$, $x10$, $x13$), spire ($x8$), and aperture ($x11$, $x12$). The representations are of maximum dimensions of structures. This approach is conventional in many biometrical studies primarily because the loci for such measurements are well defined. However, a technical question of possible significance concerns the adequacy of the data for studies in shape discrimination. A great variety of closed curves can be drawn when the only constraints are the loci corresponding to the two maximum dimensions of a structure. One suspects that



TEXT-FIG. 1. Bivariate plots of gross dimensions of shells. Scale units times 0·0084 give dimensions in millimetres. Bartlett's lines of best fit are shown.

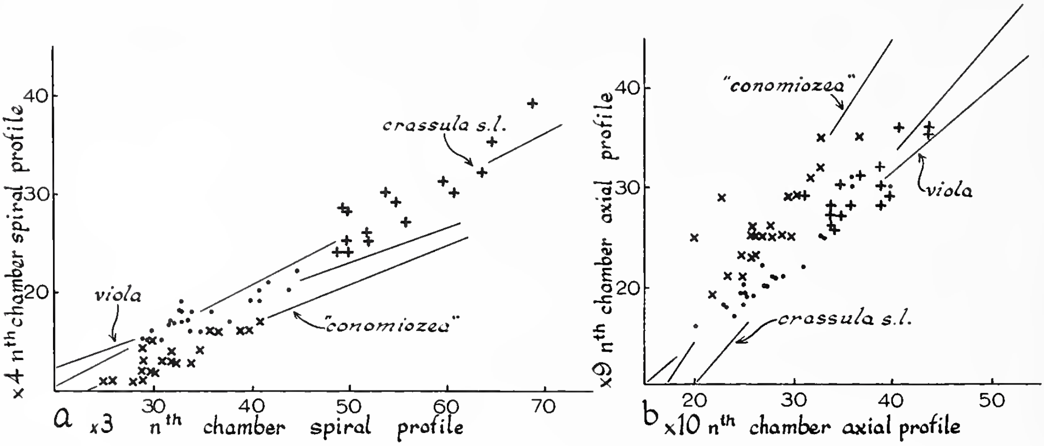
a systematist as experienced as Blow made use of much more detailed information on shape of structures than that derivable from gross dimensions. For this reason the conventional biometrical study is followed by an analysis of shell profiles represented by closely sampled coordinates.

Shell diameters, spiral orientation. The location and orientation of scatters for variates $x1$, $x2$ (text-fig. 1*a*) are closely similar in S55/f937 (*G. c.* '*conomiozea*') and F100020 (*G. c. viola*). Shells from S154120 (*G. crassula s.l.*) are considerably larger. This may reflect selective preservation or be due to bias in sampling. For F100020 and S55/f937 the intercepts of the fitted lines lie close to the origin suggesting an isometric relation between $x1$, $x2$. However, the line fitted to the much larger shell dimensions in S154120 has confidence limits (4·00–7·13, 99% level) that do not include the origin. Slight size allometry is suggested. With this reservation, the data indicate that spiral shape, as estimated from $x1$, $x2$, is stable from sample to sample and is largely size-independent.

Spiro-axial shape. In text-fig. 1*b* the cone-like shells of *G. c.* '*conomiozea*' are strongly distinguished by their axial height. There is no indication in this sample that the proportion $x1:x7$ changes with increase in $x1$ (99% confidence limits are 0·78 to −3·08). In contrast, for *G. crassula s.l.* the data suggest that axial height of shells tends to decrease, relatively, with increase in spiral diameter. Larger shells are more disc-like than smaller shells. A 'menardine' trend (Scott 1973), iteratively followed in globorotalids (Cifelli 1969), may occur during ontogeny.

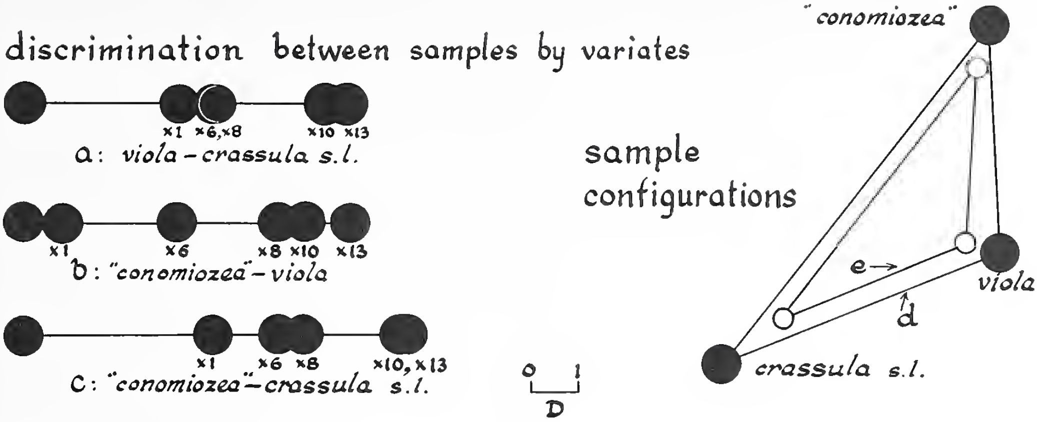
Spiral profile of n*th chamber.* Scatters for *G. c. viola* and *G. crassula s.l.* are similar in orientation (text-fig. 2*a*) although differentiated by size. In contrast, chamber height ($x4$) in *G. c. 'conomiozea'* from S55/f937 tends to be less, relative to length ($x3$).

Axial profile of last chamber. Variates $x9$, $x10$ (text-fig. 2*b*) reflect the angle formed by the intersection of the spiral and ventral surfaces of the *n*th chamber. In F100020 and S154120 $x10$ tends to be considerably greater than $x9$ (low axial profile). The data for S55/f937 reflect the extension of the chamber profile ventrally so that $x10$ is more nearly equal to $x9$. There is considerable intra-sample variation in relative proportions $x9:x10$ but the scatters for *G. crassula s.l.* and *G. c. viola* do not overlap with that for *G. c. 'conomiozea'*.



TEXT-FIG. 2. Bivariate plots of dimensions of last-formed (*n*th) chamber. Scale units times 0·0084 give dimensions in millimetres. Bartlett's lines of best fit are shown.

Multivariate discrimination. Bivariate plots indicate considerable size variation, both within and between samples. Principal component analyses of the multivariate data show that most of the intra-sample variation is due to size rather than shape differences. In each sample the largest principal axis of the covariance matrix reflects size variation (all direction cosines positive) and accounts for over 80% of the variation. The Mahalanobis measure of distance between populations and its associated linear discriminant function utilize the magnitude of variation within samples without regard to its sources. Thus, in comparisons between pairs of samples, *G. crassula s.l.* is discriminated from *G. c. 'conomiozea'* and *G. c. viola* (text-fig. 3*a*, *c*) even when only one variate ($x1$) is considered. In both comparisons the means for $x1$ differ at the 1% level (D^2(S154120: S55/f937) = 17·98; D^2 (S154120: F100020) = 11·75). Reference to the distributions for $x1$ (text-fig. 1*a*) shows that size differences are responsible. Conversely, the distribution for $x10$ (text-fig. 2*b*) suggests that the additional distance produced by this variate in text-fig. 3*c* is not due to differences in the direction of size



TEXT-FIG. 3. Effect of variates on taxon discrimination (*a*, *b*, *c*); configuration of samples (*d*) using pooled covariance matrix, and a version (*e*) correcting for some size differences. Scale is in Mahalanobis's units (D). Note that D^2 may be used to test the significance of the difference between sample means (Rao 1952). In configurations *d*, *e* all comparisons between sample means are significant at the 1% level.

increase. The patterns of variate-by-variate discrimination between samples shown in text-fig. 3*a*–*c* reflect an admixture of size and shape information.

Size differences between populations may be relevant in taxonomy. However, the absence of small individuals in S154120 suggests that this population was either selectively preserved or subject to biased sampling. On the assumption that size differences among the samples were growth or sampling effects, Mahalanobis's distances were recomputed by a technique (Burnaby 1966) that removed the effect of variation in the direction of the largest principal axis of each sample covariance matrix. These directions in the 13-variate spaces portrayed much of the intra-sample variation in size. Text-fig. 3*d*, *e* show configurations of the samples using Mahalanobis's distances that, respectively, include and exclude variation in these directions. Distances are reduced in text-fig. 3*e* but the disposition of samples is little changed. Intra-sample size variation contributes to intersample distances but does not distort them. Differences between samples means remains significant at the 1% level. The study suggests that axial shape of chambers, used in systematics by Blow, is significant in population discrimination (variates $x9$, $x10$). Interpopulation variability in spiral dimensions of the last-formed chamber (variates $x3$, $x4$) is also indicated.

HARMONIC AMPLITUDES

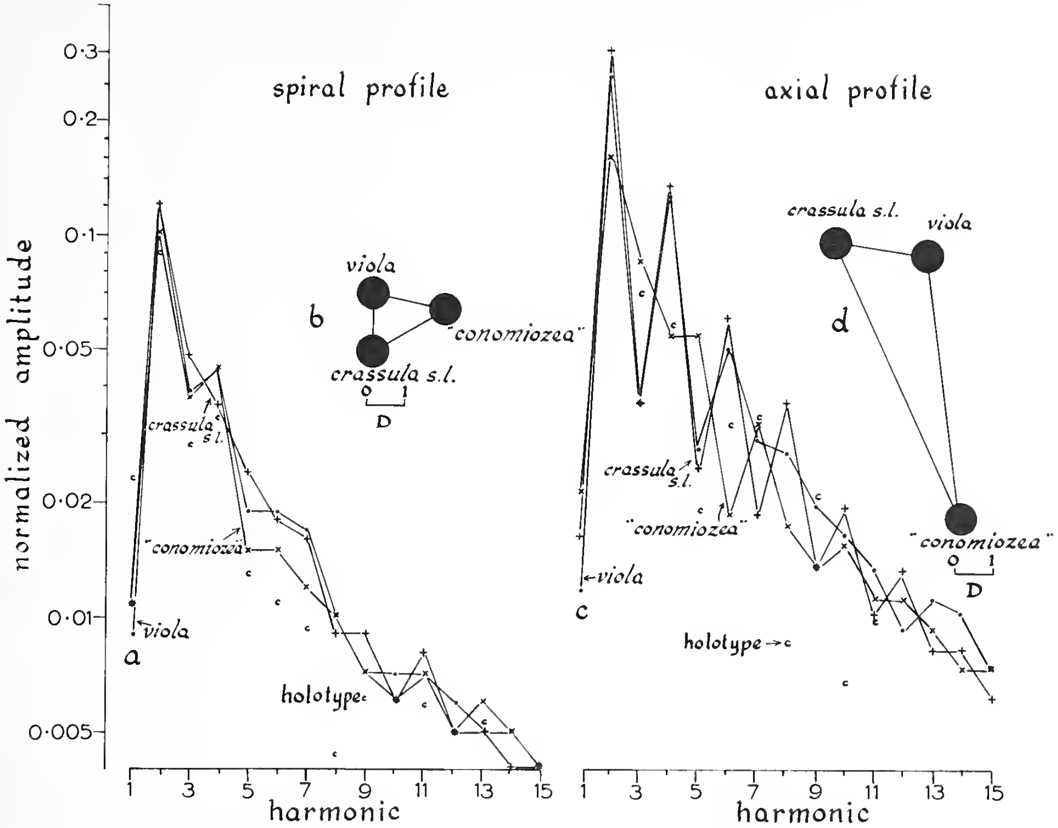
Whereas in the foregoing study variates were selected to represent shell morphology, the following analysis considers taxonomic discrimination using variates determined from quantified profiles of shells. The variates are determined by the data rather than by the investigator. The procedure perhaps matches more closely the intuitive procedure used for identification of taxa.

Spiral and axial profiles of shells were quantified with a manually guided digitizer (Scott 1975) that recorded the x, y coordinates of forty or more points around the periphery on paper tape. In numerical analysis (Hildebrand 1956) Fourier series provides a means of approximating a function over a specified period. In this application the radius at a point on the curve representing the specimen profile is taken as a function of the angle from a selected reference point. The radius at angle θ is given by $a_0+\Sigma a_k \cos k\theta+b_k \sin k\theta$ where a_0, the zeroth harmonic, is the mean radius of the figure and a_k, b_k are the determined Fourier coefficients for the $k = 1, 2, \ldots, \frac{1}{2}n-1$ harmonics (n is the number of coordinate sets recorded on the periphery). The approximation provides a least squares fit to the figure and, as terms in the expansion are orthogonal, the contribution of each harmonic towards the fit is directly obtained. Algorithms in Ehrlich and Weinberg (1970) were used for computing a_0, a_k, b_k and from these were obtained normalized amplitude coefficients $c_k = (a_k^2+b_k^2)^{\frac{1}{2}}/a_0$. The zeroth harmonic is used to remove the effects of size on amplitudes. The normalized amplitudes $c_k (k = 1, \ldots, 15)$ serve as variates for the discriminatory study.

Spiral profile of shell. In general, the amplitude of the ith harmonic reflects the extent to which the data can be approximated by a figure with i vertices. Mean amplitudes are now considered. For the spiral profile (text-fig. 4*a*) the first harmonic is, in all samples, a small contributor to the approximation, whereas the second (representing an elongate figure with two vertices) provides the largest contribution. For *G. c.* '*conomiozea*' and *G. c. viola* the amplitude of the fourth harmonic is larger than the third. This reflects the lobation produced by the four chambers that form the final whorl. For *G. crassula s.l.* the tendency, in some individuals, for the final chamber to be placed at less than 90° revolution from its predecessor seems to lead to stronger three-fold symmetry. The small amount of information provided by harmonics $\geqslant 5$ emphasizes the basically simple, quadrate, shape of the spiral profile of the shell.

Analysis of the 15-variate data by linear discriminant functions showed that amplitudes for *G. c. viola* and *G. crassula s.l.* are probably drawn from a common population ($P > 0{\cdot}05$) as are *G. c. viola* and *G. c.* '*conomiozea*' ($P > 0{\cdot}05$). The data for *G. c.* '*conomiozea*' and *G. crassula s.l.* are more equivocal as the test lies in $0{\cdot}05 > P > 0{\cdot}01$ region. A configuration (text-fig. 4*b*) using Mahalanobis's D computed with the covariance matrix pooled from the three samples reflects these results by showing the slightly greater separation of *G. c.* '*conomiozea*' from the remainder.

Axial profile of shell. Incongruity between the amplitude spectrum for *G. c.* '*conomiozea*' and those for *G. c. viola* and *G. crassula s.l.* is marked in text-fig. 4*c*. For the lower harmonics two contrasting types of spectrum are present. *G. c. viola* and *G. crassula s.l.* have larger amplitudes for harmonic 2 than *G. c.* '*conomiozea*'. This expresses the tendency for shells in the former samples to have large spiral diameter relative to axial height. Furthermore, in axial profile these shells are rather uniformly inflated to give a biconvex figure. Thus the amplitude for harmonic 4 is also strong. In contrast, in *G. c.* '*conomiozea*' shells tend to be strongly inflated ventrally whereas spire height is low. The axial shell profile is more trigonal than in other taxa and this is reflected in the amplitude of harmonic 3. The probability that mean amplitudes (fifteen harmonics) for *G. c. viola* and *G. crassula s.l.* are from a common population is between $0{\cdot}05 > P > 0{\cdot}01$. In comparisons involving *G. c.* '*conomiozea*' it is less than 0·01. Separation of *G. c.* '*conomiozea*' from remaining samples in text-fig. 4*d* is marked.



TEXT-FIG. 4. Mean amplitudes (normalized) for fifteen Fourier harmonics, spiral and axial profiles (*a*, *c*); points 'c' are values for holotype of *Globorotalia crassula crassula*. Sample configurations (*b*, *d*) scaled in Mahalanobis's units (D).

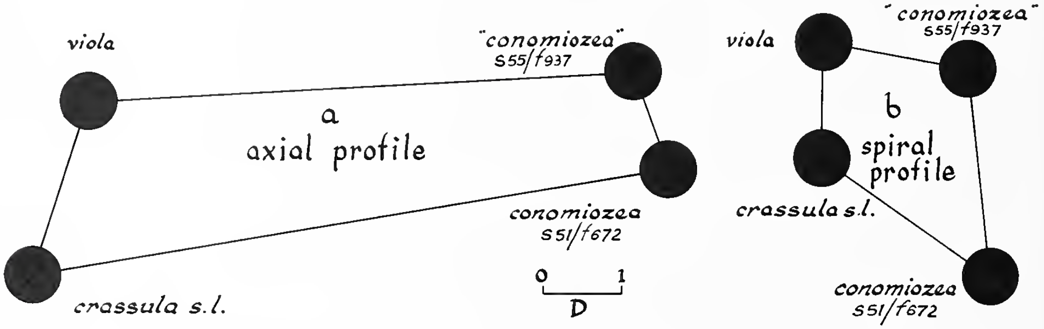
SYSTEMATIC INTERPRETATIONS

Outline drawings are commonly used to illustrate foraminiferal taxa. Ill-preserved or encrusted planktonic specimens in which chamber arrangement is obscured are still readily identified by experienced workers, mainly from information resident in shell profiles. This suggests that, of the two metrical techniques employed here, Fourier harmonic amplitudes of specimen profiles provide the closer approach to the patterns detected by direct qualitative perception. It is doubtful, for example, that linear variates such as $x4$ (text-fig. 1) of this study are perceived as such by the intuitive taxonomist.

The major result provided by analysis of amplitude spectra is that among the taxa examined there is similarity in spiral profiles and diversity in the axial profiles. Harmonic amplitudes for the spiral profile indicate similar populations. Because of the apparent significance of shell profiles in qualitative taxonomy I suggest that the pattern formed by the spiral profile was a primary unifying character in Blow's association of *G. c.* '*conomiozea*' with *G. c. viola*. Conversely, as Blow indicated, the axial profile of the shell discriminates these taxa.

Relation to G. conomiozea. Inclusion of S51/f672, a New Zealand sample studied by Kennett (1966) when he proposed *G. conomiozea*, in the sample configurations (recomputed using the pooled covariance matrix for the four samples) shows that the mean axial profile of this sample is indeed very close to that for *G. crassula* '*conomiozea*' from S55/f937 (text-fig. 5*a*). To the contrary, when spiral profiles of the shells are considered (text-fig. 5*b*) S55/f937 is closer to samples of *G. crassula* from the Atlantic region than to *G. conomiozea* from type region in New Zealand. If the shape of the spiral side of the shell is significant in systematics, the configurations support the view (Scott in press) that Blow (1969) misidentified *G. conomiozea* Kennett. *G. crassula* '*conomiozea*' of Blow appears to refer to populations of *G. crassula* in which chambers are inflated ventrally to give axial shell profiles very similar to those of *G. conomiozea* Kennett. For additional data see Scott (in press).

Holotype of G. c. crassula. This specimen provides some information about shape in *G. c. crassula* populations although it is unknown whether or not its morphology is typical. Amplitude spectra were computed from drawings of the holotype (Blow 1969, pl. 9, figs. 2, 3) in axial and spiral orientations. With the exception of that for harmonic 1 (text-fig. 4*a*), amplitudes for this specimen in spiral orientation are lower than the mean values for *G. c. viola* and for *G. c.* '*conomiozea*'. Usually they lie more



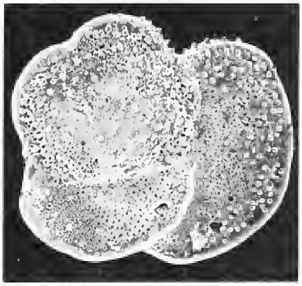
TEXT-FIG. 5. Configurations from harmonic amplitudes as in text-fig. 4 but including similar data from *Globorotalia conomiozea* Kennett, S51/f672, New Zealand (Kennett 1966).

EXPLANATION OF PLATE 16

Figs. 1–5. *Globorotalia crassula viola* Blow. FP 2558. F100020. 1, spiral orientation, ×100. 2, aperture, ×390. 3, axial orientation, ×80. 4, periphery last-formed (*n*th chamber, ×400. 5, periphery (*n*—2)th, (*n*—3)th chambers, ×240.

Figs. 6–10. *Globorotalia crassula* Cushman and Stewart *s.l.* FP 2559. S154120. 6, periphery of *n*th chamber, ×200. 7, spiral orientation, ×60. 8, aperture, ×390. 9, oblique axial orientation, ×60. 10, periphery (*n*—2)th, (*n*—3)th chambers, ×200.

Figs. 11–15. *Globorotalia crassula* '*conomiozea*' *sensu* Blow. FP 2524. S55/f937. 11, periphery *n*th chamber, ×380. 12, periphery (*n*—2)th, (*n*—3)th chambers, ×400. 13, spiral orientation, ×110. 14, aperture, ×270. 15, axial orientation, ×100.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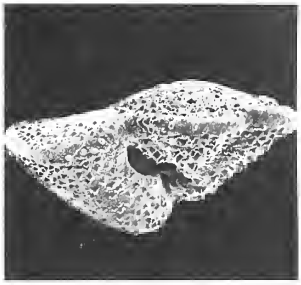
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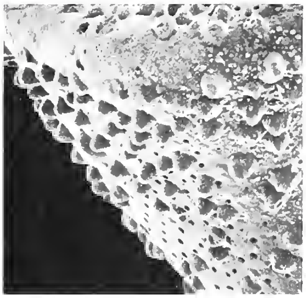
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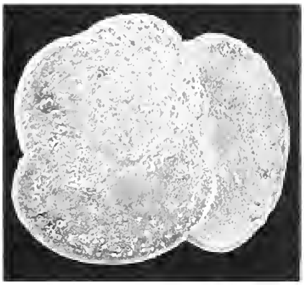
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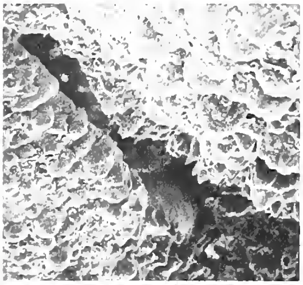
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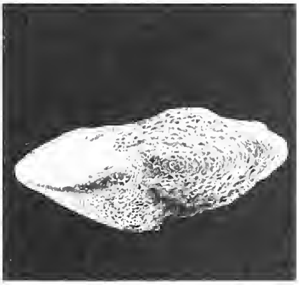
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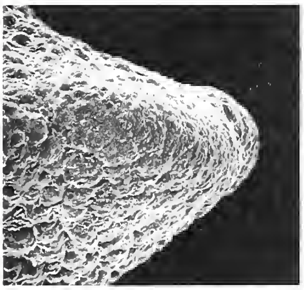
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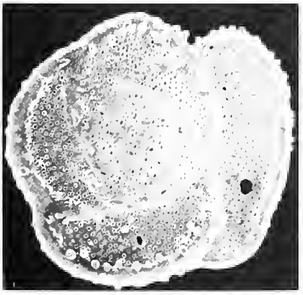
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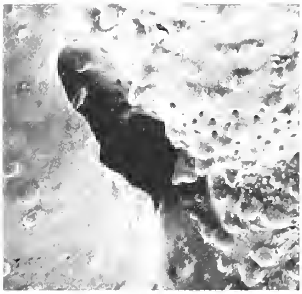
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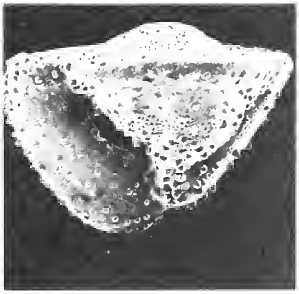
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SCOTT, *Globorotalia*

than one standard deviation away from sample means. The small amplitudes indicate that chambers do not project strongly in the outline. This is consonant with Blow's opinion (1969, p. 362) that *G. c. crassula* has a tightly coiled shell with closely appressed chambers. Of the sample spectra shown on text-fig. 4*a* the pattern for the holotype of *G. c. crassula* is closest to that for *G. c.* '*conomiozea*'. A similar result is obtained when the vector of spectral values for the holotype is projected on to the spaces defined by principal axes for the two largest roots of sample covariance matrices. Of these low-dimensional representations of the fifteen-variate sample spaces, only in that for *G. c.* '*conomiozea*' does the holotype lie within the sample scatter. Such representations are no more than a rough guide to affinity as neither the sample mean vector nor covariance matrix is known for a *G. c. crassula* population.

Blow's remarks (1969, p. 362) that *G. c. crassula* is more vaulted ventrally than *G. c. viola* and in this respect closer to *G. c.* '*conomiozea*', is supported by amplitude spectra for the holotype in axial orientation (text-fig. 4*c*). Amplitudes for harmonics 3, 4 strongly distinguish *G. c.* '*conomiozea*' from *G. c. viola* and *G. crassula s.l.* For the holotype of *G. c. crassula* the equivalent values lie close to those for *G. c.* '*conomiozea*'.

CONCLUSIONS

If qualitative classification of foraminiferal shells is viewed as a pattern establishment-recognition process then techniques such as Fourier analysis that provide approximations to curves appear to be better quantitative analogues than do conventional sets of gross dimensions.

The samples studied of *G. crassula* are united by the form of the spiral outline of the shell. Chamber lobation appears to be stronger developed in populations from the tropics (F100020, S154120) than in higher-latitude representatives (S55/f937, holotype of *G. c. crassula*).

The shape of the axial profile of the shell strongly discriminates *G. c. viola* from *G. c.* '*conomiozea*'. If typical, the holotype of *G. c. crassula* indicates that this taxon is close to *G. c.* '*conomiozea*' in characteristics of the axial profile.

While the data are insufficient to authenticate Blow's concept of *G. crassula*, they do suggest that some variant populations, widely separated geographically, possess similarities in shell form. Whereas spiral profiles are relatively uniform, axial profiles in the group are variable and may express different adaptive strategies towards constraints in planktonic environments. Samples from the tropics have relatively compressed axial profiles (*G. c. viola*, *G. crassula s.l.*); higher latitude representatives are more inflated ventrally (*G. c.* '*conomiozea*', possibly *G. c. crassula*). Both types of axial profile may improve form resistance to passive sinking, although their relative efficiencies are unknown. Convergent form, especially in the axial shape of the shell, is rife among globorotaliids and seems to reflect similar solutions to common problems in hydromechanics. It cannot be discounted in *G. crassula*. However, in defence of Blow's revision, it may be argued that the group is unified by aspects of shell form that are not directly connected with axial shape.

G. c. conomiozea of Blow (1969) does not refer to *G. conomiozea* Kennett. A new name may be required although it is possible that the populations referred to fall within the range of variation of *G. crassula crassula*.

Acknowledgements. This paper is presented in tribute to the work of the late Dr. W. H. Blow on planktonic foraminiferal systematics. His courtesy in identifying material greatly facilitated the analysis reported here. Dr. W. A. Berggren provided material and with a colleague commented on the manuscript.

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TERTIARY AND PLEISTOCENE CRABS FROM BARBADOS AND TRINIDAD

by J. S. H. COLLINS *and* S. F. MORRIS

ABSTRACT. A new species of *Hepatus* and one of *Thaumastoplax* are described from the Miocene of Trinidad; the geographical range of *Persephona* cf. *punctata* (Linné) is possibly extended southward; the geographical range of *Portunus oblongus* Rathbun is extended and a more complete description is given; *Necronectes proavitus* (Rathbun) is represented by a claw fragment. Two new species, *Falconoplax bicarinella* and *Pinnixa* (*Palaeopinnixa*) *perornata*, are described from the Lower or Middle Eocene Scotland Beds of Barbados. *Herbstia exserta* sp. nov. is described and a further eleven species in seven genera are recorded for the first time as fossils from the Pleistocene Coral Rock of Barbados. It appears that the extant species were well established in Pleistocene times and there has been little or no significant change in geographical distribution.

IN her researches on decapod Crustacea, particularly during the period 1919–1925, M. J. Rathbun made known a great number of species from the West Indies and summarized previous work. Withers (1926) added considerably to the list using material collected largely by the late Dr. C. T. Trechmann in Jamaica and Barbados. During his visits to Barbados (*circa* 1920–1964) Dr. Trechmann collected extensively from the Lower or Middle Eocene Scotland Beds and the Plio-Pleistocene Coral Rock from several localities about the island, and crabs were prominent in the collection of fossils received by the British Museum (Natural History) as the Trechmann Bequest (1964).

In 1956 the Trinidad Kern Oilfield Ltd. presented to the British Museum (Nat. Hist.) a considerable quantity of crab remains collected by Dr. N. Boutakoff and Dr. K. Glazewski from the Brasso Formation. This Formation was assigned by Kugler (1954, p. 411) to the neritic facies of the *Globorotalia fohsi* Zone (N. 12) which is considered by Berggren (1971, table 52.40) to belong to the Serravallian Stage of the Miocene, Zone N. 12 belonging in the Middle Miocene. The specimens are preserved in a friable rusty-brown sandstone with comminuted shell debris. They comprise mostly carapace and limb fragments of *Portunus oblongus* Rathbun. *Necronectes proavitus* Rathbun and *P. oblongus* have also been identified from the Lower Miocene San Sebastian Formation and Ponce Limestone of Puerto Rico by Gordon (1966). *N. proavitus* has been recorded from the Lower Miocene Loyola Formation of Ecuador (Morris 1973, p. 23) and Dr. R. Bristow has since sent us a specimen of *P. oblongus* from the Upper Miocene, Angostura Formation of Ecuador. The type locality for *N. proavitus* is the Middle Miocene, Gatun Formation, from Panama and *P. oblongus* was originally described from the Lower Miocene Cercado Formation of the Dominican Republic. Whilst *P. oblongus* ranges through the Miocene, *N. proavitus* is as yet known only from the Lower and Middle Miocene. In addition there is a single carapace of *Persephona* cf. *punctata* (Linné) and single carapaces of two new species described below as *Thaumastoplax intermedius* and *Hepatus nodosus*.

[Palaeontology, Vol. 19, Part 1, 1976, pp. 107–131, pls. 17–20.]

The crabs throw very little light on the age of the Scotland Formation except to confirm a probable Lower or Middle Eocene age. Guppy (1911) regarded the age of the Scotland Beds as Eocene. Bullen-Newton in a manuscript report (1922), the main conclusions of which were not published until 1932 (Matley), said that the mollusca suggested a Bartonian–Priabonian age. Trechmann (1925) thought that the mollusca from the Chalky Mount Conglomerate, Upper Scotland Formation, were high in the Middle Eocene to low in the Upper Eocene. Withers (1926) unfortunately thought that the presence of *Callianassa lacunosa*, a form described by Rathbun (1919*a*) from the Oligocene Culebra Formation of Haiti, indicated an Oligocene age for the Scotland Beds. Subsequently Davies and Vaughan (in Matley 1932) thought that the foraminifera and corals suggested an Eocene age for the beds. The stratigraphy of the Palaeogene of Barbados was revised by Senn (1940). He divided the Scotland Formation into five beds:

Mount All Beds
Chalky Mount Beds
Murphys Beds
Morgan Lewis Beds
Walkers Beds

The Joes River Beds, which lie uncomformably between the Scotland Beds and the Oceanic Formation, are shallow submarine mud flows. They contain erratic blocks that are of Cretaceous to Upper Scotland Formation in age. Senn collected from the lowest beds of the Oceanic Formation the foraminifer *Hantkenina*, which is an Upper Eocene indicator. The Scotland Formation thus cannot be younger than Upper Eocene. Senn later (1948) modified his views and he believed that the Scotland Beds were Lower and lower Middle Eocene. Cizancourt (1948), in her study of the nummulites from Barbados, found that by far the commonest species was *Nummulites* (*Operculinoides*) *bermudezi* which occurred in the Palaeocene erratic blocks and in the Chalky Mount Beds as well as the Murphys Beds. Of the ten species recorded from the Scotland Formation only two, *N. aster* and *N. pellatispiroides*, were not found in the Palaeocene erratics from the Joes River Beds, but *N. pellatispiroides* is known from the base of the Eocene in Mexico. Mme Cizancourt, concerned about the apparent long-ranging species, thought that care should be taken in interpretation since it was possible that secondary deposition might be involved. Two new crab species are described from these largely estuarine Scotland Beds. One is assigned to *Falconoplax*, a genus present in the Middle Eocene Jarillal Formation of Falcon Province, Venezuela (Guevara 1967) and the ?Palaeocene of Virginia, U.S.A. The second new species is a *Palaeopinnixa*, representing the second known species from the North American Eocene. All the crabs probably come from the Chalky Mount Beds.

The nummulites as well as the crab *Falconoplax* seem to suggest a Lower to Middle Eocene age for the Scotland Formation, rather than the previously thought Middle or Upper Eocene.

The Coral Rock Series occurs extensively in the central and north-western parts of Barbados, forming a cap some 61 m (200 ft) thick, resting on basal beds. The Coral Rock Series has usually been assigned to the Pleistocene but Trechmann (1937) believed the basal beds to be pre-Pleistocene, i.e. Pliocene. Trechmann considered that the presence of *Haliotis*, a form absent from the area at the present day, *Pleuroto-*

maria, and *Meiocardia* in the basal beds indicated that older beds were present. The more recent work on the molluscan fauna of Barbados by Jung (1968) supports Trechmann's view that the basal beds are indeed Pliocene in age. Mollusc fossils from these beds are internal moulds.

The Coral Rock Series rises to 334 m (1100 ft) O.D. in a series of steep wave-cut terraces which contain fossils of living species of molluscs, corals, and brachiopods, as well as crabs. We have given the terrace heights above O.D. as recorded by Trechmann. Unfortunately, it has been impossible to match these terrace heights with recent work on the chronostratigraphy of the terraces (Broecker *et al.* 1968; Matthews 1972; Bender *et al.* 1973).

Outstanding among the youngest material present is a new species of *Herbstia* whose nearest relative appears to be *H. pyriformis* (Bell), a Recent species from the Galapagos Islands. Other finely preserved oxyrhynchs include five extant species of *Mithrax*, *M. spinosissimus* (Lamarck), *M. hemphilli* Rathbun, *M. verrucosus* Milne-Edwards, *M. hispidus* (Herbst), *M. caribbaeus* Rathbun, and *M.* (*Mithraculus*) *ruber* (Stimpson). Also included are *Carpilius corallinus* (Herbst) and *Actaea rufopunctata nodosa* Stimpson, both represented by more or less complete carapaces; two species of *Portunus* and a *Pilumnus* are represented by limb fragments. None of the extant species has previously been recorded as a fossil. The genus *Mithrax* has only once before been recorded in a fossil state, from the Pleistocene of Haiti (Rathbun 1924). The Recent habitat of *Mithrax* species in this collection is generally near the shore, although some have been taken from depths ranging to 98 fathoms: they have been taken from bottoms varying from coral reefs to sand or mud. Since the degree of prominence of spines and tubercles about the carapace is subject to some variation among individuals of Recent species of this genus it would, with the limited material in the present collection, be unwise to regard the slight differences noted in *M. hispidus*, for example, as indicative of any evolutionary tendencies.

Rathbun 1925*a*, 1930, or 1937 should be consulted for intermediate synonymies of previously established species.

SYSTEMATIC DESCRIPTIONS

Infraorder BRACHYURA Latreille, 1803
Section OXYSTOMATA H. Milne-Edwards, 1834
Superfamily DORIPPOIDEA de Haan, 1841
Family TYMOLIDAE Alcock, 1896
Genus FALCONOPLAX Van Straelen, 1933

Type species. Falconoplax kugleri Van Straelen by original designation.

Falconoplax bicarinella sp. nov.

Plate 18, fig. 7

Diagnosis. Carapace with bilobed front, sharp lateral margins with two incipient spines, and a weak longitudinal ridge on each metabranchial lobe.

Holotype. A part internal mould, part decorticated carapace. In. 61353 (Pl. 18, fig. 7).

Horizon and locality. Lower or Middle Eocene, Scotland Beds, Spa, Barbados.

Description. Carapace subovate in outline, about one-third wider than long, with the widest point a little more than three-quarters of the carapace length from the front; it is moderately rounded longitudinally and transversely almost flat. The orbito-frontal margin is just under half the carapace width. The front is slightly produced and bilobed with the extremities somewhat thickened. The orbits are ovate, rather deep, and facing forward; the upper orbital margin is thin, slightly upturned with just a trace of a notch and a blunt spine forms the outer orbital angle. The anterolateral margin is short and rounded; there is a small blunt spine forward of the cervical notch and another one behind leading to a beaded line of fine granules along the postero-lateral margin. The posterior angles are broadly rounded. The posterior margin is broken, but was probably almost straight and bounded by a thin ridge. The lateral margins are sharp with the sides inclined almost at right angles behind the cervical notch and inclined slightly inwards in front of it. The regions and lobes are fairly distinct on the cast. The cervical furrow is broad and deep; from the margin it is inclined slightly forward before turning sharply back to unite with the urocardiac groove. The branchiocardiac furrow is narrower and almost parallels the downward slope of the cervical. The hepatic region is small and depressed. The somewhat tumid protogastric area is barely differentiated from the mesogastric; there is a low node close to the hepatic and another at the downward turn of the cervical. The anterior process of the mesogastric area is thin and depressed between small ovate epigastric lobes. The urogastric region is subquadrate and almost confluent with the rather urn-shaped cardiac region. The epi- and mesobranchial lobes together are shaped like a scalene triangle with the angles bluntly rounded. The epimeral adductor muscle scars are seen as two deep pits between the urogastric and mesobranchial lobes. On each metabranchial lobe a ridge composed of beaded granules nearly parallels the lateral margin. On the median side of this ridge the lobe is rounded while on the outside it is flatly depressed. The elevated parts of the carapace are densely covered in granules; on the branchial lobes they tend to become arranged in rows. The granules give way to small pits on the lateral margins and at the bases of the grooves.

A natural mould of the right chela lies along the right front of the specimen. A cast shows the hand to have been robust and more or less equal to the carapace length; the fixed finger is two-thirds the length of the palm and there is evidence of a proximal spine on the movable finger and two on the fixed finger; the basal margin

EXPLANATION OF PLATE 17

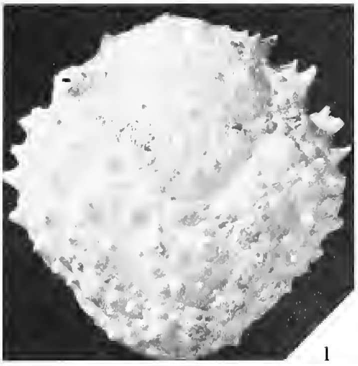
Fig. 1. *Mithrax* (*Mithrax*) *spinosissimus* (Lamarck), p. 118, Pliocene, Coral Rock; Blower's Gully, north of Bridgetown, Barbados. Dorsal view of carapace. In. 61355, ×1.

Figs. 2, 3. *Mithrax* (*Mithrax*) *hispidus* (Herbst), p. 119, Pliocene, Coral Rock 30·5 m (100 ft); Gibbons, Barbados. 2, dorsal view of carapace. In. 61191, ×1. 3, dorsal view of carapace. In. 61192, ×1·1.

Figs. 4–6. *Mithrax* (*Mithrax*) *hemphilli* Rathbun, p. 118, Pleistocene Coral Rock 104 m (340 ft); Highgate, Barbados. 4, dorsal view of carapace. In. 61208, ×1·5. 5, ventral view of carapace. In. 61208, ×1·5. 6, dorsal view of carapace. In. 61213, ×1·5.

Fig. 7. *Mithrax* (*Mithrax*) *verrucosus* H. Milne-Edwards, p. 119, Pliocene, Coral Rock 30·5 m (100 ft); Gibbons, Barbados. Dorsal view of carapace. In. 61200, ×1·5.

Fig. 8. *Mithrax* (*Mithraculus*) *ruber* (Stimpson), p. 120, Pliocene, Coral Rock 30·5 m (100 ft); Gibbons, Barbados. Dorsal view of internal mould of carapace. In. 61198, ×1·5.



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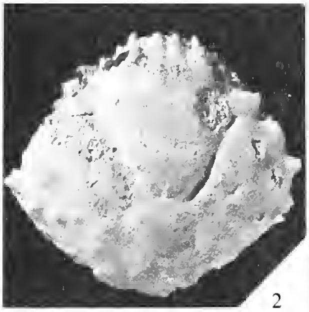

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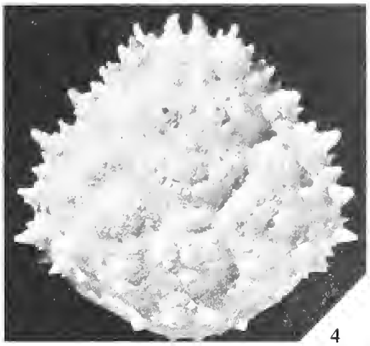

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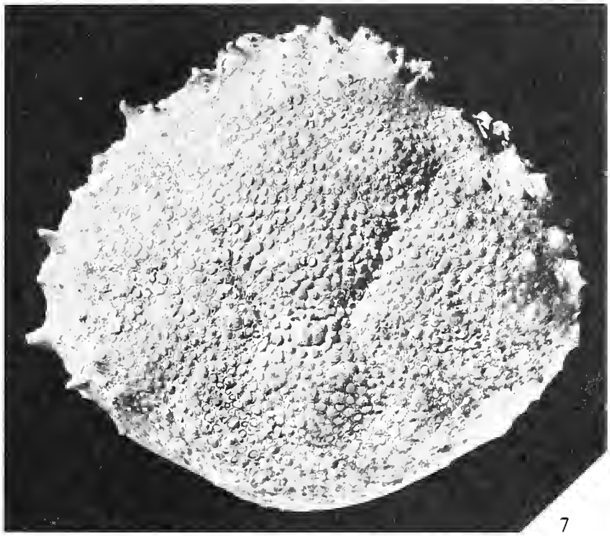

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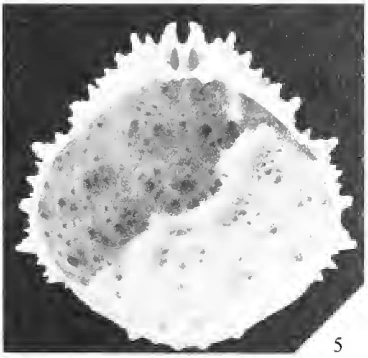

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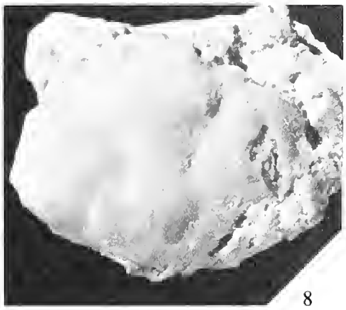

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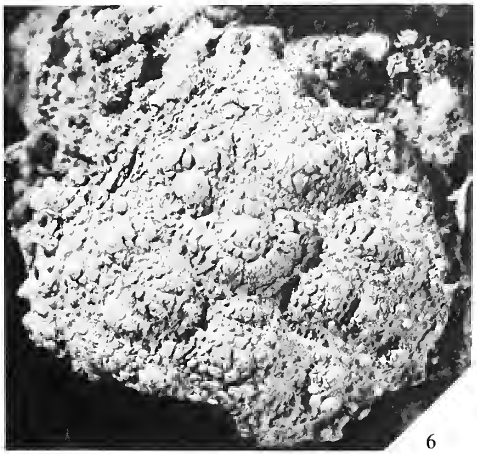

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COLLINS and MORRIS, crabs

is sinuous and the palmar surface is finely pitted. The trivial name is derived from the weak ridges on the metabranchial lobes.

Discussion. The new species differs from the type, *F. kugleri*, in having weak marginal spines at the cervical notch, clearly defined lobes, and the presence of longitudinal ridges on the metabranchial lobes. An undescribed species from the ?Palaeocene of Virginia, U.S.A. has subdued metabranchial ridges and the epi- and mesobranchial lobes are less well developed than are those of *F. bicarinella*.

Superfamily CALAPPOIDEA de Haan, 1833
Family CALAPPIDAE de Haan, 1833
Subfamily MATUTINAE McLeay, 1838
Genus HEPATUS Latreille, 1802

Type species. Calappa angustata Fabricius, 1798 by original designation.

Range. Miocene to Recent.

Hepatus nodosus sp. nov.

Plate 19, figs. 5, 6

Diagnosis. Front notched medially, not produced beyond line of suborbital cavities; anterolateral margins divided into four blunt teeth; regions marked by ovate nodes.

Holotype. An internal mould of a carapace. In. 59947 (Pl. 19, figs. 5, 6).

Horizon and locality. Middle Miocene, Brasso Formation, 'Crab Claw' Beds; Manzanilla Bay, Trinidad.

Description. Carapace sub-oblong in outline, the width a little more than twice the length; longitudinally it is strongly arched and moderately so transversely. The anterolateral margin is evenly rounded, lined with granules, and divided into four by even-sized blunt spines (but probably not so markedly as the damaged edge indicates). It forms a rounded angle with the straight front where it divides, the lower

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EXPLANATION OF PLATE 18

Fig. 1. *Mithrax* (*Mithrax*) *caribbaeus* Rathbun, p. 120, Pliocene, Coral Rock 30·5 m (100 ft); Gibbons, Barbados. Dorsal view of carapace. In. 61197, ×1·5.

Fig. 2. *Mithrax* (*Mithrax*) *caribbaeus* Rathbun, p. 120, Pleistocene, Coral Rock 104 m (340 ft); Highgate, Barbados. Lateral view of left cheliped showing crenellated cutting edge of the fixed finger. In. 61358, ×1·3.

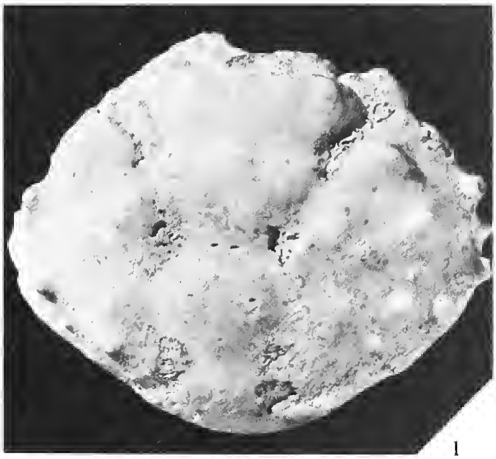
Figs. 3, 4. *Mithrax* (*Mithrax*) *spinosissimus* (Lamarck), p. 118, Pleistocene, Coral Rock 104 m (340 ft); Highgate, Barbados. 3, lateral view of right hand and carpus outstretched. In. 61207, ×1. 4, dorsal view of right hand and carpus folded. In. 61207, ×1.

Fig. 5. *Mithrax* (*Mithrax*) *verrucosus* H. Milne-Edwards, p. 119, Pleistocene, Coral Rock; Clapham, Barbados. Lateral view of right hand and carpus. In. 61357, ×0·75.

Fig. 6. *Mithrax* (*Mithrax*) *verrucosus* H. Milne-Edwards, p. 119, Pleistocene, Coral Rock; 6·1 m above sea-level, Garrison, Barbados. Lateral view of left hand and carpus. In. 61364, ×0·75.

Fig. 7. *Falconoplax bicarinella* sp. nov., p. 109, Lower or Middle Eocene, Scotland Beds; Spa, Barbados. Dorsal view of carapace. In. 61353, ×2.

Figs. 8, 9. *Persephona* cf. *punctata punctata* (Linné), p. 116, Middle Miocene, Brasso Formation, 'Crab Claw' Beds; Manzanilla Bay, Trinidad. 8, dorsal view of carapace. In. 59960, ×2·3. 9, right lateral view of carapace. In. 59960, ×2·4.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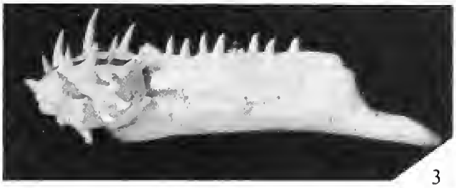
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portion continuing beneath the orbit to the buccal margin and the upper leads to, and is more or less continuous with, the upper orbital margin. Both the edges are coarsely granulated while the enclosed suborbital cavities are somewhat depressed and densely covered in fine granules. The orbitofrontal margin occupies a quarter of the carapace width; it is raised above the level of the lateral margin; there is a small median notch in the front which is not advanced beyond the suborbital margin. The orbits are small and rounded. The lateral angles are set far back and the steeply undercut posterolateral margins, lined with granules along the upper edge, converge rapidly backwards. The posterior margin is about as wide as the front.

The regions and lobes are mostly well defined; the hepatic region forms a small rather depressed triangle. The rounded mesogastric area forms the highest part of the carapace; its anterior process is depressed between tumid protogastrics, while posteriorly it is barely separated from the narrow depressed urogastric lobe. A broad depression either side of the urogastric and anterior part of the lingulate cardiac region separates them from the branchial region. The meso- and metabranchial lobes are formed by ovate even-sized nodes; the rear of the former is forward of the rear of the mesogastric, while the longer axis of the metabranchial node is level with the urocardiac juncture. Small pits of several diameters crowd the carapace surface with the exception of the nodes which are covered in irregular-sized granules.

Discussion. The narrow raised front with orbits at the same level, together with suborbital cavities not visible from above, clearly places this species within the genus as defined by Rathbun (1937) and Glaessner (1969) and serves to distinguish it from the superficially similar *Hepatella* (Upper Oligocene–Miocene, Recent) in which the front is prominent (Rathbun 1937; Glaessner 1969) and has no depression below the orbit (Rathbun 1937). The arrangement of the nodes on the dorsal surface of *H. nodosus*

EXPLANATION OF PLATE 19

Figs. 1, 2. *Thaumastoplax intermedia* sp. nov., p. 128, Middle Miocene, Brasso Formation, 'Crab Claw' Beds; 1·5 km south of Brasso on road to Gauracara, Montserrat, Trinidad. 1, dorsal view of carapace. In. 60008, ×2. 2, ventral view of carapace. In. 60008, ×2.

Fig. 3. *Carpilius corallinus* (Herbst), p. 126, Pliocene, Coral Rock 30·5 m (100 ft); Gibbons, Barbados. Dorsal view of carapace. In. 61202, ×1·5.

Fig. 4. *Pinnixa* (*Palaeopinnixa*) *perornata* sp. nov., p. 127, Lower or Middle Eocene, Scotland Beds; Spa, Barbados. Dorsal view of carapace. In. 61361, ×6.

Figs. 5, 6. *Hepatus nodosus* sp. nov., p. 112, Middle Miocene, Brasso Formation, 'Crab Claw' Beds; Manzanilla Bay, Trinidad. 5, dorsal view of carapace. In. 59947, ×2. 6, left lateral view of carapace. In. 59947, ×2.

Fig. 7. *Actaea rufopunctata nodosa* (Stimpson), p. 125, ?Pleistocene, Coral Rock; Barbados. Dorsal view of carapace. In. 61359, ×3.

Fig. 8. *Herbstia exserta* sp. nov., p. 117, Pliocene, Coral Rock 30·5 m (100 ft); Gibbons, Barbados. Dorsal view of carapace. In. 61199, ×4.

Fig. 9. *Necronectes proavitus* (Rathbun), p. 125, Middle Miocene, Brasso Formation, 'Crab Claw' Beds; Manural River, near Caparo Saca Manteca, Trinidad. Lateral view of inner margin of palm of left chela. In. 59989, ×0·8.

Fig. 10. *Pilumnus* sp., p. 126, Pleistocene, Coral Rock 91 m (300 ft); Clapham, Barbados. Outer lateral view of left propodus and carpus. In. 61360, ×1.


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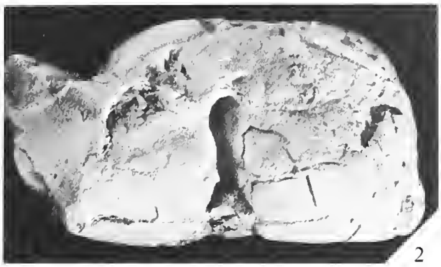
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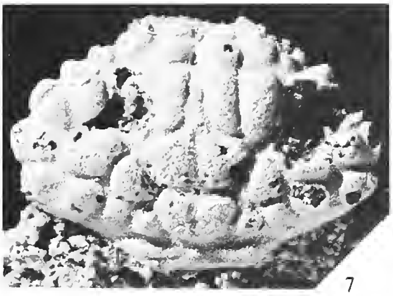
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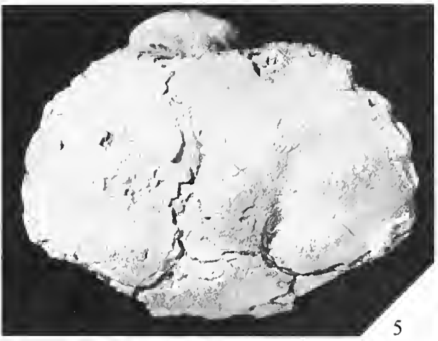
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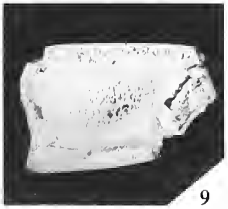
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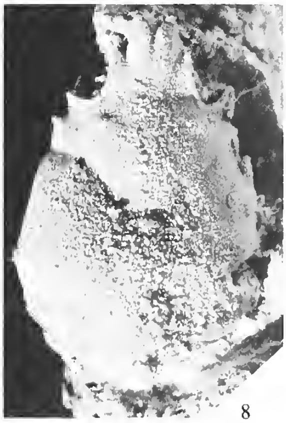
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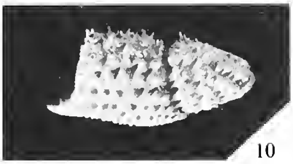
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COLLINS and MORRIS, crabs

is similar to the Recent *H. lineatus* Rathbun, but that species differs in having a more circular outline with the front slightly advanced, and a finely spinose lateral margin.

The trivial name is derived from the nodular dorsal surface of the carapace.

Family LEUCOSIIDAE Samouelle, 1819
Genus PERSEPHONA Leach, 1817

Type species. P. latreillii = *Cancer punctatus* Linné, 1758 by subsequent designation Rathbun, 1922. (ICZN Opinion 73.)

Range. Miocene to Recent.

Persephona cf. *punctata punctata* (Linné)

Plate 18, figs. 8, 9

cf. 1758 *Cancer punctatus* Linné, p. 630.
cf. 1859 *Persephona punctata* (Linné); Stimpson, p. 70.
cf. 1937 *Persephona punctata punctata* (Linné); Rathbun, p. 152, pl. 43, figs. 2, 3.

Range. Middle Miocene to Recent.

Material. A nearly complete carapace. In. 59960 (Pl. 18, figs. 8, 9).

Horizon and locality. Middle Miocene, Brasso Formation, 'Crab Claw' Beds; Manzanilla Bay, Trinidad.

Remarks. The specimen, which retains the large sixth abdominal somite of a female, conforms reasonably well with Rathbun's (1937) description and figures: the hepatic processes are less prominent on the fossil and, whereas the outer pair of posterior spines are missing, the basal scars suggest they were slenderer and approaching *P. townsendi* (Rathbun) which has sharp hepatic spines. The fossil is also remarkably close to Rathbun's figure (1937, pl. 43, fig. 4) of *P. subovata* (Rathbun) which is the Pacific analogue of *P. punctata punctata.* Rathbun's subspecies *P. p. aquilonaris*, which ranges from New Jersey to Texas, is more coarsely granulose and has a narrower front than the nominate subspecies.

In 1919*a* Rathbun described some limb fragments from the lower Miocene of San Domingo as *P. prepunctata.* She remarked that while resembling *P. punctata* they were more granulose and approached *P. townsendi.* Later (1935) Rathbun listed some limb fragments as *P. punctata* from the Yorktown Formation of Virginia, ?Yorktown of North Carolina and the Upper Miocene of South Carolina, but did not refer to her earlier work.

No persephonid limb fragments are among the present collection but as the Trinidad carapace has certain affinities with *P. townsendi* (to which Rathbun referred when discussing *P. prepunctata*) it may prove to be synonymous with *P. prepunctata.*

Section OXYRHYNCHA Latreille, 1803
Family MAJIDAE Samouelle, 1819
Subfamily PISINAE Dana, 1852
Genus HERBSTIA H. Milne-Edwards, 1834

Type species. Herbstia condyliata (Fabricius), 1787 by monotypy.

Range. Pliocene to Recent.

Herbstia exserta sp. nov.

Plate 19, fig. 8

Diagnosis. Carapace pyriform with three anterolateral spines and a prominent intestinal spine.

Holotype. An almost complete carapace. In. 61199 (Pl. 19, fig. 8).

Horizon and locality. Pliocene Coral Rock 30·5 m (100 ft) level; Gibbons, Barbados.

Description. Carapace pyriform in outline, almost flat longitudinally, depressed at the urogastric lobe, and gently curved towards the posterior margin; it is slightly arched transversely with the side narrow and almost straight. The length, including the rostrum, is one and a half times the greatest width. The short rostrum is about as broad as long, consisting of two flattened slightly divergent teeth separated by a V-shaped cleft leading to a furrow between raised backward extensions of the teeth. The orbits are small and circular with sharp pre-orbital spines extending to the base of the rostrum; the upper orbital margin is slightly ridged with a thin notch; the post-orbital spine is short. Most of the antennary region is obscured by matrix, but there is a short sharp spine on the posterior part of the basal article. The anterolateral margin is very short, occupied almost entirely by a spiniform tubercle on the small triangular hepatic lobe; a similar tubercle occurs behind the cervical furrow and a larger somewhat rounded one at the widest part of the carapace almost two-thirds the distance from the front. Two or three granular tubercles are in line with and below the larger marginal tubercles. The posterior margin is strongly produced. The cervical furrow is deep, curving back from the margin it turns abruptly inwards to cross the mid-line at about a half the carapace length. The gastric lobes are barely differentiated; there is a very weak tubercle on the mesogastric and a flattened tubercle on each protogastric lobe close to the orbital margin and a weak furrow which separates the protogastric from the hepatic lobe. The urogastric forms a narrow depressed transverse bar and has a weak median tubercle bordering the cardiac lobe. The branchial region is smooth and separated from the cardiac and intestinal regions by weak grooves. The intestinal lobe is attenuated and has a low rounded suberect median tubercle overhanging the basal margin.

Remarks. H. exserta is quite unlike other Atlantic members of the genus, but is undoubtedly analogous with the extant Pacific species, *H. pyriformis* (Bell) from which it differs mainly in having a tubercle on the protogastric and not on the mesobranchial lobes, and a somewhat blunter intestinal tubercle. Rathbun (1925*a*) recognizes only one other pair of *Herbstia* as analogous species on opposite side of America—*H. depressa* Stimpson, Atlantic and *H. tumidus* (Stimpson), Pacific.

The trivial name refers to the protruding posterior margin of the carapace.

Subfamily MITHRACINAE Balss, 1929
Genus MITHRAX Desmarest, 1823
Subgenus MITHRAX

Type species. Cancer aculeatus Herbst, 1790 = *Mithrax pilosus* Rathbun, 1892 by subsequent designation H. Milne-Edwards, 1837.

Range. Pliocene to Recent.

Mithrax (*Mithrax*) *spinosissimus* (Lamarck)

Plate 17, fig. 1; Plate 18, figs. 3, 4

1818 *Maia spinosissima* Lamarck, p. 241.
1832 *Mithrax spinosissimus* (Lamarck); H. Milne-Edwards, pls. 2, 3.
1925*a* *Mithrax* (*Mithrax*) *spinosissimus* (Lamarck); Rathbun, p. 383, pl. 135.

Range. Pliocene to Recent.

Material. A carapace. In. 61355 (Pl. 17, fig. 1); Pliocene Coral Rock, Blower's Gully, north of Bridgetown, Barbados. Hand of left cheliped and an articulating carpus. In. 61207. Pleistocene Coral Rock 104 m (340 ft); Highgate, Barbados. (Plate 18, figs. 3, 4) two fragments of meri. In. 61354, In. 61384. As above. Carpus. In. 61203. Pliocene Coral Rock 30·5 m (100 ft); Gibbons, Barbados.

Remarks. The carapace is of a young individual 28 mm in width between the fourth to fifth anterolateral spines; the frontal region is missing as far as the postorbital spine. Two small spines are preserved on the upper orbital margin in front of the postorbital spine on the right-hand side; the pair of tubercles behind the rostral horns are well developed and in line with the postorbital spines. Both the first (hepatic) and the second (epibranchial) anterolateral spines are sharply double; the fifth spine, slightly below the line of the others, is more or less in line with the gastro-cardiac groove.

This is the largest species of *Mithrax*, with the carapace in Recent specimens reaching about 170 mm over-all length by 184 mm in total width. Young and medium-sized individuals are relatively longer (Rathbun 1925*a*, p. 384) and in this respect the outline approaches that of *M.* (*M.*) *cornutus* Saussure, which may be distinguished from *M. spinosissimus* in having much longer rostral horns with the post-rostral tubercles set in advance of the postorbital spine and having only four anterolateral spines, the first being trifid and the fourth in line with the gastro-cardiac groove.

The limb fragments agree in general with Recent specimens in the British Museum (Nat. Hist.). The hand (Pl. 18, figs. 3, 4) differs from that of *M.* (*M.*) *cornutus* in having the spines on the upper margin arranged not in pairs but issuing alternately inwards and outwards from a ridged margin and in the presence of three short spines in line on the proximal half of the palmar, or inner surface. Rathbun (1925*a*, p. 384) states that two to four spines may be present. In *M.* (*M.*) *pilosus* Rathbun the spines are alternately arranged but extend only a short way along the upper margin.

Rathbun (1923) described a carapace fragment from the Pleistocene of Mole St. Nicholas, Haiti; although the specimen was not sufficiently well preserved to name she compared it with *M. spinosissimus.*

Present distribution. Carolina to West Indies in fairly shallow water down to 98 fathoms.

Mithrax (*Mithrax*) *hemphilli* Rathbun

Plate 17, figs. 4–6

1892 *Mithrax hemphilli* Rathbun, p. 263, pl. 37, fig. 2.
1925*a* *Mithrax* (*Mithrax*) *hemphilli* Rathbun; Rathbun, p. 395, pl. 139; pl. 259, fig. 2.

Range. Pleistocene to Recent.

Material. Six more or less complete carapaces. In. 61208–61213.

Horizon and locality. Pleistocene Coral Rock 104 m (340 ft); Highgate, Barbados.

Remarks. The arrangement of all the surface markings more or less agree with Rathbun's description (1925*a*, p. 395). The dorsal surface of the largest carapace (In. 61213, Pl. 17, fig. 6) is much more coarsely granulated than the smaller ones; a fragment of a robust merus on the right side, possibly of the cheliped, is armed with long sharp spines on the upper, outer, and inner margins and suggests the specimen to be a male.

This group of specimens is among the finest preserved in the present Pleistocene collection; in specimens In. 61208–61210 both the dorsal and ventral surfaces of the carapace are entirely free from matrix.

Present distribution. Rathbun (1925*a*) does not record this species from Barbados, but the range appears to be from Florida Keys to Rio de Janeiro.

Mithrax (*Mithrax*) *verrucosus* H. Milne-Edwards

Plate 17, fig. 7; Plate 18, figs. 5, 6

1832 *Mithrax verrucosus* H. Milne-Edwards, pl. 4.
1925*a* *Mithrax* (*Mithrax*) *verrucosus* Milne-Edwards; Rathbun, p. 400, pl. 144.

Range. Pliocene to Recent.

Material. Five more or less complete carapaces. In. 61200 (Pl. 17, fig. 7). In. 61201. Pliocene, Coral Rock 30·5 m (100 ft); Gibbons, Barbados. In. 61356. Pliocene, base of Coral Rock, *Amphistegina* Bed; Cluffs, Barbados. In. 61357. Pleistocene, Coral Rock; Silversands, Barbados. In. 61385. No data; Barbados. In. 61388–61389. Hands of two chelipeds, Pleistocene, Coral Rock 104 m (340 ft); Highgate, Barbados. In. 61364 (Pl. 18, fig. 6). Hand and articulating carpus. Coral Rock 6·2 m (20 ft); Garrison, Barbados.

Remarks. The width of the carapace ranges in size from 17·5 mm to 45·0 mm between the spines at the lateral angle, the largest not quite reaching the known largest size (*circa* 51·0 mm) of Recent forms. The granulation on the smallest specimen (In. 61201) is a little more flattened on the gastric region than the branchial where the spinulose granules are more conspicuous than in larger individuals. The surface ornament is rather similar to that of *M.* (*M.*) *pilosus* Rathbun, but this species has distinct spinules on the mesogastric, mesobranchial, and intestinal lobes in addition to those bordering the anterolateral spines and the four across the frontal part of the gastric region which are weakly developed in *M. verrucosus.*

Of the chelae assigned to this species, two (In. 61364, In. 61357, a left and right hand respectively, Pl. 18, figs. 5, 6) retain an articulating carpus of which the bluntly rounded tubercles along the upper margin and flattened tubercles over the outer margin of the carpus, together with the unornamented upper margin of the hand, provide readily distinguishing features from other Atlantic members of the genus. The analogous Pacific species *M.* (*M.*) *bellii* Gerstaecker has similar chelipeds.

Present distribution. From South Carolina to Fernando Noroñha, Brazil. It is a nocturnal species living near the shore, hiding in holes in rocks.

Mithrax (*Mithrax*) *hispidus* (Herbst)

Plate 17, figs. 2, 3

1790 *Cancer hispidus* Herbst, p. 245 (by error, 247), pl. 18, fig. 100.
1832 *Mithrax hispidus* (Herbst); H. Milne-Edwards, (13).
1925*a* *Mithrax* (*Mithrax*) *hispidus* (Herbst); Rathbun, p. 406, pls. 145, 146, 147, fig. 3.

Range. Pliocene to Recent.

Material. Six carapaces. In. 61191-61196.

Horizon and locality. Pliocene Coral Rock; Gibbons, Barbados.

Remarks. These specimens agree in general principles with Rathbun's (1925*a*) description and figures, but the first branchial spines, where preserved, do not appear to be as deeply bifurcated, and the line of tubercles across the gastric region is rather less prominent.

Distinguishing features between this species and *M.* (*M.*) *caribbaeus* Rathbun are discussed below.

Present distribution. Delaware Bay to São Paulo, Brazil, in shallow water to 30 fathoms.

Mithrax (*Mithrax*) *caribbaeus* Rathbun

Plate 18, figs. 1, 2

1920 *Mithrax caribbaeus* Rathbun, p. 23.
1925*a* *Mithrax* (*Mithrax*) *caribbaeus* Rathbun; Rathbun, p. 409, pls. 148, 149.

Range. Pliocene to Recent.

Material. A carapace. In. 61197 (Pl. 18, fig. 1). Pliocene Coral Rock 30·5 m (100 ft); Gibbons, Barbados. Part of a cheliped. In. 61358 (Pl. 18, fig. 2). Pleistocene Coral Rock 104 m (340 ft); Highgate, Barbados.

Remarks. Although the front and marginal spines on the left side of the carapace are missing, the two parallel transverse rows of the branchial tubercles which characterizes this species and provides a distinguishing feature from *M.* (*M.*) *hispidus*, discussed above, are clearly developed.

The cheliped (Pl. 18, fig. 2) is represented by a left-hand and articulating carpus. The crenellated cutting edge extending to the base of the fixed finger distinguishes this limb from that of *M.* (*M.*) *hispidus* in which the surface before the terminal cap is entire.

Present distribution. The northern Atlantic coast of America and West Indies, in depths ranging from about 2 to 12 fathoms.

Subgenus MITHRACULUS White, 1847

Type species. Mithraculus coronatus White, 1847 (not *Cancer coronatus* Herbst, 1785) = *Maia sculpta* Lamarck, 1818.

Range. Pliocene to Recent.

Mithrax (*Mithrax*) *ruber* (Stimpson)

Plate 17, fig. 8

1871 *Mithraculus ruber* Stimpson: 118.
1925*a* *Mithrax* (*Mithraculus*) *ruber* (Stimpson); Rathbun, p. 432, pl. 157.

Range. Pliocene to Recent.

Material. A carapace. In. 61198.

Horizon and locality. Pliocene Coral Rock 30·5 m (100 ft); Gibbons, Barbados.

Remarks. The specimen differs from Rathbun's (1925*a*, p. 432) Gibbons, Barbados description in that the branchial and cardiac tubercles are not so prominent; of those across the mesogastric only the outermost pair is present and the pair behind the rostral horns is somewhat inconspicuous.

The specimen may be distinguished from *M.* (*Mithrax*) *tortugae* Rathbun in having blunter, rounder lateral processes and the cervical furrow crosses the mid-line of the carapace nearer the front.

Present distribution. From Cuba to Barbados and Curacao; from ½ to 84 fathoms on bottoms varying from sandy, muddy, or rocky to coral reefs.

Section BRACHYRHYNCHA Borradaile, 1907
Superfamily PORTUNOIDEA Rafinesque, 1815
Family PORTUNIDAE Rafinesque, 1815
Genus PORTUNUS Weber, 1795

Type species. Cancer pelagicus Linné, 1758 by subsequent designation Rathbun, 1926. (ICZN Opinion 394.)

Range. Lower Miocene to Recent.

Portunus oblongus Rathbun

Plate 20, figs. 1-8

1920 *Portunus oblongus* Rathbun, p. 383, pl. 25, fig. 3, 3*a*.
1966 *Portunus* cf. *oblongus* Rathbun; Gordon, p. 185, text-fig. 2.

Range. Lower to Middle Miocene.

Remarks. This species was founded on a single fragmentary specimen (328229 USNM) of a male from the Lower Miocene Cercado Formation of the Dominican Republic. Since the new material shows features not present in the type and also includes specimens of females, a revision of the description, incorporating Rathbun's original remarks where appropriate, is given.

Horizon. Middle Miocene, Brasso Formation, 'Crab Claw' Beds.

Material. Fifty-nine specimens, largely fragmentary, from three localities: In. 59948-60006, Manzanilla Bay, Trinidad; In. 60001. Navarro River, Manzanilla Bay, Trinidad; In. 60009. 6·5 km (4 miles) south of Caparo Sta., Montserrat, Trinidad.

Description. Carapace length a little less than two-thirds of the width measured in front of the lateral spines. The lateral spine (In. 60006, Pl. 20, fig. 1) is long, stout, and almost conical at the base and curving upwards and forwards. The spines on the anterolateral margin are small, more or less even in size, flattened and upturned; they have slightly convex posterior and concave anterior margins. The orbitofrontal margin is a little more than half the carapace width with the front occupying about a quarter of this distance. There are four bluntly rounded spines on the front; the median pair, separated by a V-shaped sinus is a little in advance of the lateral pair and the distance measured at the outer bases of the inner pair is about a third of the frontal width. The orbital margin from the triangular inner orbital spine to a notch on the outer third is more advanced than the lateral portion; there is a thinner notch close to the outer orbital spine which is a little larger than the succeeding marginal spine. The posterior margin is a little narrower than the orbitofrontal margin. The surface of the carapace is very uneven with the proto- and mesogastric lobes tumid and the epibranchial ridge leading to the lateral spine is prominent. The cardiac region is divided anteriorly by a cleft, the portions on either side forming rounded nodes which with two others of similar size on the branchial region form a semicircle round the depressed urogastric lobe. The anterior gastric ridge is nearly straight. Fine granules of several diameters crowd the elevated parts of the dorsal surface; they become sparser posteriorly, and laterally give way to pits; both dorsal and ventral surfaces of the anterolateral spines are granulose. On the holotype the posterior of the carapace is decorticated and the exposed shell layer is rather coarsely granulated.

The ischium of the third maxilliped shows a deep furrow which is situated near the inner third and does not reach the posterior end; the basal width of the exopodite is about half that of the endopodite.

The sternum between the chelipeds is extremely wide, giving the whole sternum a more oblong shape than usual; its margin opposite the anterior base of the cheliped bears a few granules; the sternum in front of the articulating condyle of the cheliped is depressed, the line between the depression and the elevation behind it being nearly transverse, not V-shaped. The male abdomen exclusive of the first two somites is largely triangular; the length of the coalesced somite (third, fourth, and fifth combined), measured on the median line, from the transverse ridge to the distal end is two-thirds of its distal width; the sixth somite is half as wide on its distal as on its proximal margin, while the length is three-quarters of the proximal width; the telson is triangular, its width a little greater than its length. The third to sixth somites of the female abdomen are semi-eliptical in outline; the third, fourth, and to a lesser extent the fifth somites have a transverse median ridge. The median length of the sixth somite is two-fifths of its proximal width.

The chelipeds are robust. The ischium is triangular in section with two sharp spines on the upper and two smaller ones on the lower margin. The carpus is short, triangular in section with a short curved ridge running towards the middle of the outer margin and there is a sharp distal spine on the upper and lower margins. The hand is twice as long as the carpus; there are four sharp carinae extending the length of the hand on the outer margin and two on the inner; the third outer and median inner ones not reaching the distal edge but terminating in a blunt spine; the areas between the carinae

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EXPLANATION OF PLATE 20

Figs. 1–8. *Portunus oblongus* Rathbun, p. 121, Middle Miocene, Brasso Formation, 'Crab Claw' Beds; Manzanilla Bay, Trinidad. 1, dorsal view of internal mould of carapace. In. 60006, ×0·5. 2, dorsal view of internal mould of carapace. In. 59949, ×0·75. 3, ventral view of female abdomen. In. 59998, ×0·9. 4, ventral view of male abdomen. In. 59971, ×0·8. 5, lateral view of outer margin of right propodus and carpus. In. 59952, ×0·75. 6, lateral view of inner margin of right propodus and carpus. In. 59952, ×0·75. 7, lateral view of outer margin of left propodus. In. 59983, ×0·75. 8, lateral view of inner margin of left propodus. In. 59983, ×0·75.

Figs. 9–11. *Portunus gibbesii* (Stimpson), p. 124, Pleistocene Coral Rock 104 m (340 ft); Highgate, Barbados. 9, lateral view of inner margin of left propodus. In. 61204, ×1. 10, lateral view of outer margin of left propodus. In. 61204, ×1. 11, lateral view of fragment of left propodus. In. 61205, ×1.

Fig. 12. *Portunus vocans* (A. Milne-Edwards), p. 124, Pleistocene Coral Rock 104 m (340 ft); Highgate, Barbados. Lateral view of right propodus. In. 61206, ×2.


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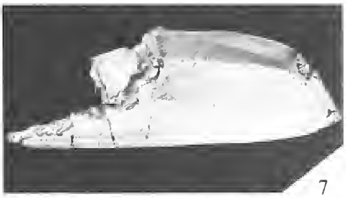
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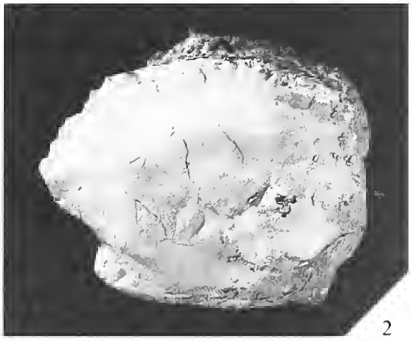
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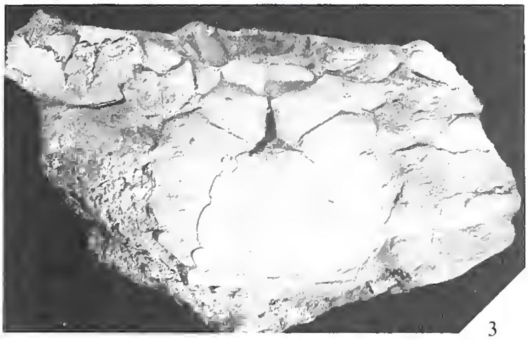
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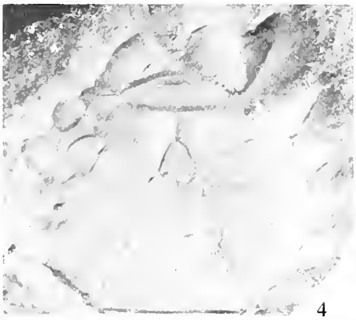
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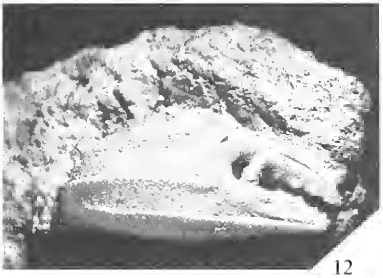
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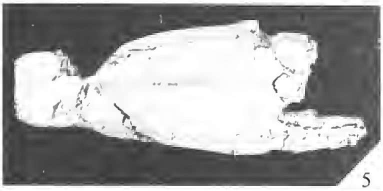
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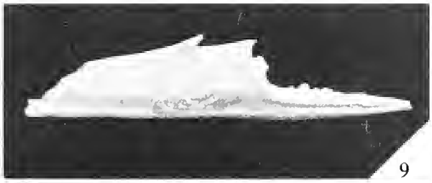
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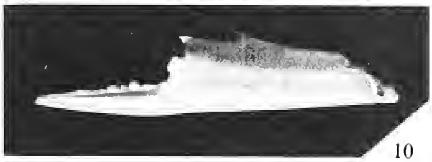
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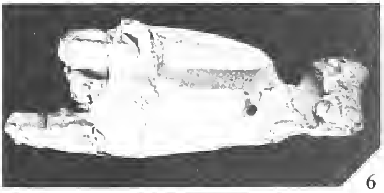
6

COLLINS and MORRIS, crabs

are concave. There is a distal spine on the upper inner carina, a smaller one on the first outer carina, and one proximal on the second. The upper margin is generally flat, although on a large natural pair of chelae, In. 59973, it is somewhat rounded. The lower outer carina extends the length of the fixed finger which is about two-thirds the length of the hand. The movable finger is bluntly carinated. The major claw seems to be generally on the right and is much the same length as the minor which is rather slimmer in transverse section. The fingers of the major claw gape rather more than the minor.

Discussion. P. oblongus closely resembles *P. gabbi* Rathbun (1919*b*), from the Lower Miocene of the Dominican Republic, particularly in the shape of the orbital margin and arrangement of the frontal spines; in the Trinidad specimens the front appears to differ from that of *P. gabbi* only in the inner pair of teeth being narrower across the base and slightly less divergent at their tips. Rathbun (1920) distinguished the two species largely on the larger carapace width of *P. oblongus* and the shape of the fifth lateral spine. So far, too little is known of the anterior part of the sternites of *P. gabbi* to allow a closer comparison of the two species.

P. oblongus differs from *P. haitensis* (Rathbun, 1923) (Lower Miocene of Haiti) in having a less-protruding frontal region, no nodes on the protogastric lobes, no median ridge, and the semicircular arrangement of the branchial nodes.

Among European forms *P. oblongus* closely resembles *P. viai* Secretan (1971) from the Burdigalian of Vaucluse, particularly in the dorsal areolation of the carapace, but differs in having a shallower sinus between the median pair of frontal spines and in the shape of the orbital margin; the ridge across the anterior sternites is inclined at much the same angle to the mid-line in both species.

Portunus (*Portunus*) *gibbesii* (Stimpson)

Plate 20, figs. 9–11

1859 *Lupa gibbesii* Stimpson, p. 57 (11).
1900 *Portunus gibbesii* (Stimpson); Rathbun, p. 140.
1930 *Portunus* (*Portunus*) *gibbesii* (Stimpson); Rathbun, p. 49, pls. 16, 17.

Range. Pleistocene to Recent.

Material. Two fragments of chelae. In. 61204, In. 61205.

Horizon and locality. Pleistocene Coral Rock 104 m (340 ft); Highgate, Barbados.

Remarks. The proximal portion on the better-preserved specimen is missing so there is no evidence of a possible spine on the upper margin near the articulation with the carpus. In the nature of the other two upper marginal spines, the five granulated carinae on the outer surface, the blunt one on the inner edge of the lower surface, and the lines of granules along the inner surface, the specimen agrees closely with Rathbun's (1930) description and figures of Recent specimens.

Present distribution. Massachusetts to Texas and Venezuela.

Portunus (*Portunus*) *vocans* (A. Milne-Edwards)

Plate 20, fig. 12

1878 *Neptunus vocans* A. Milne-Edwards, p. 225 (6).
1930 *Portunus* (*Portunus*) *vocans* (A. Milne-Edwards); Rathbun, p. 60, pl. 25, fig. 8.

Range. Pleistocene to Recent.

Material. A right chela. In. 61206.

Horizon and locality. Pleistocene Coral Rock 104 m (340 ft); Highgate, Barbados.

Remarks. The supero-subdistal and more prominent proximal spines on the hand, together with the large strong outstanding tooth on either finger readily identifies this species and serves to distinguish it from other members of the genus within the region.

Genus NECRONECTES A. Milne-Edwards, 1881

Type species. N. vidalianus A. Milne-Edwards by original designation.

Range. ?Upper Eocene to Miocene.

Necronectes proavitus (Rathbun)

Plate 19, fig. 9

1919 *Gatunia proavita* Rathbun, p. 168, pls. 54–56, p. 58, figs. 16, 17.
1966 *Necronectes proavitus* (Rathbun); Gordon, p. 184, fig. 1*a–e*.
1969 *Necronectes proavitus* (Rathbun); Glaessner, p. R512.

Range. Miocene.

Material. A fragmentary left chela. In. 59989.

Horizon and locality. Middle Miocene, Brasso Formation, 'Crab Claw' Beds; Manural River, near Caparo Saca Manteca, Trinidad.

Remarks. Although fragmentary, this left chela conforms well with Rathbun's (1919*a*) description and figures; proportional measurements of height to length agree reasonably well with those taken from the figures. The outer surface is worn and traces of the fine granulations are seen only towards the upper margin.

Superfamily XANTHOIDEA Dana, 1851
Family XANTHIDAE Dana, 1851
Genus ACTAEA de Haan, 1833

Type species. Cancer (*Actaea*) *granulatus* Audouin, 1825 (non *C. granulatus* Linné, 1758) (= *C. savignyi* H. Milne-Edwards, 1834) by subsequent designation Rathbun, 1922.

Actaea rufopunctata nodosa (Stimpson)

Plate 19, fig. 7

1860 *Actaea nodosa* Stimpson, p. 203.
1886 *Actaea rufopunctata* var. *nodosa* (Stimpson); Miers, p. 122.
1930 *Actaea rufopunctata nodosa* (Stimpson); Rathbun, p. 257, pl. 105, figs. 1, 2.

Range. Pleistocene to Recent.

Material. A carapace. In. 61359.

Horizon and locality. Part of the Trechmann Bequest, in a box subsequently labelled 'Barbados'; the matrix compares well with that of other Coral Rock material.

Remarks. The front is damaged but there is a sufficient gap between it and lobule 1F (after Dana) to distinguish the specimen from the specific analogue, *A. sulcata*

Stimpson, in which the lobule and the front are fused; similarly 4L and T are separate in *A. r. nodosa*. The nominative, Pacific, species differs in that the anterior median nodule of the mesogastric reaches as far as, or further than, the protogastric lobes; whereas in *A. r. nodosa* it extends to about the middle of that lobe. In specimen In. 61359 (Pl. 19, fig. 7) the anterior median nodule reaches to about the distal fourth of the protogastric lobe which indicates the two Recent forms were already diverging from a possible common ancestor and could therefore be considered as distinct species.

In other actaeids of the region the mesogastric and cardiac lobes are not divided by a median furrow.

Genus PILUMNUS Leach, 1815

Type species. *Cancer hirtellus* Linné, 1761 by original designation.

Range. Pleistocene to Recent.

Pilumnus sp.

Plate 19, fig. 10

Material. Chela and articulating carpus. In. 61360.

Horizon and locality. Pleistocene Coral Rock 91·5 m (300 ft); Clapham, Barbados.

Remarks. The specimen is a well-preserved left chela and freely articulating carpus, the movable finger is missing. There is a significant difference in size and structure of the major and minor chelipeds among pilumnids, with a tendency for the major cheliped to be on the right-hand side. The minor cheliped is usually the more spinose in juveniles and often so in mature females and the ornament of the Barbados specimen is approximate to several closely allied species inhabiting the Caribbean Region.

Family CARPILIIDAE Ortmann, 1894

Genus CARPILIUS Leach, 1823

Type species. *Cancer maculatus* Linné, 1758 by original designation.

Carpilius corallinus (Herbst)

Plate 19, fig. 3

1783 *Cancer corallinus* Herbst, p. 131; p. 5, fig. 40.
1825 *Carpilius corallinus* (Herbst); Leach *in* Desmarest, p. 104.
1930 *Carpilius corallinus* (Herbst); Rathbun, p. 240, pls. 97–99.

Range. Pliocene to Recent.

Material. A carapace. In. 61202.

Horizon and locality. Pliocene Coral Rock 30·5 m (100 ft); Gibbons, Barbados.

Remarks. The carapace agrees in all respects with Recent members of the species and the posterior margin to carapace width ratio of 20% suggests it to be that of a young male (Collins and Morris 1973).

Family PINNOTHERIDAE de Haan, 1833

Genus PINNIXA White, 1846

Type species. *Pinnotheres cylindricum* Say, 1818 by original designation.

Subgenus PALAEOPINNIXA Via, 1966

Type species. Pinnixa eocenica Rathbun 1926, by original designation.

Range. Eocene to ?Recent.

Pinnixa (*Palaeopinnixa*) *porornata* sp. nov.

Plate 19, fig. 4

Diagnosis. Carapace with a row of granules across hepatic and protogastric lobes, and three more on the cardiac region.

Holotype. A cast of a carapace. In. 61361.

Horizon and locality. Lower or Middle Eocene, Scotland Beds, Spa, Barbados.

Description. Carapace length about two-thirds of the width, the lateral margins are well rounded and the frontal and posterior margins nearly straight; it is moderately rounded longitudinally and nearly flat in transverse section. The orbits are ovate and occupy the outer thirds of the orbitofrontal margin which is rather narrow, being a little more than a third of the carapace width. The front is broken but appears to be depressed between two very small frontal lobes; the upper orbital margin is thin and sinuous and the weak outer orbital process is bluntly rounded. The anterolateral margin is much shorter than the posterolateral and the margin edges are acute; the posterolateral angle is sharply rounded into the posterior margin which is wider than the front and somewhat concave. The groove separating the hepatic from the gastric and branchial regions is broad and deep. Low circular nodes mark the epigastric lobes which form a line with two granules on each protogastric close to the gastro-hepatic furrow, these coincide with a pair of granules on the hepatic to form two transverse rows. Only the tip of the anterior mesogastric process is defined. The cervical groove bounding the small triangular hepatic lobes is traced by a line of fine granules. Two short elongated nodes separate the mesogastric from the urogastric which is represented by a single granule more or less absorbed into the cardiac region, the upper edges of which are drawn up into two low nodes bordering the epimeral adductor muscle scars. The surface is covered medially with fine granules which become coarser on the branchial region and towards the lateral margins.

Discussion. The only other member of *Palaeopinnixa* known from North America is *P.* (*P.*) *eocenica* Rathbun from the Eocene of Washington; it differs from *P.* (*P.*) *perornata* in having deeper gastro-hepatic grooves and the dorsal surface is devoid of granules. Absence of granules also distinguishes *P.* (*P.*) *perornata* from *P.* (*P.*) *mytilicola* Via from the Miocene of Barcelona, in which the cardiac region is trilobed. In discussing the phylogeny Via (1966) considered that *Pinnixa minuta* Rathbun formed a living representative of the subgenus and this opinion is possibly strengthened by the presence of weakly defined lateral portions of the cervical groove in *P.* (*P.*) *perornata*, but this character is shared to a greater or lesser extent by several other members of *Pinnixa.*

The trivial name, 'unusually ornamented', refers to the ornamentation of the carapace.

Family GONEPLACIDAE McLeay, 1838
Subfamily HEXAPODINAE Miers, 1886
Genus THAUMASTOPLAX Miers, 1881

Type species. Thaumastoplax anomalipes Miers, 1881, by original designation.

Range. Eocene to Recent.

Thaumastoplax intermedia sp. nov.

Plate 19, figs. 1, 2

1925*b* (?) *Thaumastoplax prima* Rathbun; Rathbun *in* Mansfield, p. 5.

Range. Middle Eocene.

Diagnosis. Carapace sub-oblong with front depressed; no furrows on dorsal surface.

Holotype. A part cast part decorticated carapace. In. 60008.

Horizon and locality. Middle Miocene, Brasso Formation, 'Crab Claw' Beds; 1½ km south of Brasso on road to Gauracara, Montserrat, Trinidad.

Description. Carapace sub-oblong in outline, about one and a half times as broad as long; longitudinally it is very convex, particularly anteriorly and nearly flat in transverse section. The orbits are ovate and occupy the outer thirds of the orbito-frontal margin which is depressed, barely visible from above and about one-third of the greatest carapace width. The front is missing. The lateral angles are sharply rounded and the sides are splayed a little outwards. The anterolateral margins are broadly rounded; the posterolateral margins are straight and diverge towards the slightly concave posterior margin which is wider than the front. The regions are poorly defined; the protogastric lobes are just sufficiently tumid to cause a median depression. Curved epimeral adductor muscle scars extend over the middle third of the carapace length; between the forwards part of the scars are two oblique mesogastric nodes and behind, on each mesobranchial lobe, is an almost obsolete node. There are two nodes of about the same size on the anterior part of the cardiac region.

Traces of outermost shell layer preserved on the dorsal surface show large crowded pits. Crowded granules occur on the cast surface; they are much coarser on the mid-branchial than other parts exposed.

The abdominal trough is very deep and narrow with the sides almost parallel and bluntly rounded apex, typical of males of the Recent species. A few pits are present on what remains of the shell surface of the sternites and a row of elongated granules lines the posterior border of the cast surface of each sternal segment.

Remarks. In the absence of dorsal furrows and relative positions of the epimeral adductor muscle scars to the mesogastric and mesobranchial nodes *T. intermedia* has affinities with *T. eocenica* Woods (1922) from which it differs in having straighter posterolateral margins and a depressed front. The general outline of the carapace of *T. intermedia* closely resembles that of *T. prima* Rathbun (1918) from the Oligocene of Panama, but this species also has a prominent front together with conspicuous dorsal furrows. There are no mesobranchial nodes on *T. prima*, the posterolateral margins are longer in relation to the carapace length and the distance between the forward gape of the mesogastric nodes is about a third of the carapace width compared to a fifth in *T. intermedia.*

Rathbun (1925*b*) listed, but neither described nor figured, *T. prima* from the Miocene of Trinidad; it is probable that this specimen rightly belongs to *T. intermedia*.

Compared with the Recent *T. anomalipes* (Miers, 1881), *T. intermedia* has shorter anterolateral margins and diverging not converging posterolateral margins.

The species name relates to affinities between *T. eocenica* and *T. anomalipes*.

CONCLUSIONS

The collection of crabs from the Caenozoic of Trinidad and Barbados in the Department of Palaeontology, British Museum (Natural History) not only allows five new species to be described but also representatives of extant species of *Mithrax* indicate the subfamily Mithracinae was firmly established by Pliocene times. *Herbstia*, a genus known by Recent species on both sides of America, is recorded for the first time as a fossil. Numerous specimens of both sexes of the Miocene species, *Portunus oblongus* Rathbun allow a more detailed description to be given and the geographical range is extended within the Central American Region. A new species each of *Thaumastoplax*, *Hepatus*, *Falconoplax*, and *Palaeopinnixa* add considerably to our knowledge of the history of these little-known genera.

Crabs are not very useful stratigraphic indicators but the Scotland Formation specimens do support Senn's (1948) contention that the Scotland Formation is of Lower or Middle Eocene age rather than Middle or Upper Eocene.

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LATE MIDDLE CAMBRIAN AGNOSTID TRILOBITES FROM NORTH-WESTERN TASMANIA

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ABSTRACT. Eighteen species of agnostid trilobites are described from three late middle Cambrian faunas from the St. Valentines Peak and Christmas Hills areas in north-western Tasmania. Two new genera, *Tasagnostus*, type species, *T. debori* sp. nov. and *Valenagnostus*, type species, *V. marginatus* (Brögger) are erected. The following new species are described, *Peronopsis gullini*, *P. ekip*, *Valenagnostus banksi*, *V. brittoni*, *Ptychagnostus* (*Goniagnostus*) *buckleyi*, *Utagnostus neglectus*, *Tasagnostus debori*, and *T. compani*. Some of the effaced agnostids are reviewed. It is concluded that the new genus *Valenagnostus* includes the following species, *V. marginatus* (Brögger), *V. imitans* (Öpik), *V. evexus* (Öpik), *V. banksi*, and *V. brittoni*. The effaced agnostids usually described under *Grandagnostus*, *Phalacroma*, or *Phalagnostus* should be split into at least three genera, namely, *Valenagnostus*, *Grandagnostus* Howell with *G. glandiformis* (Angelin) as the best-known species, and *Phalagnostus* Howell which includes *P. nudus* (Beyrich) as type species, *P. prantli* Šnajdr, and *P. scanicus* (Tullberg).

THE purpose of this paper is to describe all previously undescribed agnostid trilobites from the Christmas Hills (lat. 40° 54·1′ S., long. 144° 29·8′ E.) and St. Valentines Peak (lat. 41° 21·6′ S., long. 145° 44·3′ E.) areas in north-western Tasmania. These localities contain some of the best-preserved late middle Cambrian fossils in Tasmania. There are three faunas involved—two from Christmas Hills and one from St. Valentines Peak. Prior to this paper only five trilobite species had been described from these localities (Jago 1972; Jago and Daily 1974). Some palaeoecological aspects of the three faunas were discussed by Jago (1973).

Jago and Buckley (1971) reported the abrupt faunal change between the older and younger faunas at Christmas Hills, despite the very similar ages of the faunas. In the lower fauna *Proampyx* and *Nepea* are common. Other polymerids include an asaphiscid and very rare examples of *Dorypyge*. The agnostid trilobites described herein from the lower fauna are *Peronopsis gullini*, *Valenagnostus brittoni*, *Tasagnostus debori*, and *Utagnostus neglectus*. *Clavagnostus milli* has been described previously (Jago and Daily 1974). Of these species *T. debori* (referred to in previous papers, e.g. Jago 1973, as cf. *Oidalagnostus*) occurs in great abundance. *P. gullini* and *V. brittoni* are fairly common, but *C. milli* is scarce and *U. neglectus* is known only from a single specimen. At least two species of inarticulate brachiopods and very rare dendroids are also known from the lower fauna, which is probably of *Lejopyge laevigata* I age (Jago and Buckley 1971).

The polymerid trilobites from the upper fauna at Christmas Hills include *Centropleura*, *Pianaspis*, *Amphoton*, and others; the agnostids include *Peronopsis gullini*, *Hypagnostus* cf. *brevifrons* (Angelin), *Grandagnostus* sp., *Ptychagnostus* (*Ptychagnostus*) cf. *aculeatus* (Angelin), *P.* (*Goniagnostus*) *buckleyi*, *Diplagnostus* sp., *T. debori* and Agnostid, gen. et sp. indet., no. 3. *Clavagnostus* sp. was described in Jago and Daily (1974). The most common agnostid in the upper fauna is the effaced agnostid

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described here as Agnostid, gen. et sp. indet. no. 3; *P. buckleyi*, *Grandagnostus* sp., and *Diplagnostus* sp. are common. Dendroids and hydroids (Quilty 1971), inarticulate brachiopods, hyolithids, and sponge spicules are also known from the upper fauna at Christmas Hills which is either of *L. laevigata* I or *L. laevigata* II age (Jago and Buckley 1971; Jago 1973).

The Cambrian stratigraphy of the St. Valentines Peak area is described in Jago *et al.* (1975). Newly described agnostids from St. Valentines Peak are *Peronopsis ekip*, *V. banksi*, *Aspidagnostus* sp., *T. compani*, *Utagnostus*(?) sp., Agnostid gen. et sp. indet. no. 1 and no. 2. *C.*(?) *rawlingi* has been described (Jago and Daily 1974). Other trilobites include *Opsidiscus argusi* Jago, *Schmalenseeia gostinensis* Jago, *Nepea*, and a zacanthoid. The age of this fauna is late middle Cambrian, probably either *L. laevigata* III or *Damesella torosa–Ascionepea janitrix* Zone (Jago 1972). The latter zone was erected by Öpik (1967) as a passage zone between the middle and upper Cambrian, but it has recently been shown to be of late middle Cambrian age (Daily and Jago 1975).

All Tasmanian Cambrian fossils have undergone tectonic distortion to some extent. As noted by Henningsmoen (1960, p. 207), there are three main types of symmetrical distortion with respect to the orientation of bilaterally symmetrical fossils such as trilobites: (*a*) a dorso-ventral compression (flattening), (*b*) sagittal elongation (the L form of Henningsmoen) (e.g. Pl. 21, fig. 1), and (*c*) transverse elongation (the W form) (e.g. Pl. 23, fig. 9). Those fossils in which the distortion has been asymmetrical are stated here to have undergone intermediate distortion (i.e. the compression took place at an oblique angle to the length of the trilobite, e.g. Pl. 23, fig. 13). In cases where no comment is made about the type of distortion, it is because the distortion is so slight as to make it difficult to determine the type.

All statements made in the descriptions, such as ‘the cephalon is about as wide as is long’, are made after taking the effect of distortion into account. Admittedly, this is a subjective assessment, but I feel that, after inspecting and studying several thousand distorted agnostid specimens, such a judgement seems reasonable. Unless otherwise stated, all length measurements were taken in a sagittal or exsagittal line, all width measurements were taken in a transverse direction.

It should be noted that the trilobites from the Christmas Hills and St. Valentines Peak area are among the least distorted of Tasmanian Cambrian faunas. All trilobites from these localities are preserved as internal and external moulds in weathered siltstone. In order to prepare them for description, silicone rubber casts of the external moulds were prepared. These rubber casts were then photographed after being whitened with magnesium oxide. All specimens are housed in the collection of the Geology Department, University of Tasmania. The catalogue numbers refer to this collection.

HABITAT OF AGNOSTID TRILOBITES

Robison (1972*a*, 1972*b*) reviewed the various hypotheses regarding the mode of life of agnostid trilobites. He concluded that the distinctive agnostid morphology is the result of adaptation to a pelagic mode of life in the oceanic province. The author’s work indicates general support for this view although in the Tasmanian Cambrian sequences there is strong evidence that certain agnostid groups lived in a more open-sea type environment than others (Jago 1973). A possible explanation for this is that of Bergström (1973) who suggested that some agnostid species were pelagic while others may have been benthonic. On the other hand, the agnostids which occur in the closer-to-shore assemblages in Tasmania include species of *Peronopsis* and *Clavagnostus*. Species of these genera have a world-wide distribution.

Bergström (1973) postulated that agnostids may have been parasitic although, as he noted, there are certain agnostid characteristics which do not support such a hypothesis. In fact, such a hypothesis, although it cannot be disproved, seems unnecessary. I feel that it is much more likely that the agnostids drifted near the surface of the seas at the mercy of the currents. The diet of agnostids is still unknown.

Robison (1964, 1972*b*) noted various features of agnostid morphology which he regarded as indicating that agnostids spent most of their life enrolled. Most, if not all, of the agnostid characteristics used by Robison to suggest this mode of life seem to be simply adaptations for enrolment. Great numbers of polymerid trilobites are known to have enrolled, and it is not suggested that this was their usual way of life. Even allowing for the fact that agnostids differ in many ways from other trilobites, there is no reason why the enrolled position should be considered to be the normal mode of life of the agnostids.

In faunas with which I am familiar and in which complete agnostids are common, the unenrolled specimens by far outnumber the enrolled specimens. It is possible that in most faunas a large number of the unenrolled complete specimens could be due to moults. However, in faunas where it seems reasonable to assume that most specimens represent dead animals rather than moults there is still a very high ratio of unenrolled to enrolled specimens, e.g. the Que River fauna (Jago 1973) where only three out of twenty-six complete specimens are enrolled. Although it could be argued that some of the unenrolled specimens were enrolled when they died and that relaxation of muscles after death caused the agnostid to open out and settle to the bottom in the unenrolled state, the presence of a few enrolled specimens which have failed to open out argues against this. It is concluded that agnostids were unenrolled for the greater part of their existence. In considering the enrolled position of agnostids it is possible that the cephalo-thoracic aperture of Robison (1964) could be related to maintaining hydrostatic equilibrium when the agnostid went into the enrolled position.

Robison (1972*b*) suggested that an agnostid may have been able to swim by clapping the cephalon and pygidium together in a manner similar to a modern pectenid bivalve. Presumably, like the pectens, such swimming, if it occurred at all, would have been rather erratic and of short duration. Such swimming would probably have taken place in an attempt to escape predators or to search for food.

CLASSIFICATION AND MORPHOLOGY OF AGNOSTID TRILOBITES

Öpik (1961*b*, 1963, 1967) discussed the classification of agnostid trilobites, culminating in his detailed classification of 1967. This classification differs considerably from those of Kobayashi (1939, 1962), Hupé (1953), Howell (1959), and Pokrovskaya (1960). Bergström (1973) accepted Öpik's classification with very little modification.

Öpik's classification is accepted here as being more objective and consistent than previous classifications.

The morphology and terminology of agnostids has been discussed by Palmer (1955), Öpik (1961*a*, 1963, 1967), and Robison (1964); that of Öpik is the most complete and is usually followed herein.

SYSTEMATIC DESCRIPTIONS

Order MIOMERA Jaekel, 1909
Suborder AGNOSTINA Salter, 1864
Superfamily AGNOSTACEA M'Coy, 1849
Family AGNOSTIDAE M'Coy, 1849
Subfamily QUADRAGNOSTINAE Howell, 1935
Genus PERONOPSIS Hawle and Corda, 1847

Synonymy. See Palmer 1968, p. 31.

Type species. Battus integer Beyrich, 1845, p. 44, pl. 1, fig. 19.

Diagnosis. See Robison 1964, p. 530 and discussion on *Peronopsis ekip* sp. nov. (below).

Peronopsis gullini sp. nov.

Plate 21, figs. 1–9

Material. One large almost complete specimen, UT 86599, the holotype, and two smaller complete specimens are known. Numerous pygidia are available. It is impossible to differentiate cephala of *P. gullini* sp. nov. from those of *Tasagnostus debori* sp. nov. with certainty. However, the latter is a larger agnostid than *P. gullini*, and thus all the large cephala of this type in the lower fauna at Christmas Hills are included in *T. debori.*

Holotype. UT 86599 (Pl. 21, fig. 1).

Diagnosis. Simple basal lobes moderately large; transverse glabellar furrow arched to the posterior. Cephalic margins converge forward to a well-rounded cephalic front; pygidial margins diverge slightly to the short border spines. Posterior pygidial

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EXPLANATION OF PLATE 21

Figs. 1–9. *Peronopsis gullini* sp. nov. 1–8, from lower fauna and 9 from upper fauna at Christmas Hills (lat. 40° 54·1′ S., long. 144° 29·8′ E.). 1, UT 86599, holotype, nearly complete specimen, L form, ×7·8. 2, UT 86849b, internal mould of small complete specimen, L form, ×13·2. 3, UT 86849b, internal mould of small complete specimen, intermediate distortion, ×13·1. 4, UT 86855e, pygidium, intermediate distortion, ×12·5. 5, UT 86861b, pygidium, intermediate distortion, ×11·5. 6, UT 86853d, pygidium, W form, ×11·2. 7, UT 86853f, pygidium, L form, ×11·1. 8, UT 86845c, pygidium, intermediate distortion, ×11·3. 9, UT 92468, pygidium, W form, ×9.

Figs. 10–16. *Peronopsis ekip* sp. nov. near St. Valentines Peak, lat. 41° 21·6′ S., long. 145° 44·3′ E. 10, UT 92692, cephalon, ×13. 11, UT 92712, pygidium, ×15·2. 12, UT 92010 cephalon, ×18·2. 13, UT 92714, cephalon, ×17·9. 14, UT 92715, pygidium, ×13·1. 15, UT 92687, holotype pygidium, ×26. 16, UT 92689, pygidium, ×6·4.

Figs. 17–18. *Hypagnostus* cf. *brevifrons* (Angelin). Christmas Hills, upper fauna, lat. 40° 54·1′ S., long. 144° 29·8′ E. 17, UT 92473, almost complete specimen, W form, ×10. 18, UT 92483, cephalon and thorax, W form, ×5·8.


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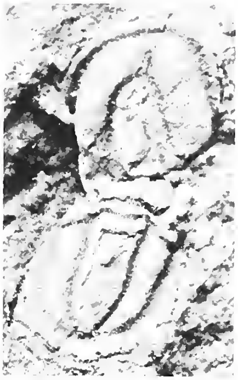
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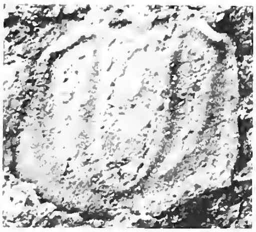
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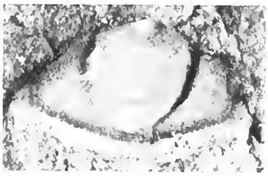
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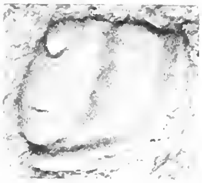
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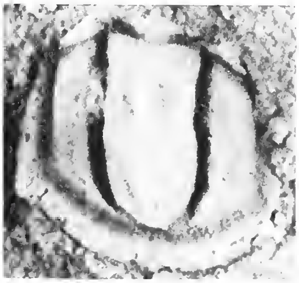
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rim wide, slightly elevated, and flatly convex; posterior marginal furrow wide and deep; both rim and marginal furrow narrow considerably to the anterior. Pygidial axis extends full length of acrolobe and in large specimens slightly on to the posterior marginal furrow. Narrow, smooth pleural fields. Lateral pygidial furrows are effaced; prominent node on second axial lobe.

Description. Moderately convex cephalon is about as wide as long. Cephalic margins converge gradually from the posterior to the broadly rounded cephalic front. Wide, shallow marginal furrow; narrow, flatly convex, slightly elevated rim. Both rim and furrow narrow posteriorly. Short, blunt posterolateral spines have a wide base. No preglabellar median furrow; smooth cheeks; moderately large simple, basal lobes.

Glabella is outlined by deep, moderately wide furrows; length about 0·7, and width about one-third, that of the cephalon. Shallow transverse glabellar furrow is arched posteriorly. Posterior glabellar lobe has length 0·7–0·75 that of glabella. On the holotype (UT 86599, Pl. 21, fig. 1) the glabellar rear is angular although the angularity is probably exaggerated by distortion (the glabellar rear is not properly visible on other cephala). Small centrally placed node on the posterior glabellar lobe.

Moderately convex pygidium is about as wide as long. From the anterior, the margins diverge slightly to short border spines placed about opposite axial posterior. Posterior margin is evenly curved between the spines. Wide, flatly convex, slightly elevated posterior rim; wide convex elevated lateral rim; wide deep marginal furrow. Both rim and furrow narrow markedly forwards. Narrow, shallow shoulder furrows; strongly geniculate shoulders with fulcra close to the axis; large, smooth, flat facets. Wide articulating furrow has a deep pit on either side of shallow central region. Narrow, convex articulating half-ring.

Wide, deep axial furrows; axis extends full length of acrolobe in mature specimens. In smallest available pygidium axial posterior is separated from posterior marginal furrow by a very short, shallow post-axial furrow. In larger specimens axis extends slightly on to marginal furrow.

Axis is slightly constricted in region of second axial lobe; lateral axial furrows are almost obsolete; well-developed node on second axial lobe. Anterior of node is a low ridge extending to anterior margin of acrolobe. Axial posterior is sharply rounded.

Discussion. P. gullini sp. nov. is quite close to *P. fallax minor* (Brögger), but differs in that it has a greater pygidial axial constriction, and the pygidial posterior is slightly more pointed. The pygidial axial rear reaches the posterior marginal furrow in all the larger specimens of *P. gullini* which is not the case with *P. fallax minor*. The basal lobes of *P. gullini* are larger than those of *P. fallax minor*. As noted above the pygidial axis of *P. gullini* extends further to the posterior in larger specimens than in smaller specimens.

Occurrence and age. Almost all specimens of *P. gullini* sp. nov. come from the lower fauna at Christmas Hills. There are four pygidia (including that figured as Pl. 21, fig. 9) tentatively assigned to *P. gullini* sp. nov. from the upper fauna at Christmas Hills. Thus *P. gullini* is probably of *Lejopyge laevigata* Zone I and possibly also extending into Zone II.

Peronopsis ekip sp. nov.

Plate 21, figs. 10–16

Material. Three partial cephala and four partial pygidia. All are well preserved.

Holotype. Pygidium UT 92689 (Pl. 21, fig. 15).

Diagnosis. Glabella has sharply rounded front and rounded rear. Transverse glabellar furrow arched strongly to the posterior. A small elongated glabellar node is placed towards glabellar posterior. Posterior glabellar lobe has a low anterior part and a relatively high posterior part. There is a vestigial preglabellar median furrow.

Subquadrate pygidium has a wide border, with short border spines. Almost parallel-sided, wide axis reaches the posterior marginal furrow; pygidial rear broadly rounded. Lateral axial furrows almost entirely effaced; axis slightly constricted at the second lobe. Prominent node on second lobe; small node towards axial posterior.

Description. Moderately convex cephalon about as long as wide. Moderately wide marginal furrow and moderately wide, slightly elevated, convex rim. Smooth cheeks. Glabella outlined by deep, wide axial furrows; it has a length about 0·7 that of the cephalon. Immediately anterior to sharply rounded glabellar front is a vestigial preglabellar median furrow which extends only a short distance towards the marginal furrow. Glabellar rear is rounded. Basal lobes, small, simple, and separated. Glabella expands slightly to the anterior; it is widest just behind the posteriorly arched transverse glabellar furrow. Anterior third of posterior glabellar lobe composed of two lobules which are outlined by faint furrows directed inwards and forwards from points on the axial furrows just to the anterior of the midpoint of the posterior lobe. The posterior glabellar lobe, particularly its posterior region, stands out strongly above the rest of the cephalon with the highest point being close to the posterior margin. Small elongated median node placed posteriorly on posterior glabellar lobe.

Subquadrate pygidium about as wide as long. Wide, shallow marginal furrow; wide, gently convex rim; short border spines. Gently geniculate shoulders with fulcra being close to the axis. Articulating furrow with a shallow central region and deep extremities. Convex articulating half-ring has a lenticular outline.

Pygidial axis distinctly convex and markedly elevated above less convex, smooth pleural fields. Axis is outlined by wide, moderately deep axial furrows which are subparallel for most of their length. Furrows shallow towards the bluntly rounded axial posterior which just reaches the marginal furrow. Axial width about two-fifths pygidial width. The two lateral axial furrows are effaced except for faint marginal indentations. Axis is slightly constricted at second lobe. The anterior and second lobes each have length about one-fifth that of axis. Very prominent node on second lobe. Small node occurs towards posterior of posterior axial lobe.

Discussion. The presence of a vestigial preglabellar median furrow may cast some doubt on the placing of this species in *Peronopsis*. However, the species described by Robison (1964, p. 531) as *Homagnostus incertus* has such a furrow, and as noted by Öpik (1967, p. 139), this species should be referred to *P. incerta* (Robison). *P. quadrata* (Tullberg), as illustrated by Westergård (1946, pl. 3, fig. 23), also shows a short preglabellar median furrow. Thus, the diagnosis of *Peronopsis* given by Robison (1964,

p. 529) should be amended to include forms with an incomplete preglabellar median furrow.

P. ekip sp. nov. has a small node placed towards the posterior of the pygidial axis; this feature is unique in *Peronopsis* as far as the author is aware.

Occurrence and age. P. ekip sp. nov. comes from near St. Valentines Peak; its age is either the *L. laevigata* III Zone or the *Damesella torosa–Ascionepea janitrix* Zone.

Genus HYPAGNOSTUS Jaekel, 1909

Hypagnostus Jaekel, 1909, p. 399; Kobayashi 1939, p. 122; Lermontova 1940, p. 129; Westergård 1946, p. 43; Ivshin 1953, p. 17; Howell 1959, p. 184; Öpik 1961*b*, p. 57; Robison 1964, p. 529; Öpik 1967, p. 82; Palmer 1968, p. 31.
Cyclopagnostus Howell, 1937, p. 1166; Howell 1959, p. 175.
Tomagnostella Kobayashi, 1939, p. 159; Howell 1959, p. 128.

Type species. Agnostus parvifrons Linnarsson, 1869, p. 82, pl. 2, figs. 56, 57.

Diagnosis. See Robison 1964, p. 529.

Discussion. Westergård (1946, p. 44) and later authors have included *Spinagnostus* Howell, 1935 in *Hypagnostus*. However, Shaw (1966, p. 848) redescribed the type species of *Spinagnostus*, *S. franklinensis* Howell, and concluded that *Spinagnostus* should be excluded from *Hypagnostus*. Shaw's interpretation is followed here until better-preserved examples of *S. franklinensis* clarify the situation.

Hypagnostus cf. *brevifrons* (Angelin)

Plate 21, figs. 17, 18

1946 Westergård, p. 48, pl. 5, figs. 24–29 (this reference gives the pre-1946 synonymy).
1959 Chu, p. 213, pl. 1, figs. 6–9.
1961*b* Öpik, p. 48, pl. 18, figs. 6–10.

Material. Two poorly preserved specimens are known from the upper fauna at Christmas Hills; one is an almost complete specimen; the other consists of a cephalon and a thorax.

Description. Moderately convex cephalon probably a little wider than long. Border consists of a moderately wide, flatly convex rim, and a narrow, shallow marginal furrow. Single lobed glabella has length about one-half that of cephalon, and at widest (at anterior of the small, simple basal lobes) it has a width about two-fifths that of the cephalon. Glabella tapers forward to well-rounded glabellar front. Basal lobes joined by narrow connecting band.

Moderately convex pygidium is probably slightly wider than long. It is widest at anterior and has a broadly rounded posterior margin. Border consists of wide, flatly convex rim and narrow, moderately deep marginal furrow. Border spines absent. Shallow, moderately wide shoulder furrows meet marginal furrows at an angle somewhat in excess of 90° and well to posterior of articulating furrow. Moderately convex shoulders with fulcra placed close to axis. Shallow articulating furrow is arched posteriorly; convex articulating half-ring. No post-axial median furrows developed; pleural fields smooth. Pygidial axis outlined by moderately deep and wide furrows. It has a fairly sharply rounded posterior and a length about 0·7 that of the pygidium. Lateral axial furrows are obsolete; axis constricted in region of the second axial lobe on which there is an elongated node.

Discussion. The over-all appearance of the form described above is thus very similar to that of *Hypagnostus brevifrons* (Angelin) as described and illustrated by Westergård (1946, p. 48, pl. 5, figs. 24–29). However, the specimens of the form described above are about one-half the size of the largest Swedish and Queensland specimens of *H. brevifrons* as described and illustrated by Westergård (1946) and Öpik (1961*b*, p. 58) respectively. A further point is that the border of the pygidium of the Tasmanian specimen appears to be slightly wider than *H. brevifrons* as illustrated by both Westergård (1946) and Öpik (1961*b*). The preservation of the Tasmanian specimens is such that it cannot be seen if the glabellar node is present in the same position as those on the Swedish specimens illustrated by Westergård (1946, pl. 5, figs. 24, 25, 28). A feature seen on rubber casts of Westergård's specimens (pl. 5, figs. 27, 26 respectively) is the presence of a small node close to the posterior of the pygidial axis; this feature was not reported by Westergård. It is in a similar position to the posterior axial node of *H. correctus* Öpik (1967, text-fig. 16). Such a feature is too small to be preserved on the poorly preserved pygidium described above. It cannot be stated with certainty that these Tasmanian specimens belong to *H. brevifrons*, and thus they are referred to as *H.* cf. *brevifrons*.

Occurrence and age. H. cf. *brevifrons* (Angelin) comes from the upper fauna at Christmas Hills; its age is either of the *Lejopyge laevigata* I or II Zone.

Genus GRANDAGNOSTUS Howell, 1935

Grandagnostus Howell, 1935*a*, p. 221; 1959, p. 181; Öpik 1961*b*, p. 65 (part); Rasetti 1967, p. 37; Poulsen 1969, p. 7.
Phalacroma Kobayashi, 1939, p. 136 (part); Westergård 1946, p. 92 (part).

Type species. Grandagnostus vermontensis Howell, 1935*a*, p. 221, pl. 22, figs. 8–11.

Diagnosis. A very large agnostid in which both cephalon and pygidium are almost completely effaced. The cephalic border, if present, is extremely narrow. Small, subcentral node on cephalon. Subquadrate pygidium with wide border which narrows only slightly to anterior. Small circular node towards pygidial anterior. Articulating half-ring is a narrow strip covering more than half the width of the pygidium.

Discussion. See discussion of *Valenagnostus* gen. nov.

Grandagnostus sp.

Plate 22, figs. 1–5

Material. About twelve somewhat crushed specimens, all of which have undergone tectonic distortion; five of the specimens are more or less complete.

Description. Very large, almost entirely effaced cephalon slightly wider than long. Lateral cephalic margins quite steep, but rest of cephalon gently convex. Cephalon has circular outline with straight posterior margin. Border not visible on most specimens, but some cephala show traces of a very narrow border. On some specimens, a narrow slightly upraised posterior rim and a narrow, shallow border are present on either side of a faintly outlined, rounded glabellar rear. Otherwise glabella is entirely effaced. Apparent centrally placed node on UT 92478 (Pl. 22, fig. 2) due to distortion.

Thoracic segments simple and have few furrows. Anterior thoracic segment decidedly longer (sag.) than posterior one.

Subsquare pygidium has evenly rounded posterior margin. Margins diverge slightly away from pygidial anterior until pygidium is widest about two-thirds of distance to posterior. Pygidium slightly wider than long. It is distinctly smaller than cephalon. This is shown well in all complete specimens and also in UT 86879g (Pl. 22, fig. 5), an enrolled specimen where the anterior end of the cephalon considerably overlaps the pygidial posterior. Almost flat pygidium has a wide border with a wide, gently convex rim, which narrows anteriorly and a wide, moderately deep marginal furrow. Shoulder furrows continuous with marginal furrows. Shoulder furrows narrow considerably adaxially; large flat facets; narrow shoulders. Articulating device not well preserved in any specimen, but in some poorly preserved unfigured specimens it is a narrow strip covering more than half the width of the pygidium. Shallow articulating furrow. Faint traces of moderately wide axis, of unknown length, at anterior of most pygidia. These traces are accentuated by the crushing of most pygidia.

Discussion. The specimens described above are not well enough preserved to be the basis for a new species. It is smaller than *G. glandiformis* (Angelin) and does not possess well-defined nodes as do *G. glandiformis* and *G. vermontensis.* However, such nodes would be difficult to see due to distortion.

Occurrence and age. Grandagnostus sp. comes from the upper fauna at Christmas Hills; its age is either of the *L. laevigata* I or II Zone.

Genus VALENAGNOSTUS nov.

Diagnosis. The almost entirely effaced cephalon has a narrow rim and a narrow marginal furrow. There is a small node on the posterior part of the cephalon. At the posterior of the pygidium the rim is wide and convex, and the marginal furrow is wide. The border narrows greatly to the anterior. A narrow, tapered vestigial axis extends to the marginal furrow; it is tapered most close to its anterior and again at about two-thirds of the distance of the posterior. There is a terminal axial node.

EXPLANATION OF PLATE 22

Figs. 1–5. *Grandagnostus* sp. Christmas Hills, upper fauna, lat. 40° 54·1′ S., long. 144° 29·8′ E. 1, UT 92477, complete specimen, W form, ×5. 2, UT 92478, complete specimen, intermediate distortion, ×8·7. 3, UT 86628, pygidium and thoracic segment, W form, ×5·2. 4, UT 86629, pygidium and two thoracic segments, W form, ×5·5. 5, UT 86879g, enrolled specimen, pygidium exposed, L form, ×5·3. Note the marked overlap of the cephalon with respect to the pygidium.

Figs. 6–11. *Valenagnostus banksi* sp. nov. from St. Valentines Peak, lat. 41° 21·6′ S., long. 145° 44·3′ E. 6, UT 92707, cephalon, L form, ×15·9. 7, UT 92720, cephalon, intermediate distortion, ×13. 8, UT 92693, pygidium and thoracic segments, W form distortion, ×19·2. 9, UT 92713, holotype pygidium, L form, ×20. 10, UT 92708, pygidium, W form, ×11·3. 11, UT 92688, pygidium, W form, ×11·5.

PLATE 22


1


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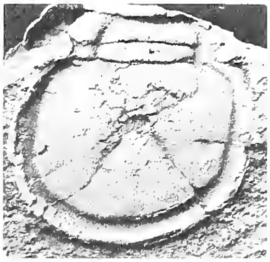
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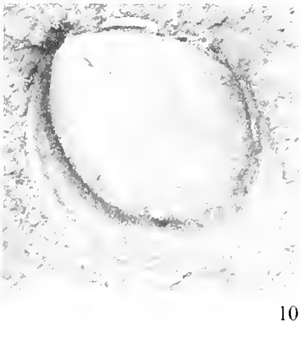
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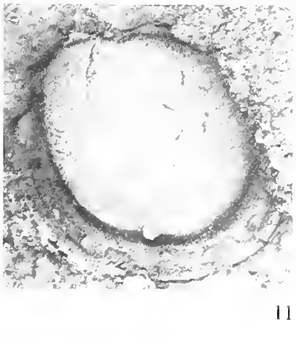
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JAGO, Tasmanian agnostids

Type species. Agnostus nudus Beyrich var. *marginata* Brögger, 1878, p. 73, pl. 6, fig. 3.

Discussion. The effaced agnostid species usually described under the generic names, *Phalacroma*, *Grandagnostus*, and *Phalagnostus* are difficult to assign to any particular genus. As noted by Öpik (1961*b*, p. 91), *Phalacroma* refers to agnostids with a wide, non-effaced pygidial axis like that of *P. bibullatum* (Barrande). Thus all species, which have both the cephalon and pygidium effaced and have been described as *Phalacroma*, must be reassigned to other genera.

Howell (1935*a*, p. 22) erected the genus *Grandagnostus* for a very large agnostid which has both the cephalic and pygidial acrolobes almost completely effaced, a wide pygidial border and a very narrow or absent cephalic border. In this genus, Howell (1935*a*) correctly included the type species, *G. vermontensis* Howell from Vermont and *A. glandiformis* Angelin from Sweden (see below). Unfortunately, *G. vermontensis* is poorly preserved. Westergård (1946, p. 96) refers to cephala of *glandiformis* up to 16 mm long and 15 mm wide.

There appear to me to be at least two and probably three distinct genera represented by the species included by Westergård (1946) in *Phalacroma*. Two of these genera are best compared by a comparison of *G. glandiformis* (Angelin) and *V. marginatus* (Brögger). The writer had at his disposal rubber casts of many of the specimens of both species that are illustrated by Westergård (1946, pls. 15, 16). Rubber casts of some of the specimens of *Phoidagnostus bituberculatus* (Angelin), *Phalacroma scanicum* (Tullberg), and *P. resectum* (Grönwall) illustrated in Westergård were also available.

The most obvious difference between *glandiformis* (Pl. 24, figs. 1-5 herein) and *marginatus* (Pl. 24, figs. 6-9 herein) is that the former is much larger. The narrow cephalic border of *marginatus* (Pl. 24, fig. 6) is much better developed than that of *glandiformis* (Pl. 24, fig. 2). Westergård (1946, p. 95) notes that no cephalon of *glandiformis* which has retained the exoskeleton shows a border, but in some of the exfoliated specimens (Pl. 24, fig. 2), including the lectotype, a narrow rim is visible.

The most marked differences of form are in the pygidia. The pygidial border of *glandiformis* (Pl. 24, figs. 3-5) consists of a very wide, shallow furrow and a gently convex rim. The rim is moderately wide at the posterior and quite narrow at the anterior. The border narrows slightly to the anterior. This is in marked contrast with the border of *marginatus* (Pl. 24, figs. 6-9). At the posterior the pygidial border of *marginatus* is very wide (in some specimens it has a length (sag.) over a quarter that of the complete pygidium). It consists of a narrow, shallow marginal furrow and a very wide, gently convex rim. The rim narrows greatly forwards where it is quite narrow; over all, the border narrows markedly forwards.

There is a faint but clear axis on *marginatus* which extends the full length of the acrolobe and has a terminal node. The axis of *marginatus* is very similar to that figured by Öpik (1961*b*, text-fig. 20) for his species *G. imitans*. The axis of *glandiformis* is poorly outlined, and there is no terminal node. The articulating half-ring of *glandiformis* is a narrow strip more than half the width of the pygidium, that of *marginatus* is lens-shaped and much less than half the width of the pygidium.

Howell (1955, p. 925) erected a new genus, *Phalagnostus*, with type species *Battus nudus* Beyrich in an attempt to solve the complex nomenclatural problem of the effaced agnostids. Howell (1955, p. 926 states: '*Phalagnostus* differs from *Grandagnostus* in being smaller, in having a less quadrate pygidium, in having the node on the axial positions of the pygidium elongate, instead of circular and in having a more circular cranidium.'

Šnajdr (1958, p. 76) restudied the Czechoslovakian forms of *B. nudus* Beyrich and also revised the genus *Phalagnostus.* Šnajdr (1958, p. 78) included the following species in *Phalagnostus*, viz. *P. nudus* (Beyrich), *P. prantli* Šnajdr, *P. eskriggei* (Hicks), *P. scanicum* (Tullberg), *P. resectum* (Grönwall), *P. marginatus* (Brögger), and *P. glandiformis* (Angelin). The last four species are included by Westergård (1946) in *Phalacroma.* However, *marginatus* and *glandiformis* are shown above to belong to separate genera. The species *marginatus* and *nudus* are also considerably different, especially in the nature of the pygidial border, pygidial axis, terminal axial node, and cephalic border. They are regarded by the present writer as belonging to different genera. Species of the *marginata*-type are included below in the new genus *Valenagnostus.*

G. vermontensis Howell is poorly preserved and difficult to compare with other species. However, it would seem from a comparison of the photographs of *vermontensis* with rubber casts of some of the specimens of *G. glandiformis* (Angelin) illustrated in Westergård (1946) that *vermontensis* and *glandiformis* do belong in the same genus *Grandagnostus* Howell, as originally suggested by Howell (1935*a*). In fact, Poulsen (1969, p. 9) regarded *G. vermontensis* as a junior synonym of *G. glandiformis*, thus making the latter the type species. Shaw (1966, p. 848) described an incomplete cephalon as *G. vermontensis* Howell(?), the query being due to the lack of the cephalic node on Shaw's specimen. A well-preserved example of *vermontensis* is required before it can be decided whether or not it is conspecific with *glandiformis.*

Because Šnajdr (1958) included both species *nudus* and *glandiformis* in *Phalagnostus*, a comparison of the two species seems warranted. Apart from the rubber casts of *glandiformis* noted above, the author has at his disposal rubber casts of one pygidium of *nudus* (figured in Šnajdr 1958, pl. 5, fig. 9, and herein Pl. 24, fig. 11) and the holotype of *P. prantli* Šnajdr (1958, pl. 6, fig. 1), and herein Plate 24, fig. 10.

The species *glandiformis* is bigger than *nudus*; the cephalic posterior of *nudus* shows more traces of the glabellar rear and basal lobes than does that of *glandiformis.* The pygidial borders of *glandiformis* and *nudus* are similar in that they do not narrow much to the anterior. The pygidial rim of *nudus* is wider than that of *glandiformis* especially in the anterior region. The pygidia of *glandiformis* generally have a more quadrate outline than those of *nudus.* Another difference between the two species is in the arrangement of the pygidial muscle scars; those of *nudus* as illustrated by Šnajdr (1958, text-fig. 11) are smaller and more numerous than those of *glandiformis* illustrated by Westergård (1946, pl. 16, fig. 2) and herein Plate 24, fig. 4.

On each shoulder region of *nudus* there is a transverse furrow which extends across the anterolateral corner of the pygidium, across the anterior of the rim, and almost to the pygidial margin (Pl. 24, fig. 11). This furrow is distinct from the marginal furrow. No such furrow is seen in *glandiformis.* A similar furrow is also seen in *P. prantli* Šnajdr, *Phalacroma scanicus* (Westergård, 1946, pl. 14, figs. 16–18—see Pl. 24, figs. 15, 16) and in the species described by Hutchinson (1962, p. 90) as *P. nudum* (Beyrich).

Rasetti (1967, p. 38) considers that it is possible that this anterolateral transverse furrow is, in fact, the shoulder furrow and that the wide rim around the pygidium is part of the acrolobe. Poulsen (1969, p. 9) supports Rasetti's suggestion that the pygidium of *Phalagnostus* may not have a true border. Both Rasetti and Poulsen consider that the anterolateral transverse furrow described above is of generic significance. The writer agrees with this conclusion but feels that the question of the presence or absence of a border cannot be determined on the available material.

Öpik (1961*b*) referred two new species, *imitans* and *velaevis*, to *Grandagnostus*, and in 1967 (p. 86) he described *G. evexus*. Öpik (1961*b*, p. 54) states that there are two groups within *Grandagnostus*: (i) species without a cephalic marginal border, e.g. *G. velaevis*, and (ii) species with a border, e.g. *G. imitans*. Öpik (1961*b*, p. 67) differentiated between *Grandagnostus* and *Phalagnostus* on the grounds that the latter has no basal lobes. This appears to the writer to be an error. Basal lobes or traces of them are seen on all but the most effaced agnostid cephala and appear to be a fundamental part of agnostid anatomy. Furthermore, species such as *G. glandiformis* (Angelin) and *P. prantli* Šnajdr do possess vestigial basal lobes. This is shown by an inspection of a rubber cast of the cephalon of *glandiformis* (figured by Westergård 1946, pl. 15, fig. 4; herein Pl. 24, fig. 1) and a rubber cast, the complete holotype of *P. prantli* (figured by Šnajdr 1958, pl. 6, fig. 1; herein Pl. 24, fig. 10). The basal lobes of these species are difficult to see in the photographs noted above but are certainly present.

No comment can be made by the author on the species described by Pokrovskaya (1958) in *Phalacroma*, because the author has not seen that paper. The pygidium figured and described by Hajrullina (1962, p. 130, pl. 4, fig. 3) as *P. rabutense* cannot be compared in detail with other species because of the poorly reproduced photo of *rabutense*. *P. thorali* Howell (1935*b*, p. 227, pl. 22, figs. 19, 20) is poorly preserved and cannot be placed with certainty into any genus although its narrow pygidial border excludes it from *Grandagnostus*. Courtessole (1973) included this species in *Leiagnostus*, but the preservation of the figured specimens of *thorali* does not allow a definite generic assignment.

Öpik (1961*b*, p. 86) suggested, and Palmer (1968, p. 32) agreed, that *Agnostus bituberculatus* Angelin, 1851, belongs in *Phalagnostus*. However, *A. bituberculatus* has no transverse furrow near the anterolateral corners of the pygidium as has *Phalagnostus*, and should not be included in that genus.

My conclusions regarding the effaced agnostids are as follows:

(i) A new genus, *Valenagnostus* must be erected to include the following species, *V. marginatus* (Brögger), *V. imitans* (Öpik), *V. evexus* (Öpik); *V. banksi* sp. nov., and *V. brittoni* sp. nov., with *V. marginata* as the type species.

(ii) The other effaced agnostids usually described under *Grandagnostus*, *Phalacroma*, or *Phalagnostus* should be divided into at least two genera, i.e. *Grandagnostus* Howell, with *G. glandiformis* (Angelin) as the best-known species, and *Phalagnostus* Howell, with *P. nudus* (Beyrich) as type species. Other species which should be included in *Phalagnostus* are *P. prantli* Šnajdr and *P. scanicus* (Tullberg).

(iii) The generic position of *A. bituberculatus* Angelin, 1851 is not yet known.

(iv) The positions of the species *velaevis* and *resecta* (Pl. 24, fig. 12) are not known.

Valenagnostus banksi sp. nov.

Plate 22, figs. 6–11; text-fig. 1

Material. Many well-preserved, almost complete, pygidia. Unfortunately, only a few external moulds of almost complete cephala are known.

Holotype. Pygidium, UT 92713 (Pl. 22, fig. 9).

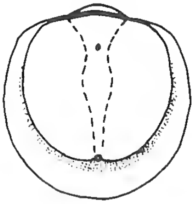
Diagnosis. Strongly convex, almost entirely effaced cephalon about as wide as long. Narrow cephalic border with short cephalic spines. Strongly convex pygidium about as wide as long. Wide border with wide elevated rim and moderately wide, shallow marginal furrow, both of which narrow greatly to the anterior. Faintly outlined axis has very prominent terminal node.

Description. Strongly convex cephalon about as wide as long. Narrow rim has similar slope to acrolobe margin and is separated from acrolobe by very narrow, shallow marginal furrow. Short cephalic spines known only from unfigured internal moulds. Cephalon is almost entirely effaced; glabella very faintly outlined at posterior and fades completely to anterior. Glabellar rear rounded. Small centrally placed node at posterior end of cephalon about one-third of distance from posterior to anterior margin. Posterior ends of basal lobes may be faintly outlined in UT 92707 (Pl. 22, fig. 6).

Strongly convex pygidium about as wide as long. Wide posterior border with wide elevated rim and a moderately wide, shallow marginal furrow. Both rim and marginal furrow narrow greatly anteriorly; near the anterolateral corners the border is quite narrow. Gently convex, narrow shoulders; narrow, shallow shoulder furrows. Basic articulating device with moderately deep articulating furrow which is arched slightly forward; lens-shaped articulating half-ring.

At centre of posterior margin border about one-fifth length of pygidium. Margins diverge slightly from anterolateral corners to a point just over half-way along pygidium; from this point posterior margin is broadly and evenly rounded. No border spines. The almost effaced narrow axis stands out very slightly above smooth pleural regions; it extends full length of acrolobe and has a prominent terminal node.

In region of axial rear acrolobe is arched slightly forward. Axis moderately wide at anterior and tapers to posterior which is slight expansion at about midpoint (text-fig. 1). Small, centrally placed anterior axial node about one-quarter distance from anterior to posterior of axis. Axis shows no trace of annulation.



TEXT-FIG. 1. Pygidium of *Valenagnostus banksi* sp. nov.

Discussion. The terminal pygidial axial node of *V. banksi* is much more prominent than those of other species of *Valenagnostus*. The pygidial marginal furrow of *V. banksi* is wider than that of either *V. imitans* or *V. marginatus*. Pygidia of *V. evexus* and *V. brittoni* are much more effaced than that of *V. banksi*.

Occurrence and age. V. banksi sp. nov. comes from near St. Valentines Peak; its age is of either the *Lejopyge laevigata* III Zone or the *Damesella torosa–Ascionepea janitrix* Zone.

Valenagnostus brittoni sp. nov.

Plate 23, figs. 1-6

Material. About fifty pygidia and cephala in varying states of preservation are available for descriptive purposes. Unfortunately, some of the best-preserved specimens are available only as internal moulds. It is on these specimens that the small cephalic spines can be seen. All figured specimens are external moulds.

Holotype. UT 86850c (Pl. 23, fig. 1).

Diagnosis. Cephalon almost effaced, with a narrow cephalic border and a small cephalic node. The pygidium has an extremely wide border which narrows greatly to the anterior. There is a faintly outlined axis with a small terminal node.

Description. Strongly convex cephalon about as wide as long. Narrow border with narrow, shallow marginal furrow and narrow convex rim. Slope of rim continuous with that of very steep acrolobe margin. Very small posterolateral spines. Margins of cephalon diverge slightly away from posterior margin; cephalon widest at mid-point; it has an evenly curved anterior margin. Cephalon almost entirely effaced with very faint traces of basal lobe posteriors and in some specimens vestiges of a moderately long and wide glabella (brought out by distortion and crushing of specimens). Cephalic node present.

Pygidium about as wide as long with acrolobe of slightly less convexity than that of cephalon. At posterior, border is very wide (about 0·3 length (sag.) of pygidium); wide, deep marginal furrow; wide, elevated convex rim. Border decreases in width considerably to anterior where it is quite narrow. Shoulder area not visible in many specimens; however, on an unfigured internal mould one shoulder is well exposed. Shoulder furrows are narrow and shallow; large concave facets; large fulcra placed about mid-way between anterolateral corners and centre of articulating device. Shallow, articulating furrow with slight depression at either end. Gently convex articulating half-ring. Faintly outlined pygidial axis extends full length of acrolobe; small axial terminal node. Small node at anterior end of axis about one-quarter of distance from anterior to posterior of axis. Axis wide at anterior (about 0·45 of

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EXPLANATION OF PLATE 23

Figs. 1-6. *Valenagnostus brittoni* sp. nov. Christmas Hills, lower fauna, lat. 40° 54·1′ S., long. 144° 29·8′ E. 1, UT 86850c, holotype pygidium, W form, ×10·6. 2, UT 86869h, cephalon, intermediate distortion, ×7·4. 3, UT 86579, poorly preserved complete specimen, L form, ×9·5. 4, UT 86879m, cephalon, W form, ×10·4. 5, UT 86877, cephalon, L form, ×10. 6, UT 86870g, pygidium, W form, ×10.

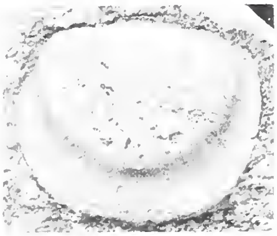
Figs. 7-11. *Ptychagnostus* (*Goniagnostus*) *buckleyi* sp. nov. Christmas Hills, upper fauna, lat. 40° 54·1′ S., long. 144° 29·8′ E. 7, UT 86880i, cephalon, L form, ×11·4. 8, UT 92472, holotype, complete specimen, W form, ×8·5. 9, UT 86873a, W form, ×10·5. 10, UT 86872f, pygidium, W form, ×9. 11, UT 86880m, pygidium, L form, ×6·6.

Fig. 12. *Ptychagnostus* (*Ptychagnostus*) cf. *aculeatus* (Angelin). Christmas Hills, upper fauna, lat. 40° 54·1′ S., long. 144° 29·8′ E., pygidium, W form, ×14·7.

Fig. 13. *Utagnostus neglectus* sp. nov. Christmas Hills, lower fauna, lat. 40° 54·1′ S., long. 144° 29·8′ E. UT 86844i, holotype, complete specimen, intermediate distortion, ×11.

Figs. 14-17. *Utagnostus*(?) sp. from near St. Valentines Peak, lat. 41° 21·6′ S., long. 145° 44·3′ E. 14, UT 92718, cephalon and part of pygidium, ×19. 15, UT 92698, holotype, almost complete specimen, ×14·5. 16, UT 92686, pygidium, ×16. 17, UT 92699, cephalon and thorax, ×15.

PLATE 23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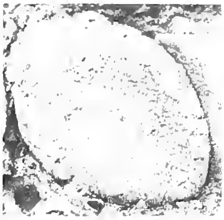
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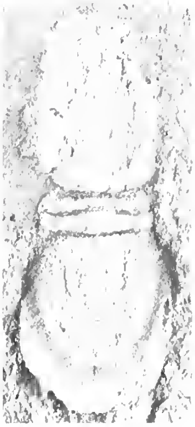
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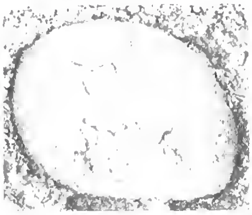
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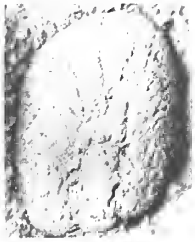
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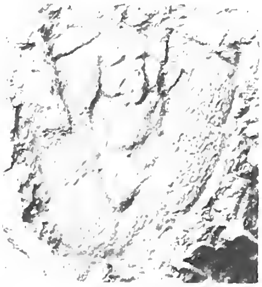
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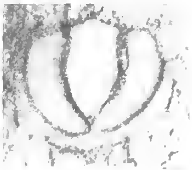
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JAGO, Tasmanian agnostids

pygidial width); immediately behind anterior margin axis narrows considerably and tapers evenly (except for a slight central widening) to terminal node.

Discussion. The pygidial border of *V. brittoni* is wider than those of *V. evexus*, *V. imitans*, and *V. banksi*. Some of the pygidia of *V. marginatus* figured by Westergård (1946, pl. 14 and herein Pl. 24, figs. 7–9) have a pygidial border of similar width to that of *V. brittoni*. However, these specimens are some of the smaller pygidia of *V. marginatus*, and the larger pygidia of *marginatus* have a narrower border than does *V. brittoni*. The pygidial axis of *V. brittoni* is less obvious than those of *V. banksi* or *V. marginatus*. *V. brittoni* does not have the elongate anterior axial node of *V. imitans*.

Occurrence and age. V. brittoni sp. nov. comes from the lower fauna at Christmas Hills; its age is probably of the *L. laevigata* I Zone.

Subfamily PTYCHAGNOSTINAE Kobayashi, 1939

Genus PTYCHAGNOSTUS Jaekel, 1909

Robison 1964, p. 522, gives the most detailed recent synonymy. The following synonymy should be added.

Ptychagnostus Šnajdr, 1958, p. 70; Pokrovskaya 1960, p. 58; Rushton 1966, p. 35; Palmer 1968, p. 28.
Goniagnostus Pokrovskaya, 1960, p. 58.
Doryagnostus Pokrovskaya, 1960, p. 58.
Triplagnostus Pokrovskaya, 1960, p. 58.

Diagnosis. See Robison 1964, p. 522.

EXPLANATION OF PLATE 24

Figs. 1–5. Rubber casts of *Grandagnostus glandiformis* (Angelin). 1 and 2, exfoliated cephalon figured by Westergård 1946, pl. 15, fig. 4. 1, top view, ×4·1. 2, side view showing very narrow rim, ×5·5. 3, pygidium from Andrarum Limestone, Kiviks-Esperöd, Scania figured by Westergård 1946, pl. 15, fig. 14, ×6. 4, pygidium showing muscle attachments from Andrarum Limestone, Andrarum, Scania, figured by Westergård 1946, pl. 16, fig. 2, ×2·4. 5, pygidium which has been damaged since figured by Westergård 1946, pl. 15, fig. 12, ×3·8.

Figs. 6–9. Rubber casts of *Valenagnostus marginatus* (Brögger). Specimens from Aborrtallet, Angermanland figured by Westergård as *Phalacroma marginatum* (Brögger). 6, cephalon figured by Westergård 1946, pl. 14, fig. 25, ×6·6. 7, pygidium figured by Westergård 1946, pl. 14, fig. 29, ×6. 8, pygidium figured by Westergård 1946, pl. 14, fig. 27, ×10. 9, pygidium figured by Westergård 1946, pl. 14, fig. 26, ×10.

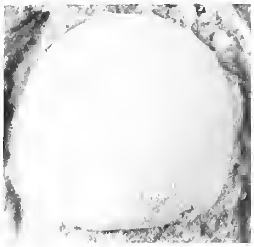
Fig. 10. Rubber cast of the holotype of *Phalagnostus prantli* Šnajdr figured by Šnajdr 1958, pl. 6, fig. 1, ×7. Note the very faint traces of basal lobes.

Fig. 11. Rubber cast of enrolled specimen showing pygidium of *Phalagnostus nudus* (Beyrich), ×6·7. Originally figured by Šnajdr (1958, pl. 5, fig. 9). Note the arrangement of muscle scars and the furrow across the anterolateral corner of the pygidium.

Fig. 12. Rubber cast of pygidium of *Phalacroma resecta* (Grönwall) from Brantevik, Scania figured by Westergård 1946, pl. 14, fig. 19, ×6.

Figs. 13–14. Rubber casts of *Phalagnostus scanicus* (Tullberg) from Gislövshammer, Scania and Andrarum, Scania, respectively. 13, pygidium figured by Westergård 1946, pl. 14, fig. 18, ×8·5. 14, pygidium figured by Westergård 1946, pl. 14, fig. 17, ×8.

Figs. 15–16. Rubber casts of *Oidalagnostus trispinifer* Westergård, figured in Westergård 1946, pl. 9, figs. 7 and 6 respectively. 15, pygidium from Torbjorntrop, Västergotland, ×9. 16, holotype pygidium from Gudhem, Västergotland, ×5.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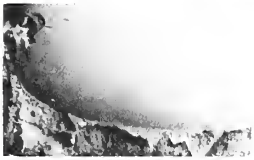
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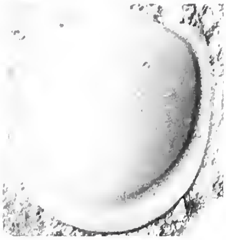
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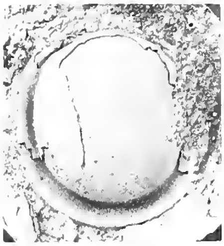
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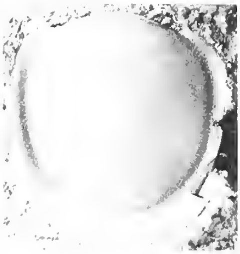
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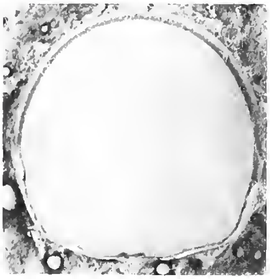
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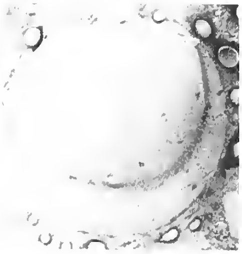
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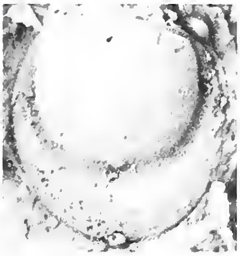
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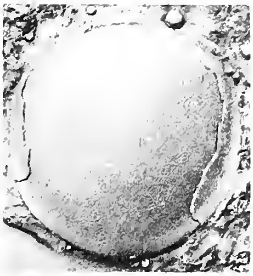
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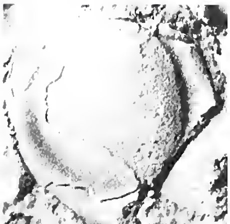
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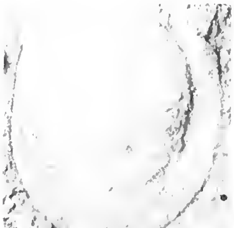
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JAGO, Tasmanian agnostids

Discussion. The Tasmanian forms add nothing to the concept of the genus *Ptychagnostus* as formulated by Öpik (1961*b*, p. 77). Any necessary discussion is given after the relevant species.

Ptychagnostus (*Ptychagnostus*) cf. *aculeatus* (Angelin)

Plate 23, fig. 12

Synonymy. See Palmer 1968, p. 28.

Material. One poorly preserved partial pygidium is known.

Description. Moderately convex pygidium with border almost entirely missing. Shoulder furrows of moderate width and depth; shoulders are narrow near lateral margins of pygidium and widen adaxially. Fulcra appear to be close to axis. Articulating device not visible. Axis outlined by moderately wide and deep furrows. Narrow, shallow post-axial median furrow appears to be present. Pleural fields covered with large granules. There also appear to be large tubercles on the first axial lobe, but they are much fainter than those on the pleural areas. Axial details are largely obscured. The axis is of the *P.* (*Ptychagnostus*) type. At anterior, axis has a width about two-fifths that of the acrolobe. From the anterior, axis narrows along first axial lobe which is tripartite, with the lateral lobules larger than the central lobule. First lateral axial furrow arched strongly forward. From anterior lobe axis tapers to the sharply rounded axial rear with a slight expansion at anterior of posterior axial lobe. Second axial lobe is also tripartite with the central lobule standing out above the lateral lobules; spine at posterior of central lobule. The poor preservation does not allow posterior extent of spine to be determined although there is a strong suggestion of quite a long spine. Posterior axial lobe slightly longer than the two anterior lobes combined.

Discussion. The Christmas Hills specimen has the following features in common with *P. aculeatus* (Angelin): (*a*) large granules over the pleural areas and on at least part of the axis, (*b*) a faint post-axial median furrow, and (*c*) a triannulated axis which may have quite a long spine.

P. aculeatus also exhibits closely spaced small granules over its surface. The Christmas Hills form does not show this feature clearly although there is a suggestion of it. The poor preservation makes retention of such features difficult. *P. aculeatus* has no border spines, but the border of the Christmas Hills specimen is not preserved and so this feature cannot be compared.

The contraction of the axis at the second axial lobe is not as marked as in the pygidia of *P. aculeatus* from Sweden, as illustrated by Westergård (1946, pl. 12, figs. 9 and 10), and from Queensland, as illustrated by Öpik (1961*b*, pl. 21, fig. 4*a*, *b*), but is similar to that figured from Alaska by Palmer (1968, pl. 6, fig. 20). The Tasmanian form is also smaller than those noted above. This fact may not be significant, but the faintness of the post-axial median furrow of the Tasmanian form may indicate that it is a quite mature specimen (see comment by Westergård 1946, p. 80). Thus, the Tasmanian form may be identical with *P. aculeatus* but it is too poorly preserved and incomplete to be sure.

If the Christmas Hills form is *P. aculeatus*, then the already widespread geographic distribution of this species is extended. It is already known from Sweden, Norway, Alaska, and Queensland. Nowhere is it common, thus, limiting its use for correlation purposes. In Sweden it is 'everywhere infrequent' (Westergård 1946, p. 80); in Alaska Palmer (1968, p. 28) records a single pygidium, and in Queensland most of the specimens came from a single bedding plane (Öpik 1961*b*, p. 80).

In Sweden *P. aculeatus* is reported only from the *Solenopleura brachymetopa* Zone. In Queensland Öpik reports it from both the *P. cassis* Zone and the *Proampyx agra* Zone which extends its range up to about the middle of the Swedish *Lejopyge laevigata* Zone (Öpik 1961*b*, fig. 15). The exact age of the Alaskan fauna in which *aculeatus* was found was not determined by Palmer (1968), but it is of a similar age to both the Swedish and Queensland occurrences.

Occurrence and age. P. (*Ptychagnostus*) cf. *aculeatus* (Angelin) comes from the upper fauna at Christmas Hills; its age is either of the *L. laevigata* I Zone or the *L. laevigata* II Zone.

Ptychagnostus (*Goniagnostus*) *buckleyi* sp. nov.

Plate 23, figs. 7–11

Material. One very well-preserved external mould of an almost complete specimen, plus about twenty separate pygidia and cephala preserved as external moulds.

Holotype. UT 92472, Plate 23, fig. 8.

Diagnosis. P. buckleyi sp. nov. has moderately long, slightly divergent posterolateral spines on both cephalon and pygidium. Cephalic axial furrows and scrobiculae are moderately deep. Narrow cephalic border; somewhat wider pygidial border. Pygidium has large shoulders and a shallow post-axial median furrow. Pygidial pleural areas covered with closely spaced small nodes.

Description. Gently convex cephalon probably a little wider than long. Narrow border with narrow, shallow marginal furrow and narrow, convex elevated rim. Posteriorly directed, slightly divergent posterolateral spines with thick bases extend to points opposite the junction of the thoracic segments.

Length of glabella about three-quarters that of cephalon. Glabella outlined by narrow, moderately deep furrows; narrow, shallow preglabellar median furrow. Almost straight transverse glabellar furrow with a slight forward deflection at centre and at either extremity. Anterior glabellar lobe is subtriangular and has a length about two-fifths that of glabella.

Posterior glabellar lobe is trilobate (including basal lobes); it has two pairs of deep lateral furrows which are directed inwards and slightly backwards from the axial furrows. Each furrow extends about one-quarter of distance across glabella. Anterior pair deeper than posterior pair. Posterior furrows (each with a deep adaxial pit) mark anterior of basal lobes. Basal lobes have length about one-third of posterior glabellar lobe. Very narrow rim beneath wide, broadly rounded glabellar rear connects posterior rims and is separated from basal lobes by narrow, shallow furrows. There is a marked decrease in width of glabella at transverse glabellar furrow.

On each highly scrobiculate cheek is a primary scrobicule which runs outwards and slightly forwards from a point near the end of the transverse glabellar furrow.

(On UT 92472, Pl. 23, fig. 8, this scrobicule appears to meet the transverse glabellar furrow, but this is a tectonic effect.) To the anterior of this scrobicule on each cheek there are three primary rugae. Scrobiculae show a radial distribution with secondary scrobiculae of various lengths between the main scrobiculae. The posterior portions of the cheeks have three or four primary rugae which are not as well defined as those in anterior part of cheeks. All these scrobiculae tend to be deepest adaxially. There is a pair of short scrobiculae in adaxial region of cheeks; each member of the pair arises from the axial furrow near anterior end of middle glabellar lobe.

Gently convex pygidium probably slightly wider than long. Pygidial border wider than cephalic border; narrow, shallow marginal furrow; moderately wide, gently convex rim. Moderately long, slightly divergent border spines; border width increases near spine bases which are about opposite end of pygidial axis. Narrow, shallow shoulder furrows; large shoulders; facets not clearly preserved but appear to be quite big; fulcra placed just abaxial of midpoints between anterolateral corners and axial furrows. Articulating furrow shallowest at centre; it is arched backwards. Small, low, convex articulating half-ring.

Pleural areas separated behind axis by narrow, shallow post-axial median furrow. Pleural areas apparently have a closely spaced reticulate veination. However, this feature is probably caused by distortion of closely spaced, small nodes. Wide, deep axial furrows. Length of axis about three-quarters that of pygidium.

Quadrilobate axis is constricted at anterior lateral furrow. Bluntly pointed axial rear. Tripartite anterior lobe with lateral lobules extending slightly more to both posterior and anterior than the central lobule. Narrow, moderately deep, anterior lateral furrow is arched slightly forward at its centre. Lateral lobules slightly wider (tr.) than the central lobule. Second lobe is tripartite with strong node on central lobule. Central lobule extends markedly to posterior so that middle transverse axial furrow is arched strongly to the posterior at the centre. Second axial lobe is slightly larger than anterior lobe. Third and fourth axial lobes are somewhat more convex than the anterior lobes; they are divided by a wide, deep furrow which is narrowest at its centre. Axis is slightly constricted at this furrow. Small node at centre of this furrow.

Discussion. This species clearly belongs in *P.* (*Goniagnostus*) as defined by Öpik (1961*b*, p. 77). The cephalic scrobiculae of *buckleyi* are deeper than those of *P.* (*G.*) *nathorsti* (Brögger), the type species of the subgenus. The pygidial border spines of *buckleyi* are much larger than those of *nathorsti*. The larger cephalic postero-lateral spines in *buckleyi* are similar to those figured for *P.* (*G.*) *fumicola* Öpik (1961*b*, text-fig. 28). *P. buckleyi* has a distinct post-axial median furrow whereas the pygidium of *fumicola* has no such furrow.

The pygidial pleural areas of *buckleyi* are covered by closely spaced, small nodules; those of *fumicola* are covered by coarse granules. The pygidial pleural areas of the Mindyallan *P.* (*G.*) *nodibundus* are also covered with coarse granules (Öpik 1967). The pygidial border spines of *P.* (*G.*) sp. aff. *nathorsti*, illustrated by Öpik (1961*b*, text-fig. 30), and of *P.* (*G.*) cf. *nathorsti*, Whitehouse (1939, p. 259, pl. 25, fig. 20), are much smaller than those of *buckleyi* as are those of *G.* aff. *nathorsti* of Chu (1965, p. 13, pl. 1, figs. 4–7). The pygidial pleural areas of this Chinese form appear to be smooth in contrast to those of *buckleyi*. The pygidium illustrated by Chu (1965, pl. 1, fig. 8) as *Goniagnostus* sp. is similar to that of *buckleyi* in that they both appear to have closely spaced, small nodes which are partly confluent. However, *buckleyi* has larger shoulders and bigger border spines.

The species described by Whitehouse (1939, p. 258, pl. 25, figs. 21–23) as *G. purus* belongs to *P.* (*Ptychagnostus*) rather than to *P.* (*Goniagnostus*). The fact that the pygidial axis is trilobed can be seen in plate 25, fig. 23 of Whitehouse. However, Whitehouse (p. 259) clearly recognized that *purus* is close to *P.* (*P.*) *gibbus* and questioned the differentiation of *Goniagnostus* and *Ptychagnostus* on the basis of the former having pygidial spines. Westergård (1946, p. 80) raised the same query. Westergård (1946, p. 81) included *scanensis* in *Goniagnostus* presumably on the basis of the small pygidial spines on this species. Only two pygidia of this species were known to Westergård, and he states (p. 82), ‘the transverse depression across the end-lobe is very weak’. A close inspection of a rubber cast of the specimen figured by Westergård (1946, pl. 12, fig. 17) reveals no such depression, and thus *scanensis* probably belongs to *P.* (*Ptychagnostus*) rather than *P.* (*Goniagnostus*).

The species described by Whitehouse (1939, p. 260, pl. 25, fig. 19) as *G. scarabaeus* is difficult to compare with *buckleyi* due to the poor photographic reproduction of *scarabaeus*. The description by Whitehouse (1939, p. 260) notes, ‘there are three or four pits on either side of the posterior glabellar lobe and one on each side of the anterior lobe’. These features are not seen in *buckleyi*. Whitehouse (1939, p. 260) gives a small line diagram of *scarabaeus* in which there is no sign of a fourth axial lobe. On the other hand, he states that *scarabaeus* is perhaps closer to *nathorsti* than it is to other members of *Goniagnostus*. This may indicate that the pygidial axis is quadrilobed and that *scarabaeus* belongs to the subgenus *Goniagnostus*. The photograph reproduced in Whitehouse (1939, pl. 25, fig. 19) is not clear on this point.

P. (*G.*) *spiniger* (Westergård) has large diverging posterolateral spines which appear slightly more divergent than those of *buckleyi* although this may be due to different preservation. However, the main difference between *spiniger* and *buckleyi* is that the pygidial axis of *spiniger* narrows all the way to its posterior. In *buckleyi* the third axial lobe is distinctly wider than the second axial lobe.

The specimen figured by Howell (1935*c*, figs. 3, 4) as *G. confluens* (Matthew) appears to belong to *P.* (*Ptychagnostus*) rather than *P.* (*Goniagnostus*). *P. confluens* is trilobed, and the apparent quadrilobation in Howell’s photograph appears to be due to distortion.

Occurrence and age. P. (*G.*) *buckleyi* sp. nov. comes from the upper fauna at Christmas Hills; its age is late middle Cambrian, probably of the *L. laevigata* I Zone or the *L. laevigata* II Zone.

Family CLAVAGNOSTIDAE Howell, 1937
Subfamily ASPIDAGNOSTINAE Pokrovskaya, 1960
Genus ASPIDAGNOSTUS Whitehouse, 1936

Aspidagnostus Whitehouse, 1936, p. 104 (cephalon only); Kobayashi 1939, p. 164 (cephalon only); Howell 1959, p. 173 (cephalon only); Pokrovskaya 1960, p. 61 (cephalon only); Palmer 1962, p. 14; Öpik 1967, p. 115; Lu 1974, p. 79.

Type species. Aspidagnostus parmatus Whitehouse, 1936, p. 105, pl. 9, fig. 5 only.

Diagnosis. See Öpik 1967, p. 116 (except for character 5).

Aspidagnostus sp.

Plate 25, figs. 1–5

Material. Three cephala and four pygidia are available for description.

Description. Moderately convex cephalon is about as wide as long. Narrow, shallow marginal furrow; narrow, convex rim. Posterolateral corners not seen clearly in any specimen. (The apparent spine in UT 92731 (Pl. 25, fig. 2) is an artifact of preservation.) Moderately large, simple basal lobes. Glabella outlined by wide, deep furrows. Preglabellar median furrow exceedingly variable in the three available specimens. In specimens UT 92701 (Pl. 25, fig. 3) and UT 92731 (Pl. 25, fig. 2) there is a well-developed preglabellar median furrow; in specimen UT 92732 (Pl. 25, fig. 1) there is hardly any sign of a preglabellar median furrow.

Single-lobed glabella well elevated above smooth cheeks. Glabellar rear angular and somewhat drawn out perhaps with an occipital collar, but this feature cannot be seen clearly. Glabella expands slightly forwards for most of its length; bluntly pointed glabellar front. Centrally placed, low ridge which extends about half length of glabella.

Zonate pygidium may be slightly wider than long. Narrow, shallow marginal furrows; narrow, convex, elevated lateral rims; median length border spines. Deep, narrow gap in pygidial collar. On either side of the gap is a strong knob. Immediately behind gap is a depressed flange bearing a median spine. At anterior of flange between posterior ends of collar knobs is a small deep pit.

Articulating device consists of a shallow articulating furrow which is arched to the posterior and an elevated articulating half-ring which does not extend full width of axis. Narrow, shallow shoulder furrows; shoulders are nowhere well preserved. Smooth pleural fields.

Very deep clavagnostid pits (*Clavagnostus* pits of Öpik 1967; clavagnostid pits of Jago and Daily 1974) about two-thirds of the distance from anterior to posterior of axis. Pits are contained in a deep depression which extends right across the axis with only a slight central ridge between the pits. Posterior one-third of axis depressed

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EXPLANATION OF PLATE 25

Figs. 1–5. *Aspidagnostus* sp. from near St. Valentines Peak, lat. 41° 21·6′ S., long. 145° 44·3′ E. 1, UT 92732, cephalon, W form, × 21. 2, UT 92731, cephalon, L form, × 22. 3, UT 92701, partial cephalon, × 22. 4, UT 92729, pygidium, W form, × 23. 5, UT 92732, pygidium, W form, × 23.

Figs. 6–9. *Diplagnostus* sp. from upper fauna at Christmas Hills, lat. 40° 54·1′ S., long. 144° 29·8′ E. 6 and 7, UT 86872c, 6, cephalon, W form, × 18; 7, internal mould of same specimen, × 21. 8, UT 92482, pygidium, W form, × 19. 9, UT 86872n, flattened cephalon, W form, × 18.

Figs. 10–16. *Tasagnostus compani* sp. nov. from near St. Valentines Peak, lat. 41° 21·6′ S., long. 145° 44·3′ E. 10, UT 92711, complete specimen with cephalon skewed with respect to the pygidium, × 6·3. 11, holotype pygidium, W form, × 14. 12, UT 92709, cephalon, W form, × 7·5. 13, UT 92717, cephalon, L form, × 8. 14, UT 92705, partial pygidium, × 13·6. 15, UT 92725, pygidium, intermediate distortion, × 16·5. 16, UT 92700, pygidium, internal mould, × 9·4.

PLATE 25


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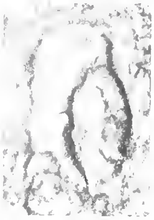
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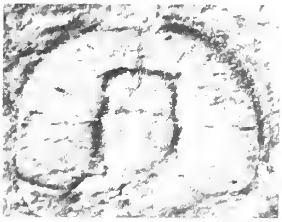
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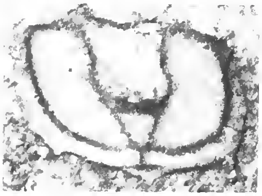
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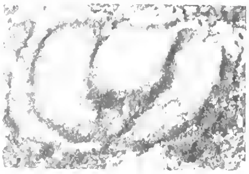
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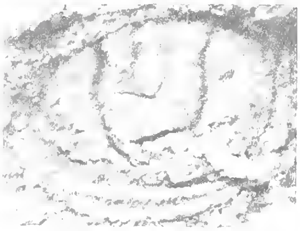
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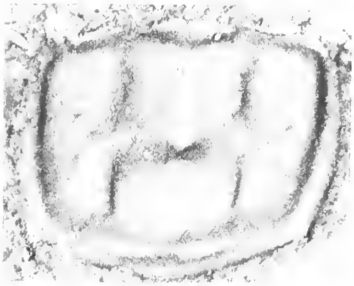
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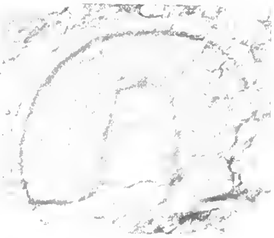
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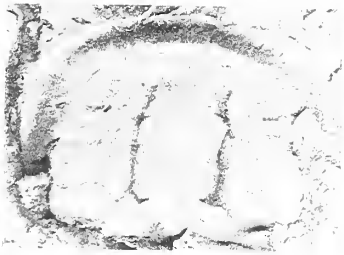
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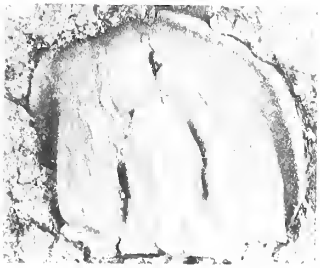
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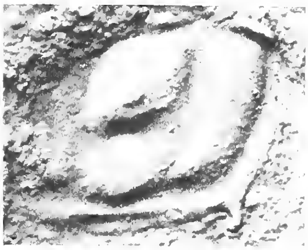
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JAGO, Tasmanian agnostids

slightly below pleural fields. No distinct lobes on anterior part of axis. Strong central keel extends entire length of axis in front of the pits; it is most prominent towards its posterior.

At anterior, axis has width about 0·45 that of pygidium. Immediately behind anterior end of axis it narrows sharply to give a sharp axial constriction; from this constriction the axis widens slightly to about its midpoint from where axis narrows sharply to clavagnostid pits. At pits axis has width between one-quarter and one-third that of pygidium. From the pits axial furrows are straight and converge evenly to pointed axial posterior. Axis extends entire length of acrolobe but does not quite extend as far to posterior as do the pleural fields.

Discussion. The species described above is tentatively placed in *Aspidagnostus*. It conforms with *Aspidagnostus*, as defined by Öpik (1967, p. 116) except that the basal lobes are simple and it has no median ogive on the anterior cephalic border. On the basis of these differences, it seems unnecessary to the writer to erect a new genus in which to place the species from St. Valentines Peak. A further factor is that both *A. laevis* and *A. rugosus* (Palmer 1962, p. 15) appear to have simple basal lobes. This is recognized by Öpik (1967, p. 120, fig. 30) for *laevis*. This is in contrast to Öpik's statement (1967, p. 116) that one of the diagnostic characters of *Aspidagnostus* is the presence of composite basal lobes.

The cephalon (UT 92731) of *Aspidagnostus* sp. (Pl. 25, fig. 2) shows an apparently well-developed preglabellar median furrow. This furrow may have been exaggerated by distortion but it appears to be genuine. On the other hand, UT 92732 (Pl. 25, fig. 1) shows no trace of a preglabellar median furrow. This may simply be intraspecific variation or there could be two species of *Aspidagnostus* present. However, at present, with the limited material available the writer prefers to place all the specimens in the one species.

Aspidagnostus sp. occurs in a late middle Cambrian fauna and is thus the oldest known species of *Aspidagnostus*. It is possible that *Aspidagnostus* sp. represents an ancestral form of the species of *Aspidagnostus*, described by Öpik (1967) and Palmer (1962), with the later forms developing a median ogive.

Occurrence and age. Aspidagnostus sp. comes from the fauna near St. Valentines Peak; its age is late middle Cambrian, the *L. laevigata* III Zone, or the *Damesella torosa*-*Ascionepea janitrix* Zone.

Family DIPLAGNOSTIDAE Whitehouse, 1936
Subfamily DIPLAGNOSTINAE Whitehouse, 1936
Genus DIPLAGNOSTUS Jaekel, 1909

Diplagnostus Jaekel, 1909, p. 396; Kobayashi 1939, p. 140; Westergård 1946, p. 61; Rusconi 1952, p. 10; Hupé 1953, p. 63; Howell 1959, p. 175; Pokrovskaya 1960, p. 57; Poulsen 1960, p. 10; Öpik 1961*a*, pp. 415 ff.; 1961*b*, p. 69; 1967, p. 126; Hutchinson 1962, p. 78; Chu 1965, p. 135; Poulsen 1969, p. 4.

Enetagnostus Whitehouse, 1936, p. 91; (*non* Lermontova 1940, p. 128).

Type species. Agnostus planicauda Tullberg, 1880 (*non* Angelin, 1851).

Diagnosis. See Öpik 1961*b*, p. 69.

Diplagnostus sp.

Plate 25, figs. 6–9

Material. One very poorly preserved almost complete specimen, six cephala, and six pygidia are available for description. All are poorly preserved.

Description. Moderately convex cephalon probably slightly wider than is long. Narrow, shallow marginal furrow; narrow, convex rim. Well-defined preglabellar median furrow shallows anteriorly. Deep axial furrows. Cheeks are probably smooth (the poor preservation makes this difficult to determine, but on most specimens the corrugations appear to be distortion effects). Glabella is about three-quarters the length and one-third the width of cephalon. Subrectangular anterior glabellar lobe contains a narrow sulcus which extends about one-third of way into the lobe. Transverse glabellar furrow is almost straight; it is arched slightly to the posterior for most of its length but is bent slightly forward at its centre. On posterior glabellar lobe is a pair of shallow, lateral furrows which turn inward and forwards from points on the axial furrows which are a little to the anterior of the centre of the lobe. High, wide, central ridge extends along anterior and central parts of posterior glabellar lobe. Angular glabellar rear; small, simple basal lobes.

Zonate pygidium probably slightly wider than long. Narrow marginal furrow; narrow, convex rim is widest at posterior. Articulating device is nowhere preserved. Narrow, shallow shoulder furrows; narrow, convex, moderately geniculate shoulders; fulcra are close to axis. Small border spines. Smooth pleural areas. Pygidial axis has length about two-thirds that of pygidium. Narrow, moderately deep axial furrows. Distinct gap between the sharply rounded pygidial posterior and the collar. There may be a faint post-axial median furrow. Narrow, shallow anterior lateral axial furrow directed inwards and forwards from either end. Posterior lateral furrow is poorly developed. Median keel about a quarter the width of axis. It extends from anterior of axis across the anterior two lobes and just on to the posterior axial lobe. Keel is highest and widest near posterior of second axial lobe. First two axial lobes are of about equal length (sag.) and together make up about 0·4–0·45 of the total axial length. Axis slightly constricted at second axial lobe. Collar seems to join rim at its extremities, which are well forward of the spines.

Discussion. The species of *Diplagnostus* described above from Christmas Hills differs from *D. planicauda vestgothicus* (Wallerius) and *D.* cf. *p. vestgothicus* (Öpik, 1961*b*, p. 71) in that these species have highly scrobiculate cephala. The pygidial axis of *D. planicauda* (Angelin) is wider than that of the Christmas Hills form. The preglabellar median furrow of the *Diplagnostus* described above is better developed than that of *D. p. bilobatus* Kobayashi. The preglabellar median furrow of *D. jarillensis* Rusconi is deeper than that of the Christmas Hills form, and *jarillensis* also has a more rounded glabellar front. The preglabellar median furrow and marginal furrows of *D. humilis* (Whitehouse) are wider and deeper than those of the species described above. *D. crassus* Öpik differs from the Christmas Hills species in that it has a broadly rounded glabellar rear.

Thus, the *Diplagnostus* found at Christmas Hills differs from all known species.

However, there are not enough well-preserved specimens to erect a new species, and it is referred to as *Diplagnostus* sp.

Occurrence and age. Diplagnostus sp. comes from the upper fauna at Christmas Hills; its age is either of the *L. laevigata* I Zone or the *L. laevigata* II Zone.

Subfamily OIDALAGNOSTINAE Öpik, 1967

The Subfamily Oidalagnostinae was defined by Öpik (1967, p. 134). A new genus, *Tasagnostus* is included herein in this subfamily. The genus *Ovalagnostus* Lu also belongs in the Oidalagnostinae. The author feels that character (2) of the subfamily (see Öpik 1967) should read, 'the median depression in the pygidial collar' rather than 'median gap'. This is because there is no distinct break in the collar of any known species of *Tasagnostus*, *Oidalagnostus*, or *Ovalagnostus* such as there is in *Aspidagnostus*.

Genus OIDALAGNOSTUS Westergård, 1946

Oidalagnostus Westergård, 1946, p. 65; Hupé 1953, p. 63; Howell 1959, p. 175; Pokrovskaya 1960, p. 57; Öpik 1967, p. 134; Lu 1974, p. 79.

Type species. O. trispinifer Westergård, 1946, p. 65, pl. 9, figs. 4–7.

Discussion. Öpik (1967, p. 134) has discussed fully the generic concept of *Oidalagnostus*. The author has at his disposal rubber casts of the two pygidia of *O. trispinifer* figured by Westergård. They are the specimens figured by Westergård as plate 9, figs. 6 and 7. The holotype (Pl. 24, fig. 16) is an exfoliated specimen, and thus shows the internal anatomy better than does the other specimen (Pl. 24, fig. 15), which has the original test preserved.

An inspection of the holotype (Pl. 24, fig. 16) reveals the presence of a long, low, rounded ruga on each pleural area. These rugae extend from near the junction of the two lateral bosses to a point near the anterolateral corners. This photograph also shows that the pleural areas are much more pitted on the abaxial sides of these rugae than on the adaxial side. An inspection of the pygidium of *O. personatus* Öpik (1967, pl. 54, fig. 8) shows what appears to be similar rugae. This type of pygidial caecal arrangement may be indicative of *Oidalagnostus*.

O. personatus Öpik from the Queensland *Lejopyge laevigata* II Zone has one pair of lateral bosses on the third axial annulation. The younger *O. trispinifer* Westergård has two well-developed lateral bosses on the posterior part of the pygidium. In Queensland *O. trispinifer* extends from the *L. laevigata* III Zone to the *Cyclagnostus quasivespa* Zone. In Sweden *trispinifer* is found in the upper part of the Swedish *L. laevigata* Zone.

The older species of *Tasagnostus*, i.e. *T. debori*, from the lower fauna at Christmas Hills is of about *L. laevigata* I age and has no distinct lateral bosses on the third pygidial axial annulation. In contrast, the younger, *T. compani* (about *L. laevigata* III age), from near St. Valentines Peak has distinct lateral bosses on the third pygidial axial annulation. Thus, in the known species of *Tasagnostus* and *Oidalagnostus* there is a trend to increase the differentiation of the lateral bosses in the younger species.

The close similarity of the pygidial structure of *Tasagnostus* or *Oidalagnostus* makes it appear probable that *Oidalagnostus* arose from *Tasagnostus* or a *Tasagnostus*-like agnostid by extension of the pygidial rim into a median spine.

Genus TASAGNOSTUS nov.

Type species. T. debori sp. nov.

Diagnosis. Cephalon with smooth cheeks; wide marginal furrow; wide, convex elevated rim. There is usually an incomplete preglabellar median furrow; deep axial furrows; shallow transverse glabellar furrow. Simple basal lobes; angular glabellar rear; small, wide posterolateral spines.

Zonate pygidium has a wide border and a pair of small border spines. In some specimens there is a transversely elongated pair of knobs on the collar directly behind the axis; knobs are separated by a low depression. Axis extends to the collar; it is divided into two parts by a pair of broad and deep laterally elongated pits found in the posterior part of axis. Anterior to these pits are three axial lobes, on which is an elongated ridge which is much lower on the third lobe than on the anterior pair. Axis widens considerably posterior to second axial lobe and is widest near the lateral pits. There is a low intranotular axis in the wide posterior segment of the axis.

Discussion. Tasagnostus has a zonate pygidium and is rather similar to *Oidalagnostus*. The genera are differentiated by the fact that *Tasagnostus* has two border spines whereas *Oidalagnostus* has a trispinose pygidium. *T. compani* sp. nov., described below, from near St. Valentines Peak has gently pitted pleural fields. The diagnosis given above and this latter fact show that *Tasagnostus* clearly belongs in the Subfamily Oidalagnostinae as defined by Öpik (1967, p. 134).

Oedorhachis Resser and *Baltagnostus* Lochman differ from *Tasagnostus* in that they have only three pygidial axial annulations whereas *Tasagnostus* has four annulations. *Dolichagnostus* Pokrovskaya differs from *Tasagnostus* in having a much better-defined preglabellar median furrow and a much less well-defined quadrilobation of the pygidial axis. The pygidium of *Dolichagnostus* has a constricted acrolobe whereas that of *Tasagnostus* is unconstricted. The posterior pygidial margin of *Dolichagnostus* is angulate; that of *Tasagnostus* is evenly rounded. *Oidalagnostus*? *dubius* Westergård is related to *Dolichagnostus* (Öpik 1967, p. 132), but differs from both *Dolichagnostus* and *Tasagnostus* in having a median pygidial spine.

The only figured specimen of the type species of *Ovalagnostus*, *O. changi* (see Lu *et al.* 1974, p. 82, pl. 1, fig. 8) is rather poorly preserved. However, it appears that the pygidial collar of *O. changi* is placed much further forward than in *Tasagnostus*; the marginal furrows (particularly in the pygidium) of *O. changi* are considerably wider than those of either species of *Tasagnostus*. The transverse glabellar furrow of *O. changi* appears to be much deeper than in either species of *Tasagnostus*. It cannot be determined from the photographs given in Lu *et al.* (1974) if *O. changi* has a third pygidial spine. It is possible that *Tasagnostus* could be placed in synonymy with *Ovalagnostus*. However, until better-preserved specimens of *O. changi* are available, I prefer to place the Tasmanian forms in a separate genus.

Tasagnostus debori sp. nov.

Plate 26, figs. 1-13

Material. The illustrated specimens are selected from the hundreds of available specimens.

Holotype. Pygidium, UT 86869e (Pl. 26, fig. 1).

Diagnosis. Cephalon in which preglabellar median furrow usually incomplete. Shallow transverse glabellar furrow; angular glabellar rear; large, simple basal lobes. Zonate pygidium may have a very low pair of transversely elongated knobs on collar. Smooth pleural areas. Broadly rounded pygidial axis extends slightly on to posterior marginal furrow. A little to the posterior of the centre of the axis is a lateral furrow with a pair of pits, one on each side of a low central rise. This furrow does not quite extend right across axis and at either extremity is distinctly separated from the axial furrow.

Description. Cephalon about as wide as long. Border wide at anterior, narrows markedly to posterior. Rim is wide, convex, and elevated at anterior, becoming narrow posteriorly. Wide, moderately deep marginal furrow narrows posteriorly. Cephalon has subparallel margins in posterior half and a broadly rounded anterior outline. Deep, wide axial furrows. Glabella has length about 0·7 that of cephalon. Glabellar front may be slightly pointed. Preglabellar median furrow is generally incomplete being widest and deepest at the posterior and fading to the anterior. Angular glabellar rear; large, simple basal lobes extend about one-third of way to glabellar front. From anterior ends of basal lobes to shallow transverse glabellar furrow the glabella is parallel sided with a slight increase in width just behind the furrow. Transverse furrow arched gently backwards. Long, narrow, node placed just forwards of centre of glabella. At transverse furrow, glabella has a width just under one-third that of cephalon. Smooth cheeks. No connective band behind glabella. Short, wide, blunt posterolateral spines arise from wide bases.

EXPLANATION OF PLATE 26

Figs. 1-13. *Tasagnostus debori* sp. nov. 1-12 from Christmas Hills, lower fauna and 13 from Christmas Hills, upper fauna, lat. 40° 54·1′ S., long. 144° 29·8′ E. 1, UT 86869e, holotype pygidium, W form, ×7·4. 2, UT 86869d, pygidium, W form, ×7·4. 3, UT 86877f, pygidium showing slightly raised intranotular axis, intermediate distortion, ×12·2. 4, UT 86877e, cephalon, L form, ×9·3. 5, UT 86869d cephalon, intermediate distortion, ×12. 6, UT 86856n, cephalon, intermediate distortion, ×7·3. 7, UT 92467, pygidium and thorax, L form, ×7·8. 8, UT 86877d, immature pygidium, W form, ×7·9. 9, UT 86877e, cephalon intermediate distortion, ×7·7. 10, UT 92480, pygidium, intermediate distortion, ×6·1; note the furrows outlining the intranotular axis, which have been accentuated by distortion. 11, UT 86846, cephalon, W form, ×11·2. 12, UT 86869g, pygidium, W form, ×10. 13, UT 86879e, pygidium, intermediate distortion, ×8·9.

Fig. 14. Agnostid, gen. et sp. indet. no. 1, from St. Valentines Peak, lat. 41° 21·6′ S., long. 145° 44·3′ E., pygidium, ×25.

Fig. 15. Agnostid, gen. et sp. indet. no. 2, from St. Valentines Peak, lat. 41° 21·6′ S., long. 145° 44·3′ E., pygidium, ×12.

Fig. 16-19. Agnostid, gen et sp. indet. no. 3, from upper fauna, Christmas Hills, lat. 40° 54·1′ S., long. 144° 29·8′ E. 16, UT 86620, complete specimen, W form, ×6. 17, UT 86878m, cephalon, W form, ×8. 18, UT 86620, cephalon, W form, ×8·2. 19, UT 86880c, pygidium, W form, ×14.


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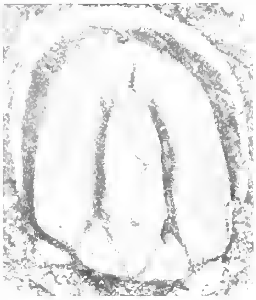
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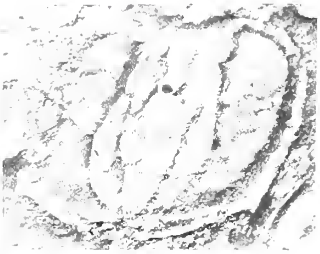
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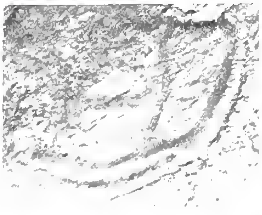
11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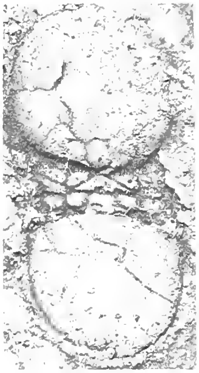
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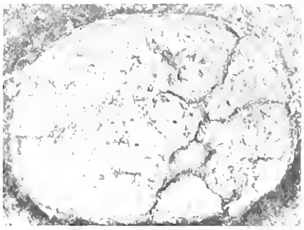
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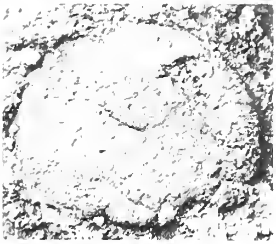
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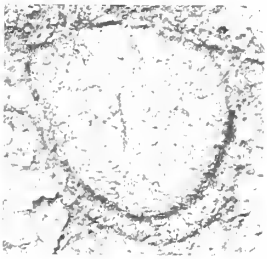
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JAGO, Tasmanian agnostids

Zonate, gently convex pygidium appears to have smooth pleural fields; it is probably slightly wider than long. Wide border with a wide, elevated convex rim which narrows quite considerably to anterior. Wide, moderately deep marginal furrows. Moderately geniculate, strongly elevated shoulders; the fulcra occur mid-way between abaxial acrolobe margin and axial furrows; facets are gently concave. Articulating device consists of a deep, posteriorly arched articulating furrow and a narrow elevated half-ring. Two small border spines present.

Between the spines the convex posterior rim is evenly curved but does not stand out as markedly as do the lateral rims. Narrow, shallow, crescentic furrow between rim and collar. Collar and rim join to form slightly thickened abaxial rim portions. Collar is sometimes slightly depressed at mid-point. On either side of this depression (if present) the collar may be slightly thickened and elevated to form a pair of weak, transversely elongated knobs. The thickening of the collar is present on most specimens, but the central depression in the collar is seen in only about 15% of the specimens. Posterior marginal furrow is curved gently to the posterior at its mid-region where the axis protrudes slightly to the posterior of the pleural areas.

Pygidial axis outlined by moderately wide, deep furrows. It is divided into two parts by what appears in many specimens to be a broad lateral pygidial furrow, which is present just to the posterior of the centre of the axis. This feature does not extend abaxially to the axial furrow and in fact is a pair of clavagnostid pits as described below. Anterior half of axis has almost parallel axial furrows and three annulations, the anterior two of which are outlined by widening of the axis around each annulation. From posterior end of second annulation axis expands evenly until it is widest in region of clavagnostid pits, from which axis contracts to broadly rounded posterior which extends slightly on to posterior marginal furrow.

On the three anterior annulations there is a prominent elongated median ridge just under a third the width of axis; ridge is best developed on the two anterior annulations and is outlined by shallow longitudinal furrows. On the third annulation the ridge is less elevated than it is on the two anterior annulations and extends slightly on to the lateral furrow. The lateral furrow has a raised central region immediately behind the node with small clavagnostid pits on either side.

There are notular lines (not visible on all specimens) on posterior axial lobe. On UT 92480 (Pl. 26, fig. 10), one of the largest available specimens, these notular lines have been accentuated by distortion and occur as distinct furrows. Intranotular axis is set very slightly above extranotular axis.

Discussion. Tasagnostus debori sp. nov. is compared with *T. compani* in the discussion on the latter species. There is some intraspecific variation in *T. debori*, e.g. the pygidial collar on some specimens is wider than on others. As noted in the description, the central collar depression is present in only about 15% of the specimens. The pygidial rear of some specimens is much more broadly rounded than on others even when the effects of distortion are taken into account. The preglabellar median furrow is well developed on some specimens and almost absent on others. In the immature pygidium, UT 86877d (Pl. 26, fig. 8), the clavagnostid pits are placed further to the posterior than in more mature specimens.

Occurrence and age. T. debori sp. nov. occurs in great abundance in the lower fauna at Christmas Hills and in very small numbers in the upper fauna from Christmas Hills; its age is probably of the *L. laevigata* I or II Zones.

Tasagnostus compani sp. nov.

Plate 25, figs. 10–16

Material. A total of about thirty individual cephala and pygidia are available for description.

Holotype. Pygidium, UT 92724 (Pl. 25, fig. 11).

Diagnosis. Highly convex cephalon; very faint transverse glabellar furrow; moderately sized basal lobes. Zonate pygidium has a pair of transversely elongated knobs on collar. Collar is only a little wider than axial posterior. Third axial annulation has a distinct lateral boss at either extremity; they protrude slightly into the pleural areas. Pleural areas are gently pitted, particularly opposite third axial annulation. Just to posterior of centre of axis is a lateral furrow with a pair of pits on either side of low central rise. This furrow shallows abaxially. Posterior axial lobe is subsquare.

Description. Strongly convex cephalon about as wide as long. Wide, shallow marginal furrow; moderately wide, elevated, convex rim. Glabella outlined by moderately deep axial furrows which shallow forwards; it is divided by a very shallow transverse glabellar furrow which in most specimens is a change of slope rather than a distinct furrow. Very shallow short preglabellar median furrow does not extend to marginal furrow. Glabella has length about two-thirds that of cephalon; it has a broadly rounded anterior. Anterior glabellar lobe has length about one-quarter that of glabella. Narrow, elongated node at anterior end of posterior glabellar lobe. Glabellar rear is angular. Basal lobes do not meet beneath the glabellar rear.

Strongly convex, zonate pygidium about as wide as long. Elevated, gently convex rim moderately wide at posterior, narrows markedly to anterior. Wide, deep marginal furrow. Moderately wide and deep shoulder furrows; slightly geniculate, narrow, elevated shoulders, fulcra placed near centre of shoulders. Agnostoid articulating device includes posteriorly arched articulating furrow; half-ring arched to posterior at its centre. Small border spines. Posterior rim between spines is slightly convex with narrow, shallow furrow between rim and collar. Collar has width only a little greater than that of pygidial rear. Collar has two transversely elongated knobs which are separated by a small central saddle.

Pygidial axis is divided into two parts by a broad transverse furrow which occurs slightly to the posterior of the centre of the axis. This furrow is basically a pair of large pits (clavagnostid pits) separated by a small, central higher area; abaxial ends of furrow are shallow and curve slightly to posterior. Axis outlined by broad, moderately deep axial furrows. Over all the axial furrows are parallel; there is a slight constriction at the second axial lobe, and a slightly expanded posterior axial lobe.

Anterior portion of the axis contains three lobes of approximately equal length. Third lobe has a small lateral boss at either extremity. These bosses protrude slightly into pleural areas; axis is widest at this point. A prominent median ridge, about one-third the width of the axis, extends the length of the three anterior lobes. It is composed of three connected large nodules and is most prominent on the second annulation where it is outlined by prominent longitudinal furrows. Steep drop from the second lobe nodule down to third lobe nodule. Ridge has a short posterior extension from third lobe on to the wide, deep lateral furrow. This extension is mirrored on the enlarged subsquare posterior pygidial lobe. Posterior lobe has two faint ridges extending longitudinally in the position where notulae would be expected. Between these ridges the intranotular axis stands out very slightly above the extranotular axis; it extends slightly but distinctly further towards the collar than does the extranotular axis. Axis extends slightly further to posterior than do pleural areas. Pleural areas of some specimens are slightly pitted.

Discussion. T. compani sp. nov. differs from *T. debori* sp. nov. in that it has a less distinct transverse glabellar furrow and a less well-developed preglabellar median furrow. The third pygidial lobe has a distinct pair of lateral bosses which is not the case in *T. debori*. The pleural areas of *compani* may be slightly pitted; those of *debori* are smooth. The lateral pygidial furrow housing the clavagnostid pits is bigger in *compani* than *debori*. The collar of *compani* is not as wide (tr.) as that of *debori*, but the knobs are more distinct.

Occurrence and age. T. compani sp. nov. comes from the St. Valentines Peak area; its age is of either the *L. laevigata* III Zone or the *Damesella torosa-Ascionepea janitrix* Zone.

Subfamily Unknown

Genus UTAGNOSTUS Robison, 1964

Utagnostus Robison, 1964, p. 532.

Type species. Utagnostus trispinulus Robison, 1964, p. 533, pl. 82, figs. 21–28.

Diagnosis. See Robison 1964, p. 532.

Discussion. Utagnostus has constricted acrolobes and a simplimarginate, smooth pygidium. These features, plus the presence of only a faint transverse glabellar furrow in *U. trispinulus* and the absence of a transverse glabellar furrow in the new species, *U. neglecta*, could indicate affinities with the subfamily Clavagnostinae (family Clavagnostidae). However, the pygidial axis of *Utagnostus* bears no resemblance to those of the Clavagnostidae. Of the Diplagnostidae only *Oidalagnostus* (Oidalagnostinae) and *O.*? *dubius* (Diplagnostinae) have a trispinose pygidium as has *Utagnostus*. There is a great range of variation within the Diplagnostidae and the Clavagnostidae, and the characters of *Utagnostus* do not allow it to be placed in any particular subfamily. However, I follow Öpik (1967, p. 78) who placed *Utagnostus* in the Diplagnostidae. The new species, described below, *U. neglecta*, from the *L. laevigata* I Zone at Christmas Hills is of very similar age to the type species, *U. trispinulus* from the *Bolaspidella contracta* Subzone of Utah. *Utagnostus*(?) sp. from St. Valentines Peak and an undescribed specimen, a possible *Utagnostus*, from Sugarloaf Gorge in north-western Tasmania (referred to as cf. *Clavagnostus* sp. in Table 2, Jago 1973), are also of late middle Cambrian age. This may indicate that *Utagnostus* is largely confined to late middle Cambrian rocks.

Utagnostus neglectus sp. nov.

Plate 23, fig. 13

Material. One well preserved, complete specimen, UT 86844i, the holotype (Pl. 23, fig. 13).

Diagnosis. Moderately convex small cephalon with long spines. Preglabellar median furrow absent. Anterior one-third of apparently single-lobed glabella is markedly narrower than rest of glabella, probably indicates a bilobed glabella. Simple basal lobes connected behind subangular glabellar rear. Trispinose pygidium with central spine smaller than lateral spines. Pygidial axis extends almost to posterior border furrow. No lateral axial furrows and very little constriction at anterior of axis. Bluntly rounded axial rear.

Description. Moderately convex small cephalon about as wide as long. Narrow shallow marginal furrow; slightly elevated gently convex rim. Long cephalic spines arise from wide bases and extend along thoracic margins to anterior of posterior thoracic segment. Preglabellar median furrow absent. Smooth cheeks. Glabella outlined by moderately wide and deep axial furrows; it has a bluntly rounded front. Length of glabella about 0·7 that of cephalon. Small, simple basal lobes connect behind subangular glabellar rear. Anterior one-third of the apparently single-lobed glabella is markedly narrower than posterior part of glabella. This marked change in width probably represents the trace of a bilobed glabella. At the centre of the posterior glabellar lobe is a broad rounded high area rather than a distinct node.

Small pygidium about as wide as long. Narrow, shallow marginal furrow; slightly elevated, gently convex rim is moderately wide between the moderately long lateral border spines but narrows anteriorly. There is a short median marginal spine. Narrow, shallow shoulder furrows, abaxially placed fulcra; articulating device unknown. Pygidial axis extends almost to marginal furrow. Axis outlined by narrow, shallow furrows. No lateral furrows. Axis is very slightly constricted at position of a second axial lobe. Axial rear bluntly pointed. Broad rounded area at position of second axial lobe rather than a distinct node.

Discussion. The cephalon of *Utagnostus neglectus* differs from that of *U. trispinulus* in that *trispinulus* has a more clearly defined transverse glabellar furrow. The three pygidial spines of *trispinulus* are of approximately equal size, but the central spines of *neglectus* appears to be smaller than the lateral spines. However, it should be noted that the central spine of *neglectus* is not very well preserved. The pygidial axis of *trispinulus* differs from that of *neglectus* in that it extends further to the posterior and it widens more at the posterior and has a more marked anterior constriction. The rim of the pygidium of *trispinulus* is wider than that of *neglectus.*

Occurrence and age. U. neglectus sp. nov. comes from the lower fauna at Christmas Hills; its age is probably *L. laevigata* I Zone.

Utagnostus(?) sp.

Plate 23, figs. 14–17

Material. Two partially complete specimens, one individual cephalon and an individual pygidium. All are reasonably well preserved.

Description. Strongly convex cephalon about as wide as long. Narrow, shallow marginal furrow; slightly elevated, narrow convex rim. Long cephalic spines arise from wide bases; spines extend along lateral thoracic margins almost to anterior margin of pygidium. No preglabellar median furrow (the apparent furrows in UT 92698 (Pl. 23, fig. 15) and UT 92699 (Pl. 23, fig. 17) are distortion features). Smooth cheeks. Glabella outlined by wide, deep subparallel axial furrows; it has a bluntly rounded front. Length of glabella about two-thirds that of cephalon. Small, simple basal lobes connected behind glabellar rear. Posterior part of glabella is very high and is greatly elevated above the cheeks and also the flat anterior third of the glabella which is below the level of the surrounding cheeks. The marked change in elevation from the low anterior third of the glabella to the high posterior portion may represent the vestige of a bilobed glabella. Glabellar rear not seen clearly in any available specimen.

Pygidium about as wide as long; it is not as strongly convex as the cephalon. Narrow, shallow marginal furrow; slightly elevated, gently convex rim is moderately wide between the long border spines but narrows anteriorly. Small median salient in pygidial border. Narrow, shallow shoulder furrows; narrow convex shoulders; the fulcra are not visible. Articulating device is unknown.

Strongly convex pygidial axis stands out strongly above smooth pleural fields which are separated behind the axis by a short, narrow, shallow post-axial furrow. Axis lacks lateral furrows; it is somewhat constricted at the position of a second axial lobe. Axial rear bluntly pointed. Axis has length about 0·7 that of pygidium. Low, elongated node on anterior half of axis.

Discussion. Apart from the lack of a third pygidial spine, the species described above fits into *Utagnostus*. It is referred to *Utagnostus*(?) sp. and is the species referred to as cf. *Clavagnostus* sp. in Jago (1973, p. 411).

Occurrence and age. *Utagnostus*(?) sp. comes from the St. Valentines Peak area; its age is either *L. laevigata* III Zone or the *Damesella torosa-Ascionepea janitrix* Zone.

Family and Subfamily unknown

Agnostid, gen. et sp. indet. no. 1

Plate 26, fig. 15

Material. Two incomplete pygidia.

Remarks. These pygidia appear to be of a similar type to those described by Rasetti 1967, p. 38, as Agnostida, pygidium, no. 1. The Tasmanian specimens do not show the articulating device, and the shoulder area is seen only in the smaller specimen. These specimens do not permit anything to be added to or any comments to be made on the discussion given by Rasetti (1967). Rasetti's specimens are associated with *Centropleura* and are hence of a similar but slightly older age to the two pygidia from St. Valentines Peak. These pygidia are referred to here as Agnostid, gen. et sp. indet. no. 1.

Occurrence and age. Agnostid, gen. et sp. indet. no. 1 comes from the St. Valentines Peak area; its age is either late middle Cambrian, the *L. laevigata* III Zone, or the *D. torosa-A. janitrix* Zone.

Agnostid, gen. et sp. indet. no. 2

Plate 26, fig. 14

Material. Two pygidia, UT 92690 and UT 92691. UT 92691 is well preserved, and the following description is based almost entirely on that specimen.

Description. Pygidium about as wide as long. It has a convex anterior end and a flat posterior. Acrolobes are unconstricted; wide border with a wide convex elevated rim which becomes less convex and quite narrow to the anterior. Rim has a low posterior median salient. Wide, moderately deep marginal furrow. Shoulder areas are poorly preserved, but the shoulder furrows are narrow and shallow; the shoulders appear to be low and convex with no geniculation. The fulcra seem to be very close to the axis, which is outlined by wide, moderately deep, axial furrows. Axis is wide at anterior; it tapers fairly evenly to the posterior with a slight constriction about one-third of the distance to the sharply rounded posterior. Immediately to the posterior of the axis is a large depression caused by the meeting of the axial furrows and the posterior marginal furrow. Border spines absent; smooth pleural fields. Small axial node placed just to the anterior of the axial constriction. No details of the articulating device are visible.

Discussion. As far as I can determine, these pygidia have no affiliation with any known agnostid genus or species. They are referred to as Agnostid, gen. et sp. indet. no. 2.

Occurrence and age. This species comes from the St. Valentines Peak area; its age is either the *L. laevigata* III Zone or the *D. torosa-A. janitrix* Zone.

Agnostid, gen. et sp. indet. no. 3

Plate 26, figs. 16-19

Material. Numerous poorly preserved cephala and pygidia. Two poorly preserved complete specimens are known including UT 88620 (Pl. 26, fig. 16).

Description. Moderately convex cephalon probably about as wide as long. When undistorted, it would have had a subcircular outline with a straight posterior margin; cephalon is widest near the posterior end about one-quarter of the distance to the broadly rounded anterior margin. Narrow border rarely visible due to overhanging acrolobe margins. Apart from faint traces of a slightly elevated rounded glabellar rear, the cephalon is smooth.

Pygidium probably slightly longer than is wide. Wide, gently convex, elevated rim, narrows considerably forwards; narrow, shallow marginal furrow. The shoulder and marginal furrows meet at an angle of just over 90°. Narrow, elevated shoulders. Articulating device consists of a moderately convex articulating half-ring which is arched gently forward and a moderately deep articulating furrow which is also arched forward. The only dorsal features on the acrolobe are shallow axial furrows at the anterior end of the pygidium where the axis has a width about two-fifths that of the pygidium.

Discussion. This effaced agnostid cannot be placed with certainty into any genus as all specimens have been considerably crushed and distorted. The pygidial border is wide, thus excluding *Lejopyge*; it may be a species of either *Grandagnostus* or *Pseudophalacroma*. The high degree of effacement and poor preservation makes detailed classification out of the question. This species is referred to as Agnostid, gen. et sp. indet. no. 3.

Occurrence and age. This species comes from the upper fauna at Christmas Hills; its age is either the *L. laevigata* I Zone or the *L. laevigata* II Zone.

Acknowledgements. This work was commenced as part of a doctoral thesis at the Geology Department, University of Adelaide: later stages of the work have been supported by a grant from the Australian Research Grants Committee. I thank my supervisor, Dr. B. Daily (Geology Department, University of Adelaide) for much valuable advice, guidance, and criticism during my doctoral studies, and for making available the rubber casts of the type material of Swedish and Bohemian agnostids referred to in the text. I also thank Mr. G. Pike for originally showing me the St. Valentines Peak locality and Mr. J. Buckley for valuable field assistance over a number of years. Mr. M. R. Banks (University of Tasmania) kindly arranged the transfer of specimens to Adelaide; Associated Forest Holdings Limited generously allowed me access to their forest concessions in the St. Valentines Peak area.

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UPPER PALAEOCENE SALVINIACEAE FROM THE WOOLWICH/READING BEDS NEAR COBHAM, KENT

by A. R. H. MARTIN

ABSTRACT. A sample from near the base of a section through organic lacustrine deposits exposed in a road cutting near Cobham, Kent, contained abundant megaspore and microspore massulae of *Azolla anglica* sp. nov. and *Salvinia cobhamii* sp. nov. The former is described as a new member of the subgenus *Florschuetzia* and is compared with several more or less contemporaneous species. The latter is described and compared with *S. boveyana* Chandler.

The environment in which the Salviniaceae existed at the site has been interpreted from a histogram of the section. It is suggested that the climate was warm temperate and that the lake was subsequently invaded by reeds and possibly tree growth, under which conditions the Salviniaceae locally died out.

POLLEN and spores were first recorded in Palaeocene–Eocene sediments of southern England by Ma Khin Sein (listed in Chandler 1964). More recently Gruas-Cavagnetto (1970) has recorded pollen and spores from the Woolwich and Reading Beds at Swanscombe, Kent.

Improvements to the A2 road close to its junction with the M2 motorway (grid ref. TQ/6730 6980) near Cobham, Kent, in 1964, made fresh exposures of the Upper Palaeocene deposits of the Woolwich and Reading Beds at Shorne Wood, some 10 km from the site described by Gruas-Cavagnetto. The stratigraphy at this site has been figured by Chandler (1923), and includes a prominent organic horizon, originally described as lignite, though it seems not to contain macroscopic wood and is better described as a lake mud. Four equally spaced samples, each representing 15 cm in vertical extent, from a 60 cm exposure of the seam were generously submitted to me for pollen study by Professor W. G. Chaloner.

Samples given to me by Professor Chaloner from an already-existing exposure of the organic band, contained a rather disappointing pollen flora. These samples were no doubt somewhat weathered. The new samples, besides a rich angiosperm flora, also contained megaspore remains of the two salviniaceous water ferns *Azolla* and *Salvinia*, as well as abundant microspore remains of the latter.

Subsequent cutting back of the exposure revealed 120 cm thickness of the lake deposit (Chaloner, pers. comm.) and samples of this were independently examined by Professor L. V. Hills, who reported (in correspondence, 1970) the occurrence of *Azolla*, *Salvinia*, and *Minerisporites*. *Minerisporites* appears to be absent from the material seen by the author (even after a careful re-examination) and none of these genera is recorded by Gruas-Cavagnetto. Nor, at the time of writing, have Salviniaceae been found in further sampling of the same site by Miss L. Allen (in correspondence, 1974). Such very local distribution of megaspores suggests the profitability of a more three-dimensional study of this site. Such is beyond the scope of the present communication which is of necessity confined to a study of those samples originally submitted. Within these bounds, it was thought useful to make a simple

[Palaeontology, Vol. 19, Part 1, 1976, pp. 173–184, pls. 27–28.]

pollen diagram to reveal as much as possible of the ecological conditions round the site at the time when Salviniaceae grew there. It is felt, too, that subsequent weathering or further destruction of the site may have made future comparisons difficult, without recording of these data. This analysis immediately follows the taxonomic part of the paper.

METHODS

Clean hand-picked pieces of the sediment were washed in distilled water, crushed to a coarse powder, and treated with 5% KOH for 24 hours. This was enough to disintegrate all samples. They were then diluted, washed several times with distilled water, and transferred to 50% glycerol. Thirty seconds treatment with a sonic probe at 15000 cycles helped to disperse superficial dirt from the pollen. Only the basal sample, R1434, required HF treatment, which was given after KOH disintegration.

Massulae and megaspores of Salviniaceae were present only in R1434, from which they were quite easily isolated and concentrated by decanting the pollen suspension. Once observed, more were obtained by further macerations, specimens being collected by pasteur pipette under a low-power binocular microscope. A total of 40 megaspore and 400 microspore massulae of *Salvinia* were obtained from one sample of 5 gm. Eighteen megaspore massulae and a number of microspore massulae of *Azolla* were obtained in this way from the same sample, but the ratio of the two types could not be assessed as the microspore massulae tend to be attached to the megaspores, often in groups, while free ones remain suspended longer and are more easily lost in decanting. Some of these were recovered later on slides prepared for pollen counting, forming the bulk of the described material of the microspore massulae.

Material for sectioning was prepared according to the method described by Hughes *et al.* (1962), sections being cut at *circa* 0·5 μm. Despite difficulties, some short serial sequences were achieved.

Spores for scanning electron microscopy were stored in 98% ethanol and when required were pipetted on to a clean microscope slide and the ethanol allowed to evaporate. The specimens were oriented on the slide without picking them up. An SEM stub coated with double-sided adhesive tape was then lowered gently on to the spores and usually all of them adhered at once. By this method handling with forceps was avoided. Once attached, the spores cannot be handled but can be detached with xylol, washed carefully, and re-attached.

SYSTEMATIC DESCRIPTIONS

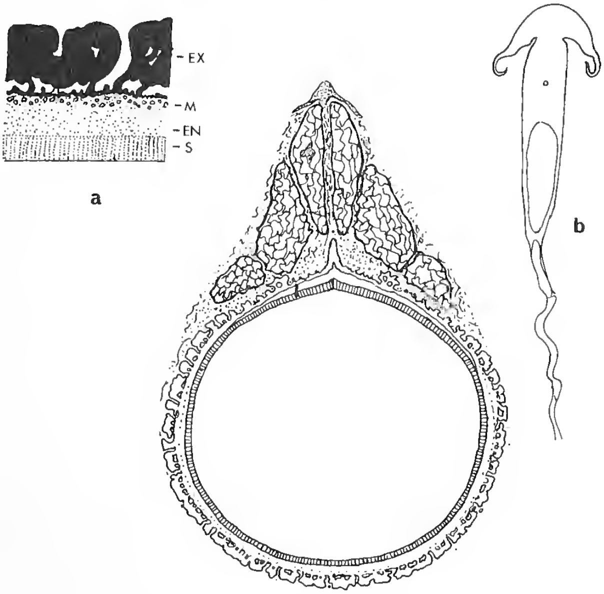
SALVINIACEAE Dumort
Genus AZOLLA Lamarck, 1783
Subgenus FLORSCHUETZIA Kempf, 1968

Type species. A. teschiana Florschütz, 1945.

Azolla anglica sp. nov.

Plate 27, figs. 1–3, 6; Plate 28, figs. 1, 2; text-fig. 1

Description. Megaspore massula with up to twenty-four floats in three tiers; diameter of spore with perispore coat 324–413 μm (mean 355 μm, 10 specimens); polar length of spore 308–364 μm, total length with floats 446–599 μm (mean 531 μm, 10 specimens); upper third of spore covered by floats of lower tier; trilete mark not obvious, sporoderm 3–4 μm thick, usually firmly attached to perine at base and detached and often appearing collapsed apically but laesurae not easily separating; total thickness, including perine wall, *circa* 15–18 μm; surface of perispore regularly foveolate, lumina of foveae *circa* 1·0–2·5 μm diameter, width of muri *circa* 3–5 μm, surface lacking excrescences but thinly hairy, diameter of hairs *circa* 1·0–1·5 μm; column solid and narrow in section, *circa* 9 μm wide at the base and 30 μm in maximum length; maniculae occurring on alveolate ridges *circa* 9 μm high, 16 μm wide, about 50 μm from column and between inner ends of lower two tiers of floats; maniculae short, *circa* 2 μm long, spicate, rarely hooked; upper tier of floats somewhat longer than two lower ones, all externally densely hairy.



TEXT-FIG. 1. Scale reconstruction of sectional view of *Azolla anglica* (× 125). a = interpretation of sporoderm-perispore stratification (× 1000); b = glochidion; EX = exoperine; M = mesoperine; EN = endoperine; S = sporoderm (*Sens. str.*).

Microspore massulae more or less circular to elliptical in outline, 103 × 103–137 × 233 μm (mean 118 × 153 μm, 10 specimens); number of microspores, 4, 8 or 12; diameter of microspores 20–29 μm (mean 24 μm, 20 measurements), laesurae 7–9 μm, wall thickness *circa* 0·7 μm; glochidia 30–40 μm, of which upper 10–15 μm usually wide and solid, with a single small central bubble 0·5–2·0 μm diameter, attenuated and gyrose towards base, alveolate with at least one septum, maximum width at barbs 9–12 μm; width 3·5–5·0 μm below barbs, 1–2 μm at base, barbs sometimes 3 in number.

Holotype. Slide V58333, Plate 27, fig. 1; repository: B.M. (N.H.).

Paratypes. Slide V58334, Plate 28, fig. 1; repository: B.M. (N.H.). Slide V58335, Plate 27, fig. 2: repository: B.M. (N.H.). SEM stub V58336, Plate 28, fig. 2; repository: B.M. (N.H.).

Locality. Shorne Wood, near Cobham, Kent: from drainage ditch connected with road widening. Ordnance Survey 1:50 000 2nd Series East London Sheet No. 177 (1–74); Nat. Grid. ref. TQ/6730 6980.

Horizon. Woolwich/Reading Beds, base of exposure of 60 cm of organic lacustrine sediment (nekron mud).

Sample. Chaloner palynological sample collection; sample No. R1434, Botany Department, Birkbeck College, London.

Remarks. A. anglica has a very thin apical region to the perispore, only *circa* 1·5 μm thick with a seemingly discontinuous exoperine resembling the layer of small globules below the tectum (Pl. 27, figs. 2, 3). This may explain why a large part of the population has lost the float apparatus and gapes open at the apex. The distinction between mesoperine and endoperine cannot be made out at the apex. Around the sides and base of the spore, on the other hand, the wall structure is well defined and reminiscent of some angiosperms in having a close semblance of a perforate tectum (Pl. 27, fig. 3). The sporoderm is rather thin.

A. anglica differs from *A. teschiana* Florschütz (Dijkstra 1961) in its regularly foveolate exoperine without excrescences (Pl. 28, figs. 1, 2). The outline of the whole structure with floats is more ovoid, with a lower length to breadth ratio, the floats being lower placed laterally, but they are less distinct individually, possibly because of a thicker coating of hairs (text-fig. 1). The maniculae are less well developed, though the column is almost identical (Pl. 27, fig. 2). The stratification of the perispore (Kempf 1969) is more regular in *A. anglica* with a uniform layer of small rods *circa* 1–2 μm in diameter and length, comparable to columellae (= bacula). *A. teschiana* has a thicker sporoderm (5–6 μm).

The differences between *A. anglica* and *A. schopfii* Dijkst. (1961) are more marked. The shape is not dissimilar and the column of *A. schopfii* is described as small, but the number of floats is described as only fifteen and the exoperine pattern as papillate. Sweet and Chandrasekharam (1973) consider *A. extincta* Jain to be conspecific with *A. schopfii*. If so, it was heterosporangiate as well.

A. velus (Dijkst.) Jain and Hall (1969) is distinguishable in section (Martin, in press)

EXPLANATION OF PLATE 27

Fig. 1. *Azolla anglica* sp. nov. Entire megaspore, in section (× 290). Holotype, slide V58333. col = column; f = float; h = hair mass; ma = ridge with maniculae; p = perispore; s = sporoderm.

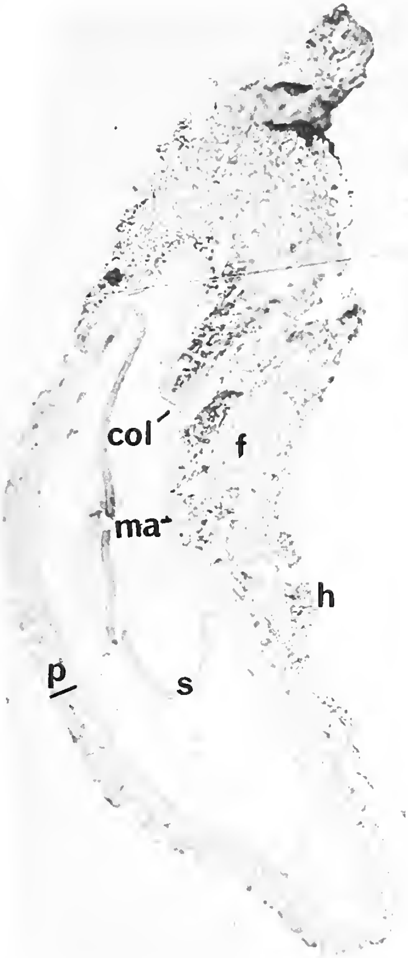
Fig. 2. *Azolla anglica*. Section through perispore apex (× 1150). col = column; f = float; h = hair mass; m = manicula; s = sporoderm. The very thin perispore wall should be compared with the appearance in fig. 3. Paratype, slide V58335.

Fig. 3. *Azolla anglica*. Microtome section of perispore and sporoderm. ex = exoperine; m = mesoperine; en = endoperine; s = sporoderm; c = columella (× 1250).

Figs. 4–5. Undescribed monoporate pollen grain associated with Salviniaceae in sample R1434. It shows resemblance to *Aglaeoreidia* and to *Sparganiaceaepollenites* but appears distinct from both (× 1000).

Fig. 6. *Azolla anglica*. Small microspore massula showing four microspores and short glochidia (× 550).

Fig. 7. *Salvinia cobhamii*. Microspore massula (× 290). The light area in centre is typical of all the microspore massulae examined. Paratype, slide V58339.



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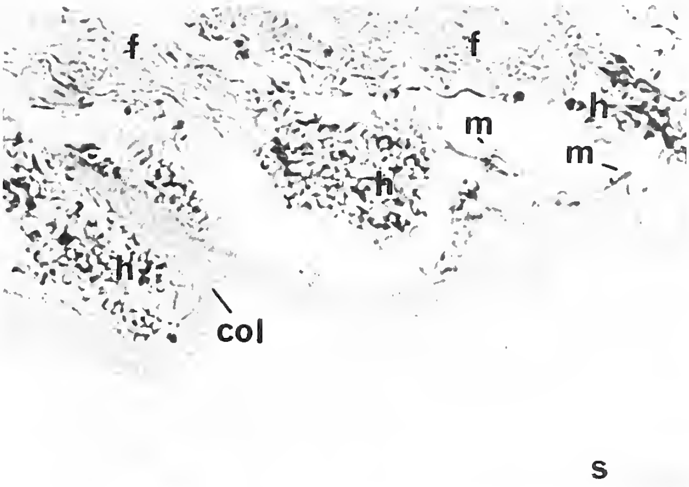

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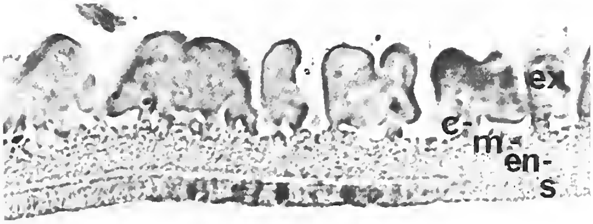

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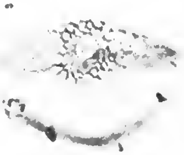

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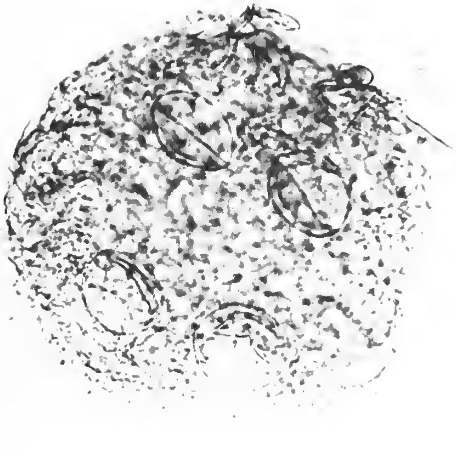

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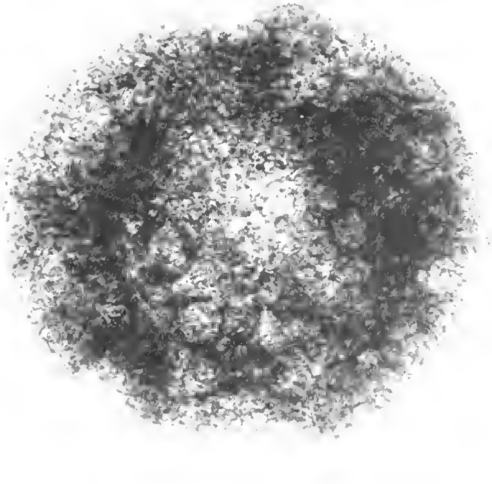


7

MARTIN, Salviniaceae

by its very different float apparatus in two tiers connected to the long column by well-developed maniculae. The exospore stratification is rather similar in the two species and the external pattern though reticulate rather than foveolate, could be confused. As the float apparatus of both species is likely to be obscured by hairs, there is a real possibility of confusion unless it is carefully examined. The size range overlaps considerably though *A. velus* is some 80 μm smaller in mean over-all length.

A. prisca Reid and Chandler (1926) is smaller than *A. anglica* in all dimensions and with only nine floats should be easily distinguishable. It is, in any case, very much younger in age (Oligocene).

Fowler (1975, and pers. comm.) proposes the separation of *A. prisca* from its present position in Sect. *Rhizosperma* into a new subgeneric Section of the genus, based in the main on a re-examination of the float apparatus. Such a systematic change in no way alters the validity of float number as a distinguishing character between the two species.

It is probably futile to try to distinguish *Azolla* species on microspore massula characters. Among the earlier species of *Azolla*, septate glochidia are perhaps uncommon (they are only recorded in *A. indica* Trivedi and Verma, 1971), though small alveoli often appear in the shafts which may simulate a septum (text-fig. 1*c*). Occasional three-barbed glochidia are not unusual among these species. Possibly some reliance can be put on glochidial length. Those of *A. prisca* are 45–52 μm long, *A. teschiana* 25–55 μm long (measured from photograph), *A. anglica* 30–44 μm long (Pl. 27, fig. 6), *A. schopfi* 30 μm (Sweet and Chandrasekharam 1973), and *A. velus* only 18 μm.

Genus SALVINIA Seguier

Type species. S. natans (L.) All., 1785.

Salvinia cobhamii sp. nov.

Plate 27, fig. 7; Plate 28, figs. 3–5

Description. Megaspores with three-lipped convoluted perispore, equatorial diameter 292–405 μm (mean 345 μm, 13 measurements); axial length 340–380 μm; diameter of contained megaspore 220–267 μm (mean 238 μm, 13 measurements), length 210–250 μm (mean 233 μm, 4 measurements), thickness of sporoderm *circa* 6 μm, trilete mark inconspicuous, laesurae 15–20 μm long and *circa* 6 μm wide at base with raised tapering lips; thickness of perispore *circa* 60 μm, surface elaborately convoluted,

EXPLANATION OF PLATE 28

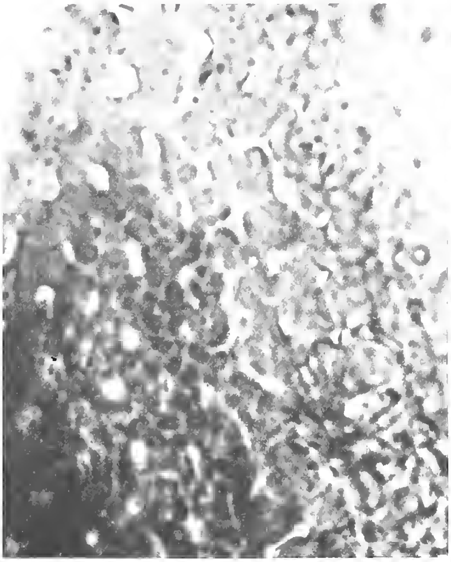
Fig. 1. *Azolla anglica.* Tangential section of perispore showing lumina, muri, and columellae (×1150). Paratype, slide V58334.

Fig. 2. *Azolla anglica.* Perispore surface (×1625). Paratype, SEM stub V58336.

Fig. 3. *Salvinia cobhamii* sp. nov. Entire megaspore (×230). Holotype, slide V58337.

Fig. 4. *Salvinia cobhamii.* Part of apex of perispore (×550). Paratype, SEM stub V58338.

Fig. 5. *Salvinia cobhamii.* Two microspores in alveolar mass. The left-hand arrow indicates the individual perine coat of one spore; the centre and right-hand arrows indicate the perispore apices (×1150). Slide V58339.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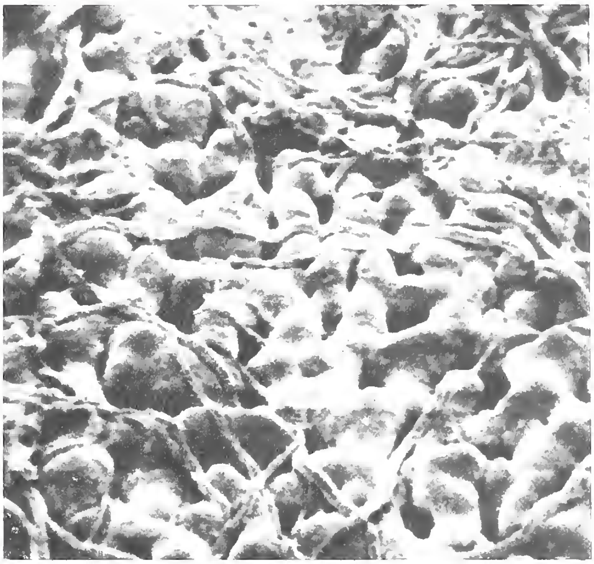
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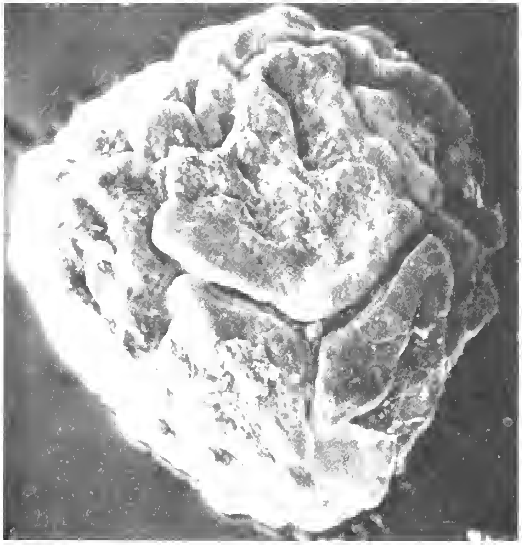
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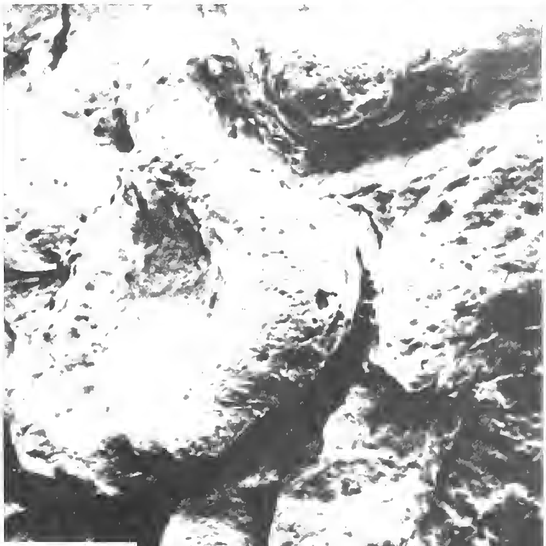
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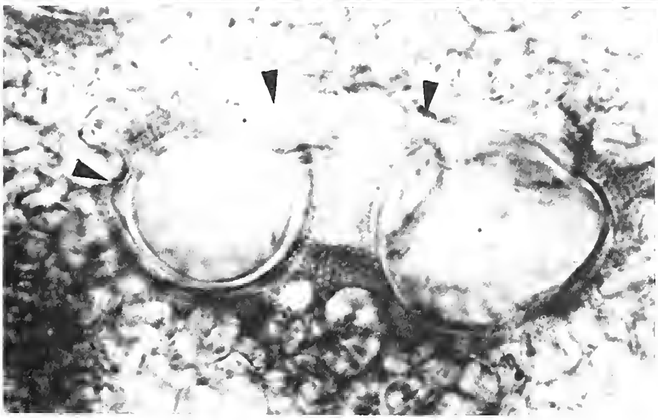
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MARTIN, Salviniaceae

forming obtusely angled and rounded cushion-like masses up to 100 μm in diameter, often with depressed centres, irregularly foveolate with foveae *circa* 1 μm in diameter; lips of perispore bluntly triangularly lobed in outline, extending about half the width of the entire spore, separated by a trifurcate cleft *circa* 6–10 μm wide, each arm *circa* 100 μm long and bifurcated at the distal end into recurved arms about 50 μm long. Massulae of microspores more or less circular-elliptical 227–306 × 215–292 μm (mean 271 × 253 μm, 6 measurements), with dark margin and pale centre, microspores peripheral, in 6–8 clusters (minimum number of spores seen 24, maximum 42), diameter of spores 22–31 μm (mean 27 μm, 32 measurements from 3 massulae), thickness of sporoderm *circa* 1·0–1·5 μm, length of trilete mark 18 μm across, each laesura *circa* 13 μm, each spore enclosed in individual perine coat within the massula.

Holotype. Slide V58337, Plate 28, fig. 3; repository: B.M. (N.H.).

Paratypes. SEM stub V58338, Plate 28, fig. 4; repository: B.M. (N.H.). Slide V58339, Plate 27, fig. 7; Plate 28, fig. 5; repository: B.M. (N.H.).

Locality. Shorne Wood, near Cobham, Kent: from drainage ditch connected with road widening. Ordnance Survey 1:50 000 2nd Series East London Sheet No. 177 (1–74); Nat. Grid. ref. TQ/6730 6980.

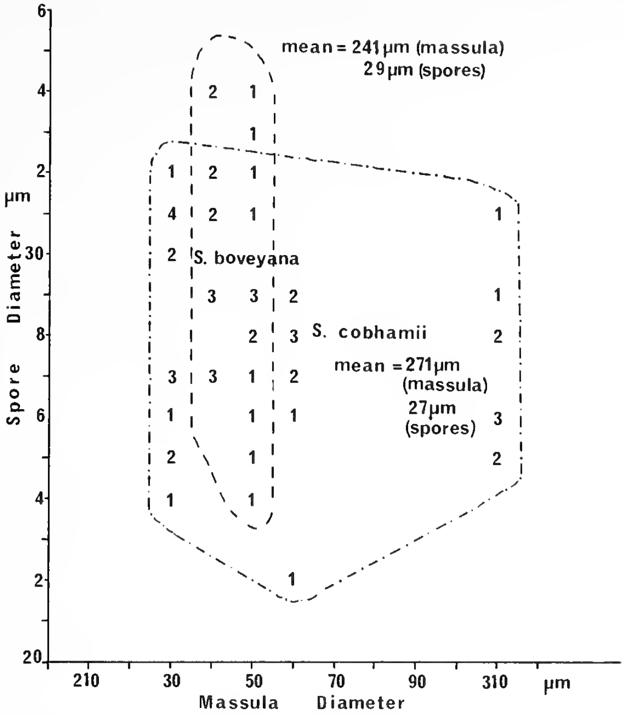
Horizon. Woolwich/Reading Beds, base of exposure of 60 cm of organic lacustrine sediment (nekron mud).

Sample. Chaloner palynological sample collection; sample No. R1434, Botany Department, Birkbeck College, London.

Remarks. *S. cobhamii* appears to be the oldest known species from the British Isles, possibly the oldest from western Europe, though the genus is now known from the Upper Cretaceous of Canada. The classification of fossil *Salvinia* species depends both on the leaves and on the spore bodies. As these are not often found together, the number of species described might exceed the true number. However, the number of early Tertiary species is small. As far as possible this form has been compared with *S. boveyana* Chandler (1957) of the Oligocene. The holotype of *S. boveyana* is a microsporocarp with its contained massulae, and megaspores have not been described. Text-fig. 2 shows that there is no fundamental difference in size between the microspores and massulae of the two species. The slightly more restricted size range of *S. boveyana* may be simply due to both the massulae being from a single sporocarp.

The main objections regarding the new form being *S. boveyana* are that it is much older and there is little evidence that microspore massulae are at all species-diagnostic. Where megaspores are available it seems better to base the species diagnoses on them and not to overweight the similarity of the microspore massulae, though one should keep open the possibility that they may prove to be conspecific.

The only other species of comparable age and sufficiently well described to compare with *S. cobhamii*, are *S. aureovallis* Jain and Hall (1969), and *S. intertrappea* Mahabale (1950). The former, of the United States Eocene, has smaller megaspores, *circa* 240–320 μm in diameter, but large microspore massulae which are described as of the same size as the megaspores. The microspores are small, 20–26 μm with laesurae measuring up to 9 μm. *A. intertrappea*, also of the Eocene, is a silicified fossil and therefore not easy to compare directly; its microspore massulae (originally described as *Massulites coelatus* Sahni and Rao) are hollow, as in modern *S. auriculata*. Those of *S. cobhamii* may have been hollow, but the microspores of all species are probably peripheral and



TEXT-FIG. 2. Scatter diagram for microspores and massulae of *Salvinia cobhamii* and *S. boveyana*. The vertical columns of numbers on the graph refer to the numbers of microspores of each diameter (as measured along the greatest axis) in each massula.

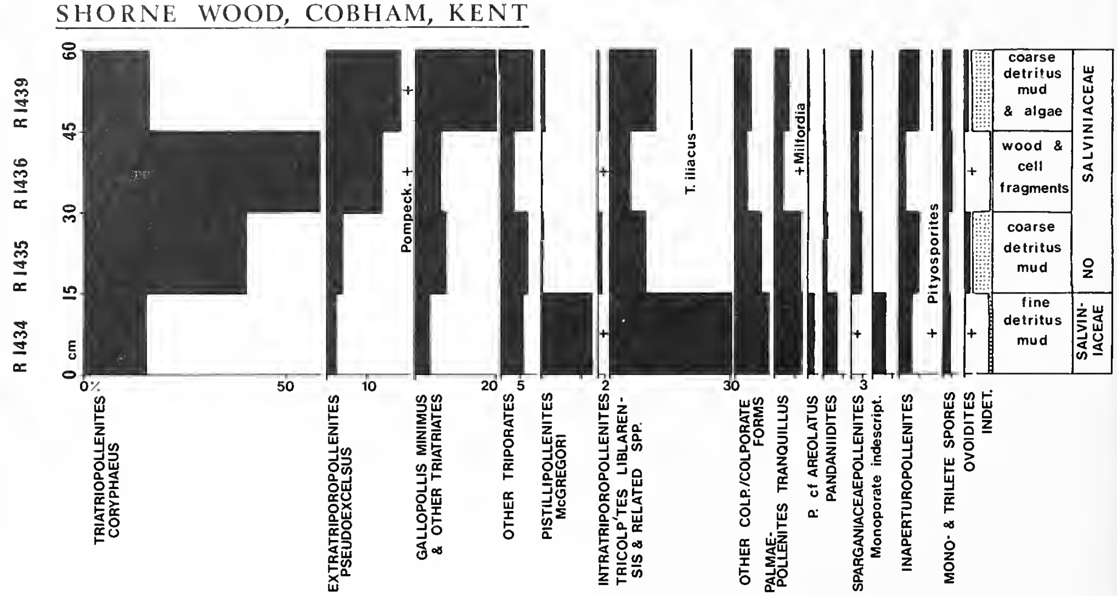
the appearance of a dark ring and pale centre (Pl. 27, fig. 7) would result equally if the centre consisted of large and the surface of small alveoli. The even older *S. stewartii* Jain (1971) of the North American Upper Cretaceous, was a species with very large megaspores up to 950 μm in length and large microspores over 50 μm in diameter.

It is of interest that *S. cobhamii* microspores have individually distinguishable perines. Kempf (1971) has shown from ultra-thin sections that while microspores in a massula always have a triradiate opening to the exterior preformed in the perine of the massula, the perine of some species is also differentiated into a trizonate layer round each microspore, e.g. *S. cerebrata*. Other species have only slight differentiation of the perine, e.g. *S. rhenana* and the modern species *S. natans*. While direct comparison with the EM-sectioned material is not possible, examination of entire massulae of *S. cobhamii* shows that the microspores have a separate distinguishable perine coat which is patterned inside the massula. The apex of each separate perine has a triradiate opening to the exterior (Pl. 28, fig. 5). It seems that *S. cobhamii* was more like the Lower Miocene species *S. cerebrata* than the Plio-Pleistocene species *S. rhenana* or modern *S. natans*, in this respect.

THE ASSOCIATED POLLEN AND SPORE FLORA

The samples obtained were equally spaced and represent the entire vertical extent of the exposure (60 cm). A simple pollen diagram showing the quantitative variation of the commoner pollen and spore types through this short profile is given in text-fig. 3. The flora contains about forty species, most of which are similar to or identical with forms from the European lower Tertiary or the North American (Wilcox) Palaeocene–Eocene (Fairchild and Elsik 1969). The sample in which Salviniaceae occur is distinguished by an abundance of *Pistillipollenites mcgregori*, tricolpate pollen of the *Tricolpopollenites liblarensis–T. microhenrici* group, and a small undescribed monoporate grain (Pl. 27, figs. 4, 5) which resembles *Aglaeoreidia* in being elliptical but differs from both described species of *Aglaeoreidia* in being more uniformly reticulate. (I am indebted to Mr. K. Fowler for pointing this distinguishing character out to me.) This species appears unique among monoporate grains of this general description in being operculate. There are also more of the two forms *Palmaepollenites tranquillus* and *Pandaniidites* sp. in this level.

The upper three samples are dominated by *Triatriopollenites coryphaeus*, *Gallopollis*, and species of *Extratriporopollenites*. Especially in R1436 and R1439 these forms tend to be corroded. The comparative rarity of Gymnosperms, particularly the bisaccate groups, and of fern spores is interesting. Fairchild and Elsik (1969) comment on the greater abundance of Normapolles in the Wilcox as compared with younger strata. The relative abundance of Normapolles (*Extratriporopollenites*



TEXT-FIG. 3. Pollen diagram of Shorne Wood, near Cobham, Kent; profile from which *Azolla anglica* and *Salvinia cobhamii* were isolated. The pollen percentages are based on counts of at least 300 pollen grains in each sample. Pompeck = *Pompeckjoideaepollenites* sp. Tricolp'tes = *Tricolpopollenites*.

spp. (up to 18%), and *Pompeckjoideaepollenites*), at the Cobham site perhaps helps to confirm the Late Palaeocene–earliest Eocene age of the Woolwich/Reading Beds.

The section seems to record the shallowing of a lake with encroachment of reeds (*Sparganiaceaepollenites*) upon a more open phase with floating Salviniaceae, then a possible reflooding. *P. tranquillus* and *P. areolatus* have been equated with Palmae, the *Tricolpopollenites liblarensis* group with Cupuliferae and *Triatriopollenites coryphaeus* with Juglandaceae, while the Normapolles and *Pistillipollenites* are of unknown source. The total flora suggests warm temperate, rather than subtropical conditions. The simplest explanation of the diagram might be that Juglandaceae and perhaps the Normapolles sources formed riparian forest which advanced and was consequently strongly over-represented during the drying phase, while the Cupuliferae represent a more long-distance component. The *T. coryphaeus* pollen in R1436 is often clumped as if anthers were falling directly into the supposed reed swamp. *Pistillipollenites*, judging by its striking association with the lake phase, may have been a waterside or even an aquatic plant. Thus the Salviniaceae at this site seem to have died out through a plant succession, or '*verlandung*', though in the absence of macroscopic wood remains it would be unwarranted to infer that some kind of swamp forest was the highest stage reached.

Acknowledgements. I wish to thank Professor W. G. Chaloner for offering me this problem to study. Professor Chaloner and Dr. M. Muir are also thanked for their kindness in offering the facilities of their respective departments during periods of leave. The nomenclature of text-fig. 3 has been adopted after discussion with Miss Lynn Allen and Mr. K. Fowler, for which I am very grateful. Mrs. P. Thiem and Mrs. S. Kilkeary are thanked for their technical assistance.

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A WESTPHALIAN EURYPTERID FROM SOUTH WALES

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ABSTRACT. The first known eurypterid from the Coal Measures of Wales is a well-preserved prosoma described here as *Adelophthalmus* cf. *moyseyi* (Woodward, 1907). It is of upper Westphalian A or lower Westphalian B age, and is compared with other approximately contemporaneous species.

EURYPTERIDS are rare in the Coal Measures (late Carboniferous) of Britain, with only some twenty undoubted specimens known, reported in the literature from the Somerset, Derbyshire–Nottinghamshire, and Lanarkshire coalfields, and all are of Westphalian age. (Three specimens (BM 16539–16541) from the Old Hards Coal (Westphalian A) of Hartley Bank Colliery, Horbury, Yorkshire, first mentioned by Stainier (1915, p. 614) and then by Kjellesvig-Waering (1948, p. 9) were subsequently re-examined by Dr. Kjellesvig-Waering in 1949, and his notes which now accompany the specimens identify them not as eurypterids but as the centipede-like arthropod *Arthropleura*.)

A number of specific names have been proposed for these British eurypterids. In a comprehensive review Kjellesvig-Waering (1948) recognized three English species, which he described as *Lepidoderma wilsoni* (Woodward, 1888), *L. moyseyi* (Woodward, 1907) (with *Eurypteris derbiensis* Woodward, 1907 as a junior synonym), and *L. kidstoni* (Peach, 1888), while Waterston (1957) later redescribed the single Scottish specimen as *Eurypterus minutisculptus* (Peach, 1905). Earlier reviews of some of the material were published by Stainier (1915), Moore (1936), and Van Oyen (1956), and in 1958 Kjellesvig-Waering emended the nomenclature to include all the English species in the genus *Adelophthalmus* Jordan and von Meyer, 1854 and the Scottish specimen questionably in *Campylocephalus* d'Eichwald, 1860. Waterston (1968) subsequently erected *Vernonopterus* to accommodate the latter.

The first eurypterid from the Coal Measures of Wales, a well-preserved though slightly crushed prosoma, was presented to the National Museum of Wales in July 1974 by Mr. David Old of Ynysawdre Comprehensive School, near Bridgend in Mid Glamorgan; it was found by his father in loose material at the head of Garw Colliery, Blaengarw. The horizon from which the specimen came is not known with certainty, but there is no doubt that it was from the colliery itself. The sequence in the colliery includes Lower and Middle Coal Measures, with workable coals ranging from the Gellideg Seam upward through the Amman Marine Band to the Two-Feet Nine Seam. Over the last few years or so work has concentrated on the Gellideg and Upper Nine-Feet seams, but there have also been workings on intervening coals. The horizon of the specimen can therefore be tied down only within these limits, indicating an upper Westphalian A or lower Westphalian B age, within the uppermost

[Palaeontology, Vol. 19, Part 1, 1976, pp. 185–190, pl. 29.]

communis, *modiolaris* or lower *similis-pulchra* non-marine bivalve zones (see Woodland and Evans (1964) and Thomas (1974) for summaries of stratigraphy).

Because of its rarity and good preservation the specimen is described here, and its relationship to other species is discussed. Other comparative British material is figured on Plate 29.

Family HUGHMILLERIIDAE Kjellesvig-Waering, 1951

Genus ADELOPHTHALMUS Jordan and von Meyer, 1854

Type species. Adelophthalmus granosus Jordan and von Meyer, 1854.

Remarks. Three generic names have been used in the past for a group of similar late Carboniferous eurypterids—*Adelophthalmus*, *Lepidoderma* Reuss, 1855, and *Anthraconectes* Meek and Worthen, 1868 and their possible synonymy has been discussed by a number of authors (e.g. see Wills 1964, pp. 474–475, Størmer 1973, p. 148 for summaries).

There is general agreement among most authors that *Lepidoderma* is a junior synonym of *Adelophthalmus*, and Kjellesvig-Waering (1958, pp. 1140–1143) and Størmer also included *Anthraconectes* in probably synonymy. However, Wills (1964, pp. 474–475) preferred to retain *Adelophthalmus* and *Anthraconectes* as separate genera until more became known of the ventral organs of the former. Here we agree with Kjellesvig-Waering and Størmer, and believe that the senior name *Adelophthalmus* should be used until such time as the ventral organs can be shown to differ from those in *Anthraconectes*.

Adelophthalmus cf. *moyseyi* (Woodward, 1907)

Plate 29, fig. 1

Material. One prosoma, NMW 74.20G.1, from Coal Measures, Westphalian A or B, loose material beside stop-lock at head of railway, Cwm Nant-hir, 180 m ENE. of Garw (Ocean) Colliery, Blaengarw, Mid Glamorgan (SS 9317 9073).

EXPLANATION OF PLATE 29

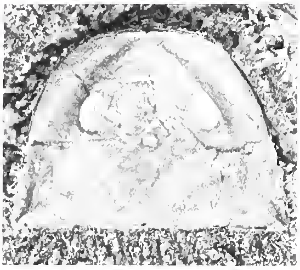
Fig. 1. *Adelophthalmus* cf. *moyseyi* (Woodward, 1907). Prosoma, NMW 74.20G.1, Coal Measures, Westphalian A or B, stop-lock at head of railway 180 m ENE. of Garw (Ocean) Colliery, Blaengarw, Mid Glamorgan (SS 9317 9073), ×2.

Figs. 2, 5. *Adelophthalmus wilsoni* (Woodward, 1888). 2, mesosomal and metasomal segments, CMB Ca7193, Coal Measures, Westphalian D, Camerton Colliery, near Radstock, Avon (orig. Moore 1936, p. 354, fig. 58), ×1. 5, holotype mesosoma, BM I1463, Coal Measures, Westphalian D, Ludlow's Colliery, Radstock, Avon (orig. Woodward 1888, p. 420, text-fig.), ×1.

Fig. 3. *Adelophthalmus kidstoni* (Peach, 1888). Holotype prosoma, GSM 49452, Coal Measures, Westphalian D, Radstock, Avon (orig. Peach 1888, pl. 20, fig. 1), ×2.

Fig. 6. *Adelophthalmus* cf. *wilsoni* (Woodward, 1888). Almost complete dorsal surface, BM In35610, Coal Measures, Westphalian C, Bromley Colliery, near Pensford, Avon (orig. Moore 1936, p. 357, fig. 59), ×1·25.

Figs. 4, 7. *Adelophthalmus moyseyi* (Woodward, 1907). 4, latex cast of dorsal surface of prosoma, mesosoma, and part of metasoma, GSM 30250, Coal Measures, Westphalian B, Shipley Clay Pit, near Ilkeston, Derbyshire (orig. Moore 1936, p. 367, fig. 63), ×1·5. 7, latex cast of incomplete dorsal surface of small specimen, GSM 30197, horizon and locality as fig. 4 (holotype of *Eurypterus derbiensis* Woodward, 1907, pl. 13, fig. 3), ×2.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OWENS and BASSETT, *Adelophthalmus*

Description. Prosoma of low relief, roughly trapezoidal, about three-quarters as long as wide. Anterior margin more or less transverse, gently curved forwards, anterolateral margins strongly but smoothly curved. Lateral margins weakly curved outwards to within about 5 mm of the genal angle, thereafter nearly straight. Posterior border straight, genal angles acutely rounded, about 80°, not produced as spines.

Along the anterior margin is a narrow, weakly concave flange, about 0·4 mm wide sagittally, narrowing to zero in front of lateral eyes. Sagittally, a small triangular notch just indents posterior margin of flange.

A pair of median ocelli, apparently almost conjoined, is situated centrally on the prosoma, slightly closer to posterior than to anterior margin. Lateral compound eyes reniform, about one-fifth the length of prosoma, with posterior ends at about the mid-length and anterior ends nearly equidistant from anterior and lateral margins.

A depressed zone runs from the middle of the anterior margin backwards and outwards outside the eyes to the genal angles, being widest just behind the eyes and narrowing almost to a point at either end. This zone defines a triangular elevated area between the genal angles, eyes, and the centre of the anterior margin. The anterolateral areas of the prosoma are also slightly elevated.

Prosoma apparently smooth, with the exception of a zone about 1 mm wide along the posterior margin, which has a scaly sculpture, with the convex edges of the scales directed backwards.

Dimensions. Sagittal length, 13·5 mm. Width across posterior margin, 18·5 mm.

Comparison. Of British species, our prosoma compares closely with both *Adelophthalmus kidstoni* and *A. moyseyi*. *A. wilsoni* is known only from mesosomal and metasomal segments, but occurs at about the same horizon as *A. kidstoni* in the Somerset coalfield. Moore (1936, p. 355) provisionally referred the holotype of *A. kidstoni* to *A. wilsoni*, and (ibid., p. 356) described a fairly complete specimen from a somewhat lower horizon in the same area as *Eurypterus* (= *Adelophthalmus*) cf. *wilsoni*. The prosomal differences between *A. kidstoni* and Moore's *A.* cf. *wilsoni* are small, although the anterior ends of the lateral eyes are somewhat further from the anterior than the lateral margin in the former, while they are equidistant in the latter. Kjellesvig-Waering (1958, p. 1143) placed *A.* cf. *wilsoni* in *A. wilsoni*. *A. moyseyi* is known only from partially complete material. The prosoma is similar to those of both *A. kidstoni* and *A.* cf. *wilsoni*, the eye position being closer to that of the latter. Most of the prosoma of the latter two is covered with a sculpture of small scales. The sculpture is similar in *A. moyseyi*, but is more localized, being best developed close to the posterior margin and on the posterior half of the prosoma. A further prosoma, from the Namurian Limestone Coal Group of Scotland, was described by Waterston (1968, p. 2, pl. 3, figs. 4, 5) as *A.* cf. *wilsoni*, and is the oldest British representative of the genus.

Eurypterids from Westphalian A and B of Limburg, southern Netherlands, have been figured as *A. imhofi* (Reuss, 1855) by Van Oyen (1956) who placed many different upper Carboniferous forms in synonymy with this species. This assignment was challenged by Kjellesvig-Waering (1963, pp. 98–100), who considered the Dutch material to belong to *A. cambieri* (Pruvost, 1930). *A. cambieri* itself, from the Westphalian B of Belgium (Pruvost 1930, pl. 13, fig. 1, 1*a*, text-fig. 7) is based on a poorly preserved specimen in which details of the prosomal sculpture are not known, but the Dutch material assigned by Kjellesvig-Waering (1963) to this species has scales covering most of the prosoma; the lateral eyes are similar in position to those of *A. moyseyi*, but are proportionately smaller. We have examined collections in the Sedgwick Museum and British Museum (Natural History) from the Limburg coalfield which confirm these relationships between *moyseyi* and *cambieri*.

Of North American species, *A. mazonensis* (Meek and Worthen, 1868) is similar to all the above, and the lateral eyes are similar in size and position to those of *A. moyseyi*. As in *moyseyi* the surface sculpture of the prosoma is rather localized, occurring at the posterior end and in the central region between the eyes. There is also general resemblance to *A. kidstoni* and Kjellesvig-Waering (1948, p. 29) noted that *wilsoni* (*sensu* Moore, 1936 = *kidstoni* herein) and *mazonensis* might be subspecies.

Our specimen compares with *A. moyseyi*, *A.* cf. *wilsoni* (of Moore), *A. cambieri* (*sensu* Kjellesvig-Waering 1963), and *A. mazonensis* in eye position, and with all except *A. cambieri* in eye size. It is particularly distinctive in its very restricted surface sculpture; this seems primary rather than preservational, as the specimen shows no sign of having been worn or weathered. None of the species mentioned above has similarly restricted sculpture, although it is more restricted in *A. moyseyi* and *A. mazonensis* than in the others. As there are so few British specimens known, there is no information on variation within species, or whether such features as surface sculpture vary much between individuals, or from population to population. Van Oyen (1956) illustrated a large number of specimens of *A.* '*imhofi*' from the Netherlands, and examination of his plates suggests that the amount of prosomal sculpture remains fairly constant. Should this apply to other taxa, then it is likely that our specimen belongs to a new species, but as yet there is insufficient material to describe it as such. At present, we consider that it most closely resembles *A. moyseyi* in its prosomal outline and general morphology. It is from a similar horizon to the type material of *A. moyseyi*.

Acknowledgements. We thank Mr. David Old for presenting the specimen on which this paper is based, and Mr. F. L. Evans (Ynysawdre Comprehensive School) and Mr. A. J. Thomas (National Museum of Wales) for first bringing it to our attention. Dr. W. G. Thomas (National Museum of Wales) kindly gave us information on seams mined in Garw Colliery, and Dr. M. L. K. Curtis (City Museum, Bristol—CMB), Dr. R. A. Fortey (British Museum (Natural History)—BM), Mr. M. Mitchell (Institute of Geological Sciences, Leeds—GSM), and Dr. R. B. Rickards (Sedgwick Museum, Cambridge University) allowed us to borrow specimens in their charge for comparative purposes. Dr. R. A. Fortey supplied the photograph for Plate 29, fig. 6.

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THE TAXONOMIC POSITION OF THE CHALICOTHERIID PERISSODACTYL *KYZYLKAKHIPPUS ORLOVI* FROM THE OLIGOCENE OF KAZAKHSTAN

by MARGERY C. COOMBS

ABSTRACT. The type of *Kyzylkakhippus orlovi*, reaffirmed as probably teeth dp^2–dp^4 from Oligocene deposits at Kyzyl-kak, Kazakhstan, is compared to upper deciduous teeth of *Schizotherium priscum*. This comparison, and the known presence of *S. turgaicum* in the Kyzyl-kak fauna, suggest that *K. orlovi* is a junior synonym of *S. turgaicum*. Upper teeth of *S. turgaicum* are otherwise poorly known. Because '*K. orlovi*' is thereby referable to the Schizotheriinae, there is no definite evidence of the Chalicotheriinae in the Old World prior to the Aquitanian or Burdigalian. *Chalicotherium* and *Nestoritherium* alone can at present be included in the Chalicotheriinae.

IN 1964 Gabunia and Belyaeva erected a new genus and species, *Kyzylkakhippus orlovi*, for a deciduous upper dentition from middle Oligocene deposits at Kyzyl-kak, Kazakhstan. They identified the type, from the collection in the Palaeontological Institute of the Academy of Sciences of the U.S.S.R., Moscow (specimen no. PIN 2259-330), as dp^2–dp^4 of an anchitheriine equid. Thenius (1968), however, noted morphological differences between the type dentition and that of known horses, and the zoogeographic difficulties of suggesting that an equid or palaeotheriid had existed in Kazakhstan in the middle Oligocene; he correctly referred the genus to the Chalicotheriidae. Thenius also reinterpreted the type dentition as dp^3–M^1 and suggested especially close affinity to the Chalicotheriinae. Malcolm C. McKenna, who also questioned the referral of *Kyzylkakhippus* to the Equidae (pers. comm.), made the cast of the type specimen shown in text-fig. 2. My study of this cast and of the drawing of the type figured by Gabunia and Belyaeva (1964, fig. 6) leads me to accept the original identification as dp^2–dp^4 but also to accept Thenius's placement of *Kyzylkakhippus* in the Chalicotheriidae. However, I consider that it belongs to the Schizotheriinae rather than to the Chalicotheriinae.

The family Chalicotheriidae is thought to have arisen in the late Eocene or early Oligocene from members of the family Eomoropidae (Radinsky 1964). Two subfamilies, the Chalicotheriinae and Schizotheriinae, are recognized. Generally speaking, the Chalicotheriinae, consisting only of the genera *Chalicotherium* and *Nestoritherium*, have undergone quite pronounced changes in foot structure, and on this basis are easily distinguished from all known schizotheriines. Chalicotheriine dentition is conservative, however, and the upper molars remain low-crowned and quadrate. In the Schizotheriinae (*Schizotherium*, *Borissiakia*, *Moropus*, *Phyllotillon*, *Ancylotherium*) postcranial modifications have occurred much more gradually than in the Chalicotheriinae, and never attain the derived state seen in even the most primitive known representatives of *Chalicotherium* (*C. pilgrimi*, *C. rusingense*). Schizotheriines modify the dentition more than do chalicotheriines, elongating the

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molars and increasing the crown height, but they do so gradually. Over a short span of time, changes in schizotheriine dentitions are relatively few. *Schizotherium* lacks the derived foot structure of the Chalicotheriinae, but its teeth are less elongated than in most other schizotheriines. The exact relationship of *Schizotherium* to chalicotheriines and other schizotheriines is not clear, but it is probably very near the common ancestry of all schizotheriines. It is possible also that ancestry of the Chalicotheriinae is close to *Schizotherium* and perhaps lay within a species which at the present state of knowledge would be placed within *Schizotherium.*

The best-known species of *Schizotherium*, *S. priscum* and *S. turgaicum*, are represented by both dental and postcranial remains. Postcranial elements provide the most certain means both for allying and differentiating the two species. Compared to elements of other schizotheriine genera, the footbones are of smaller absolute size, metatarsals are longer compared to their width (see, for example, Coombs 1974, table 1), metacarpals and metatarsals are not so closely interarticulated, and fusion between phalanges is unknown. (*Schizotherium* shares the latter three character states with *Borissiakia* but differs from that genus in, among other features, the absence of a cuboid facet from the distal surface of the astragalus.) Among features which differentiate known postcranials of *S. turgaicum* from those of *S. priscum* are the loss or strong reduction of a trapezium in the carpus, and the apparent loss of articulation for the ectocuneiform on metatarsal II in the former species (Coombs, manuscript). Loss or reduction of the trapezium occurs more than once within the Schizotheriinae and seems to allow additional flexion of the manus. *S. priscum* is known primarily from Oligocene fissure fillings in France (Phosphorites of Quercy), and *S. turgaicum* is an element of the middle Oligocene indricothere fauna well known from Kazakhstan.

Lower teeth have been regularly used to differentiate between species of *Schizotherium* (Matthew and Granger 1923; Gabunia 1951; Belyaeva 1954; Dashzeveg 1974), but upper teeth are poorly known, except in *S. priscum*, and have been little used in interspecific taxonomy. Because of their low crowns and lack of obvious elongation, *Schizotherium* upper molars have on occasion been referred to *Chalicotherium* by workers who did not take postcranial characteristics into sufficient account. Gaudry (1875*a*), before the association between chalicothere teeth and postcranials had been recognized, gave the name '*Chalicotherium modicum*' to some upper cheek teeth from the Phosphorites. Filhol (1894) later suggested that '*C. modicum*' might be the same animal as *S. priscum* (which he then referred to *Ancylotherium*), a conclusion with which I fully agree. Similarly, the worn upper molariform tooth of *S. turgaicum* figured by Borissiak (1921, pl. 7, fig. 1) led von Koenigswald (1932, p. 22) to classify the species as *C. turgaicum*. I believe that the same mistake has been made in the case of *Kyzylkakhippus orlovi*, and that this is really a junior synonym of *S. turgaicum*.

SYSTEMATIC PALAEONTOLOGY

Class MAMMALIA
Order PERISSODACTYLA
Suborder CHALICOTHERIOIDEA Gill, 1872
Family CHALICOTHERIIDAE Gill, 1872
Subfamily SCHIZOTHERIINAE Holland and Peterson, 1914
Genus SCHIZOTHERIUM Gervais, 1876
Species *Schizotherium turgaicum* Borissiak, 1920

1921 *Schizotherium turgaicum*: Borissiak, p. 43 (English version of Borissiak 1920, above); Matthew 1929, p. 519; Colbert 1935, p. 6; Gabunia 1951, p. 282; Belyaeva 1954, p. 52; Dashzeveg 1974, p. 76.
1932 *Chalicotherium turgaicum*: von Koenigswald, p. 22.
1935 *Macrotherium turgaicum*: Colbert, p. 12.
1964 *Kyzylkakhippus orlovi* Gabunia and Belyaeva, p. 129.
1968 *Kyzylkakhippus orlovi*: Thenius, p. 347.
1969 *Kyzylkakhippus orlovi*: Thenius, p. 573.

Discussion. PIN 2259-330, a deciduous upper dentition, is the holotype and only specimen referred to '*K. orlovi*'. PIN 1442-253, designated as the lectotype of *S. turgaicum* (see Belyaeva 1954), is a lower jaw ramus containing P_4–M_2. The only published upper tooth hitherto referred to *S. turgaicum* is a worn quadrate molariform tooth figured by Borissiak (1921, pl. 7, fig. 1). Although both Borissiak (1921, p. 43) and Belyaeva (1954, p. 52) identified this tooth as an upper molar (?M^2), it is small (17·5 mm long according to Borissiak 1921, p. 43). The lower teeth of the lectotype of *S. turgaicum* are also smaller than their very few known counterparts in *S. priscum*. On the other hand, metatarsals of *S. turgaicum* figured by Borissiak (1921) are in general larger than known metatarsals of *S. priscum*. It is not possible on the basis of limited specimens to reach a conclusion on the relative sizes of feet and teeth in the two species. Size sexual dimorphism in chalicotheriids (Coombs 1975) is a further confusing factor in such a determination. The length of the upper molariform tooth figured by Borissiak (1921) may have been reduced by the wear it shows, but the small size suggests that identification as M^1 or even dp^3 or dp^4 is not unreasonable. In any case, though I detect no particular differentiating features between the two specimens, it is so badly worn that it cannot be meaningfully compared with PIN 2259-330. In the absence of any other published upper teeth of *S. turgaicum*, I have compared PIN 2259-330 with upper teeth of *S. priscum*.

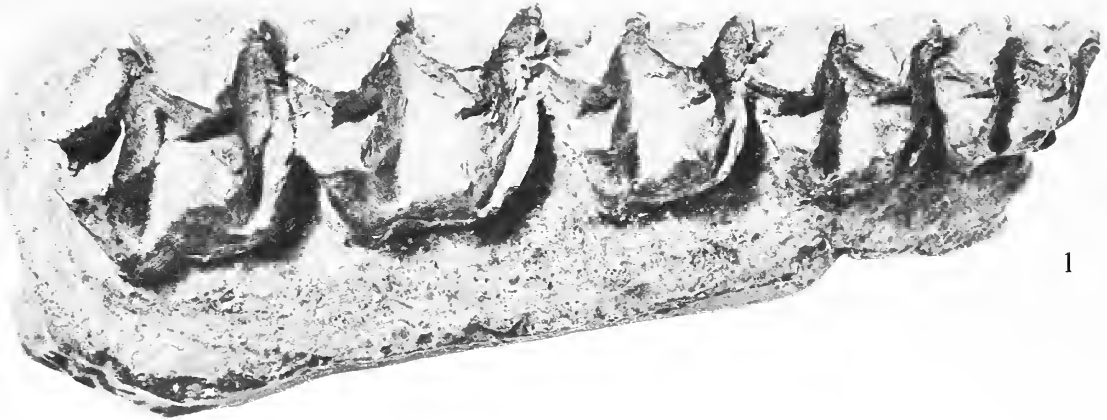
For purposes of comparison with PIN 2259-330, the most useful specimen is a maxilla from the Phosphorites of Quercy; this was given the numbers PQ 359–PQ 362 at the Muséum d'Histoire Naturelle de Lyon, Lyon, France, but was cast as specimen no. AMNH 10494 in the collection of the Department of Vertebrate Paleontology of the American Museum of Natural History, New York. The teeth in this specimen (text-fig. 1) can be identified as dp^2–M^2 and are probably referable to *S. priscum*. The posterior two teeth, M^1 and M^2, are generally similar to M^1 and M^2 on left and right uncatalogued maxillae of *S. priscum* in the Muséum National d'Histoire Naturelle, Paris, figured respectively by Filhol (1877) and Gaudry (1875*b*). (The specimens figured by Filhol and by Gaudry are very similar to one another and, if from the same locality, might be two sides of the same individual; M^2 is slightly more symmetrical than M^2 of AMNH 10494, but both molars are approximately as quadrate as those of AMNH 10494.) The most posterior tooth of AMNH 10494 is probably not an M^3, because M^3 of *S. priscum* is strongly asymmetrical, with the posterior part of the ectoloph especially reduced (text-fig. 3). The anterior three teeth of AMNH 10494 should therefore be regarded dp^2–dp^4. These teeth are of similar morphology to one another and are all molariform. The molariform structure of dp^2, as thus identified, is remarkable in the sense that dp^2 in *Moropus*, where several immature maxillae are known, is closer in morphology to P^2 than it is to dp^3, dp^4, or to the permanent molars. Permanent premolars, including P^2, of *S. priscum* are generally similar to those of *Moropus*. Lower deciduous teeth known in *Schizotherium* and other schizotheriines are not helpful in elucidating this question. Tooth dp$_2$ of *Moropus* sp. from Aquitanian deposits of St-Gérand-le-Puy, France, is elongated compared to its width but is clearly not molariform (Coombs 1974). A dp$_3$ in an uncatalogued specimen of *S. priscum* (Field Lot Bach 1893-11 in the Muséum National d'Histoire Naturelle, Paris) corresponds closely in morphology to dp$_3$ of *Moropus* and thus suggests a possible correspondence of dp$^2_2$ as well. Tooth dp$_2$ of *Ancylotherium* (*Ancylotherium*) *pentelicum* from Samos (AMNH 23001; see Coombs 1973) is, however, partly molariform.

Identification of the upper teeth of AMNH 10494 as dp^2–M^2 makes it more likely that Gabunia and Belyaeva (1964) correctly identified PIN 2259-330, the type of '*K. orlovi*', as dp^2–dp^4. Further examination and comparison with AMNH 10494 suggest that the size difference between the posterior two teeth of PIN 2259-330 is approximately the same as that between dp^3 and dp^4 of AMNH 10494 (see Table 1); it is also about the same order of magnitude as the size increment from dp^2 to dp^3. This observation conflicts with Thenius's view that there is a proportionately large size difference between the posterior two teeth. In fact, abrupt size increase does not seem to be a good method of distinguishing dp^4 from M^1 in *Schizotherium*. In AMNH 10494 the increase from dp^4 to M^1 is not much more than the size increments between dp^2, dp^3, and dp^4. In that little-worn specimen there is also a notably small size increase from M^1 to M^2, despite the fact that in many chalicotheriid specimens M^1 is shorter than M^2, possibly because of loss of length by wear during life. The teeth of PIN 2259-330 correspond closely in size to dp^2–dp^4 of AMNH 10494 but, in view of the difficulties mentioned above in making comparisons between *S. priscum* and *S. turgaicum* in tooth and foot size, one must not put undue emphasis on this similarity.

TABLE 1. Greatest length in millimetres along ectoloph of upper molariform teeth of PIN 2259-330 and AMNH 10494. Measurements of PIN 2259-330 from Gabunia and Belyaeva (1964, p. 129).

Tooth	PIN 2259-330	AMNH 10494
dp^2	Broken (approx. 14·0)	16·1
dp^3	17·0	18·0
dp^4	19·5	19·7
M^1	—	22·6
M^2	—	22·8

As thus identified, dp^2–dp^4 of PIN 2259-330 and of AMNH 10494 are very similar



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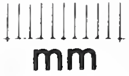

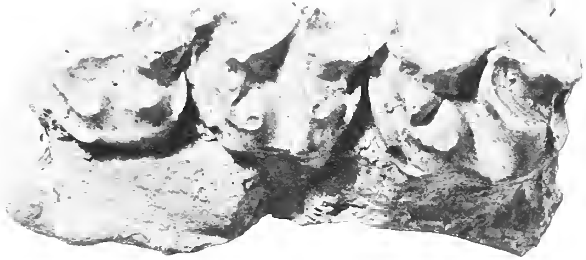

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TEXT-FIG. 1. Right dp^2–M^2 referred to *Schizotherium priscum*, AMNH 10494, a cast of PQ 359–PQ 362 of the Muséum d'Histoire Naturelle de Lyon. From the Phosphorites of Quercy, Oligocene, of France.

TEXT-FIG. 2. Cast of PIN 2259-330, left dp^2–dp^4, holotype of '*Kyzylkakhippus orlovi*'. From Oligocene deposits of Kyzyl-kak, Kazakhstan.

TEXT-FIG. 3. Left M^3 of uncatalogued specimen (Lot Number Bach 1903-20 at the Muséum National d'Histoire Naturelle, Paris) referred to *S. priscum* from the Phosphorites of Quercy, Oligocene, of France.

All figures × 1·5.

in morphology. Particularly noticeable in both are the complete molarization of dp^2 and the presence of a crista on at least dp^4. On PIN 2259-330, dp^4 is less worn than that of AMNH 10494, and therefore the origin of the metaloph from the ectoloph is closer to the mesostyle; such a variation as a result of differential wear is also seen within a single species of *Moropus*. Other minor differences between the two specimens, for example the stronger protoconule on dp^4 of PIN 2259-330, are also attributable to individual variation or differential wear. The small cuspule near the anterolabial base of the mesostyle on dp^3 and dp^4 of PIN 2259-330 is of uncertain significance. Clearly M_1 had not yet erupted in PIN 2259-330, for the posterior part of dp^4 is unworn. This is consistent with the relative lack of wear on the other teeth. In general, few differences occur between AMNH 10494 and the type of '*K. orlovi*', and most of the differences that do occur can be interpreted in the light of wear. Even if the two specimens were to be identified respectively (after Thenius) as dp^3–M^3 and dp^3–M^1, the basic similarity between them would not be changed. Certainly the generic identity of *Kyzylkakhippus* cannot be maintained.

Thenius (1968, p. 348) listed the following members of the Oligocene Indricotherium fauna previously described from Kyzyl-kak, the type locality of '*K. orlovi*': *Cricetodon deploratus*, *C. caducus*, *Hyaenodon aymardi*, Tragulidae indet., *Colodon orientalis*, *Ergilia kazachstanica*, *Indricotherium transouralicum*, *Allacerops* sp., *Schizotherium turgaicum*, and '*K. orlovi*'. The occurrence of *S. turgaicum* is especially important. The lack of described unworn upper teeth of *S. turgaicum* makes it difficult to make a direct comparison with PIN 2259-330, but probably explains why Gabunia and Belyaeva misidentified this specimen as an anchitheriine equid. Clearly the presence of *S. turgaicum* in the Kyzyl-kak faunal assemblage increases the likelihood that '*K. orlovi*' is a junior synonym of *S. turgaicum*. The absence of significant differences from the worn upper tooth of *S. turgaicum* figured by Borissiak (1921) completes the case for synonymy.

Though a full rediscussion of the genus *Schizotherium* would be helpful at the present time, such work is hampered by fragmentary material. In view of Colbert's (1935) conclusion that *S. turgaicum* is an unusually primitive representative of the genus, it is worth pointing out that his notion was based partly on the worn upper tooth figured by Borissiak (1921), and also that upper molars of all *Schizotherium* species are quadrate relative to those of other schizotheriines. *S. turgaicum*, it should be remembered, shows some character states that are clearly not primitive—for example, the loss or reduction of the trapezium in the manus, and the apparent loss of ectocuneiform contact with metatarsal II in the pes. The similarity of PIN 2259-330 to upper deciduous teeth of *S. priscum* adds to the postcranial evidence that *S. turgaicum* clearly belongs to *Schizotherium* and does not represent the separate, primitive genus that Colbert (1935) suggested.

Because '*K. orlovi*' can be referred to *Schizotherium*, there is still no definite evidence of representatives of the Chalicotheriinae prior to the Aquitanian or Burdigalian of the Old World. Skinner (1968, p. 12) attributed *Oreinotherium bilobatum* (Cope, 1891) from the Cypress Hills Oligocene of Saskatchewan, Canada, to the Brontotherioidea *incertae sedis* as a *nomen inquirendum*. After re-examining the heavy mandibular ramus and separate lower deciduous tooth referred to this species, I fully agree with Skinner's assessment. *O. bilobatum* had been previously referred to the

Chalicotheriinae (Cope 1891; Russell 1934), but there is no evidence that the Chalicotheriinae were present in the New World during the Oligocene, or indeed at any other time.

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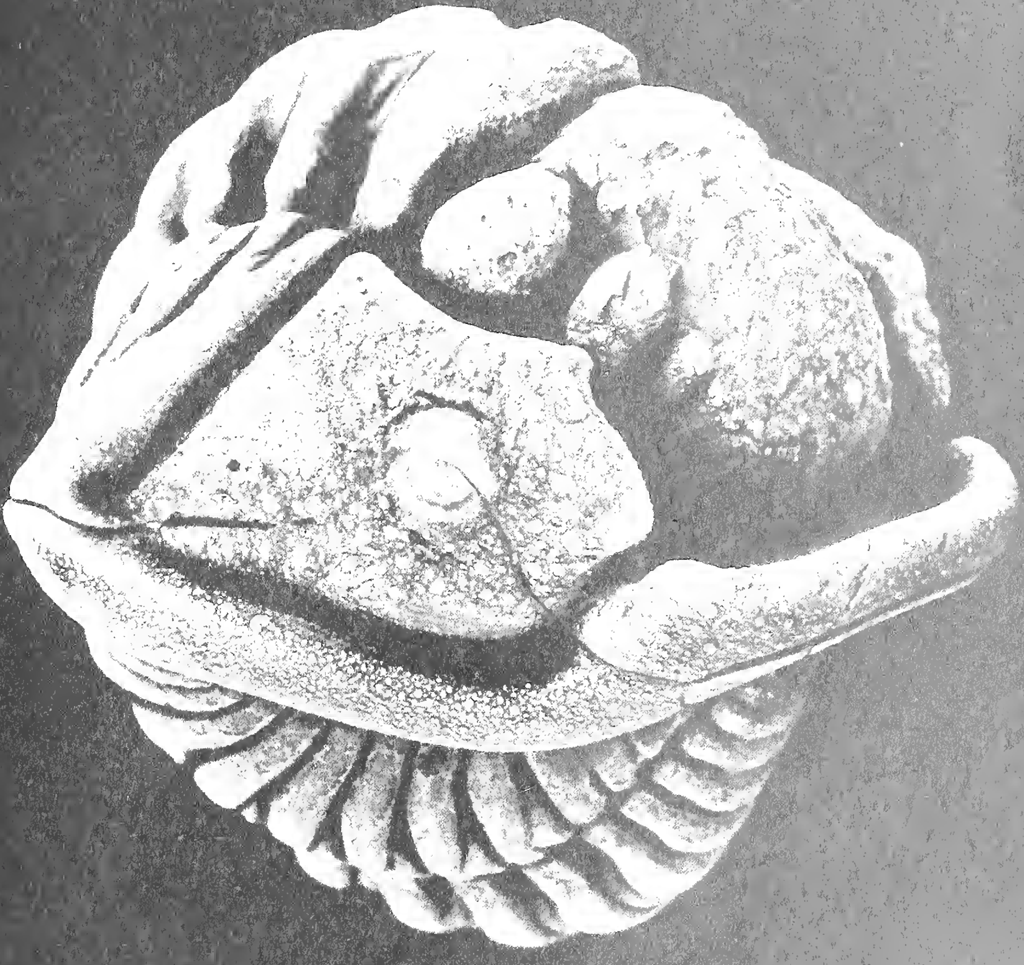

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Cover: *Calymene frontosa* Lindström, from Visby Beds (Silurian) of Gotland, Sweden.
Specimen Ar 27038 from Naturhistoriska Riksmuseet, Stockholm, photographed by
Dr. D. J. Siveter, Trinity College, Dublin.

A NEW CAMBRIAN LOPHOPHORATE FROM THE BURGESS SHALE OF BRITISH COLUMBIA

by S. CONWAY MORRIS

ABSTRACT. A single specimen (part and counterpart) of a new genus and species, *Odontogriphus omalus*, from the Burgess Shale (middle Cambrian) is described. Despite poor preservation its affinities appear to lie with the lophophorates. The simple lophophore contains tooth-like elements that are similar to certain Cambrian conodonts. It is suggested that this new genus and species is an example of a conodontophorid.

DURING a search in March 1974 through the very extensive collections of Burgess Shale fossils in the National Museum of Natural History (formerly the U.S. National Museum), Washington, D.C., a sawn slab bearing the specimen described here was noticed and set aside for further study. Shortly afterwards the counterpart was found elsewhere in the collections. The specimen had evidently never been noted by any other worker. No other specimens have been found.

STRATIGRAPHY

The Burgess Shale was discovered by C. D. Walcott in 1910, a year after he had found a dislodged slab containing soft-bodied fossils. Quarrying of the rock unit that yielded the soft-bodied fossils, the 7 ft 7 in. (2·31 m) thick Phyllopod bed, continued intermittently until 1917. An enormous number of specimens (*c.* 50 000) was collected and shipped to the U.S. National Museum (USNM). The broad history of the discovery of the Burgess Shale and research on its fauna and flora has been reviewed by Whittington (1971). The Burgess quarry was reopened in 1966 and 1967 by a party from the Geological Survey of Canada (GSC), with the co-operation of authorities of the Yoho National Park and the Parks Canada, Department of Indian and Northern Affairs, Ottawa, and the fauna and flora is currently receiving critical and detailed study by several workers, based principally at Cambridge. This article is the first in a series which will deal with worms and miscellaneous other fossils from this famous locality.

The stratigraphic position of the Burgess Shale is now fairly well understood (Fritz 1971). The shale forms a lentil in the otherwise impure limestone and shale sequence of the Stephen Formation. The Phyllopod bed occurs near the base of the Burgess Shale (Walcott 1912*b*). The Stephen Formation was deposited in a basin that lay to the south of a prominent and steep carbonate bank whose trend was roughly north-north-west (McIlreath 1974). Fritz (1971) was able to show that the Burgess Shale itself was laid down in water several hundred feet deep. There is considerable evidence that the Phyllopod bed, at least, was deposited from a succession of mudflows or turbidites (Piper 1972; Whittington 1971).

[Palaeontology, Vol. 19, Part 2, 1976, pp. 199–222, pls. 30–34.]

The larger slab of rock, which bears the counterpart, is labelled 35k. This is the USNM locality number for the Phyllopod bed (Walcott 1912*a*). The specimen is associated with *Eldonia ludwigi* Walcott, 1911*a*, *Ottoia prolifica* Walcott, 1911*b*, semi-isolated scales of *Wiwaxia corrugata* Walcott, 1911*b*, arthropods, and unidentifiable debris of organic origin. GSC collections show that *E. ludwigi* is most abundant at the level 3 ft 7 in.–4 ft 0 in. (1·09–1·22 m) above the base of the quarry, and Walcott (1912*a*) noted a similar distribution. This strongly suggests that *Odontogriphus omalus* also comes from this horizon.

SYSTEMATIC PALAEONTOLOGY

Superphylum LOPHOPHORATA
Phylum UNCERTAIN
Class CONODONTOPHORIDA Eichenberg, 1930?
Family ODONTOGRIPHIDAE fam. nov.
Genus ODONTOGRIPHUS gen. nov.

Type and only known species. Odontogriphus omalus sp. nov.

Derivation of name. Odontogriphus is derived from the Greek and means 'toothed riddle', a reference to its uncertain affinities.

Diagnosis. Bilaterally symmetrical, dorso-ventrally compressed lophophorate. Body tapering at posterior, head poorly differentiated from the annulated trunk. Head bears double-looped lophophoral apparatus containing tooth-like elements and a pair of lateral palps. Gut straight, mouth ventral, anus probably terminal. Lateral longitudinal muscles running along edges of trunk.

Odontogriphus omalus sp. nov.

Plates 30–34; text-figs. 1, 2, and 4

Derivation of name. The trivial name *omalus* (Latin) refers to its originally dorso-ventrally compressed nature.

Diagnosis. As for the genus.

Holotype and sole specimen. USNM 196169, and counterpart 196169a. The new species is from the Stephen Formation (middle Cambrian), Burgess Shale Member (*Pagetia bootes* faunule of the *Bathyuriscus-Elrathina* Zone: Fritz 1971). The Phyllopod bed (7 ft 7 in., 2·31 m) lies within division h. of the Burgess Shale (Walcott 1912*b*). The Phyllopod bed is exposed in the Burgess quarry, which is situated on a ridge connecting Wapta Mountain to Mount Field at an elevation of about 7500 ft (2286 m). The Burgess quarry is 3 miles (4·8 km) north of Field, southern British Columbia.

A note on the photography and interpretation of the specimen

The part and counterpart have been photographed in air with ordinary white light using Ilford N5/31 film (Pl. 30, fig. 1; Pl. 31, fig. 1; Pl. 32, fig. 1) and ultra-violet light using Panatomic-X film (Pl. 33, figs. 1–3; Pl. 34, figs. 1–2), and under alcohol with white light using Ilford N5/31 film (Pl. 30, fig. 2; Pl. 31, fig. 2; Pl. 32, fig. 2). The white light was produced by four lamps, two intensity lamps, and a directional spot lamp. Alcohol was used because some details of the specimen which are obscure or invisible when dry become obvious when wet. The ultra-violet light was produced from a directional lamp. The lamp was inclined to the horizontal specimen at about 60°, the specimen was then tilted through about 10° towards the lamp until maximum reflectivity, as observed down a focusing tube, was obtained. Focusing was undertaken in ordinary light.

Camera-lucida drawings are placed beside or with Plates 30, 31, 33, and 34 as a guide to their interpretation.

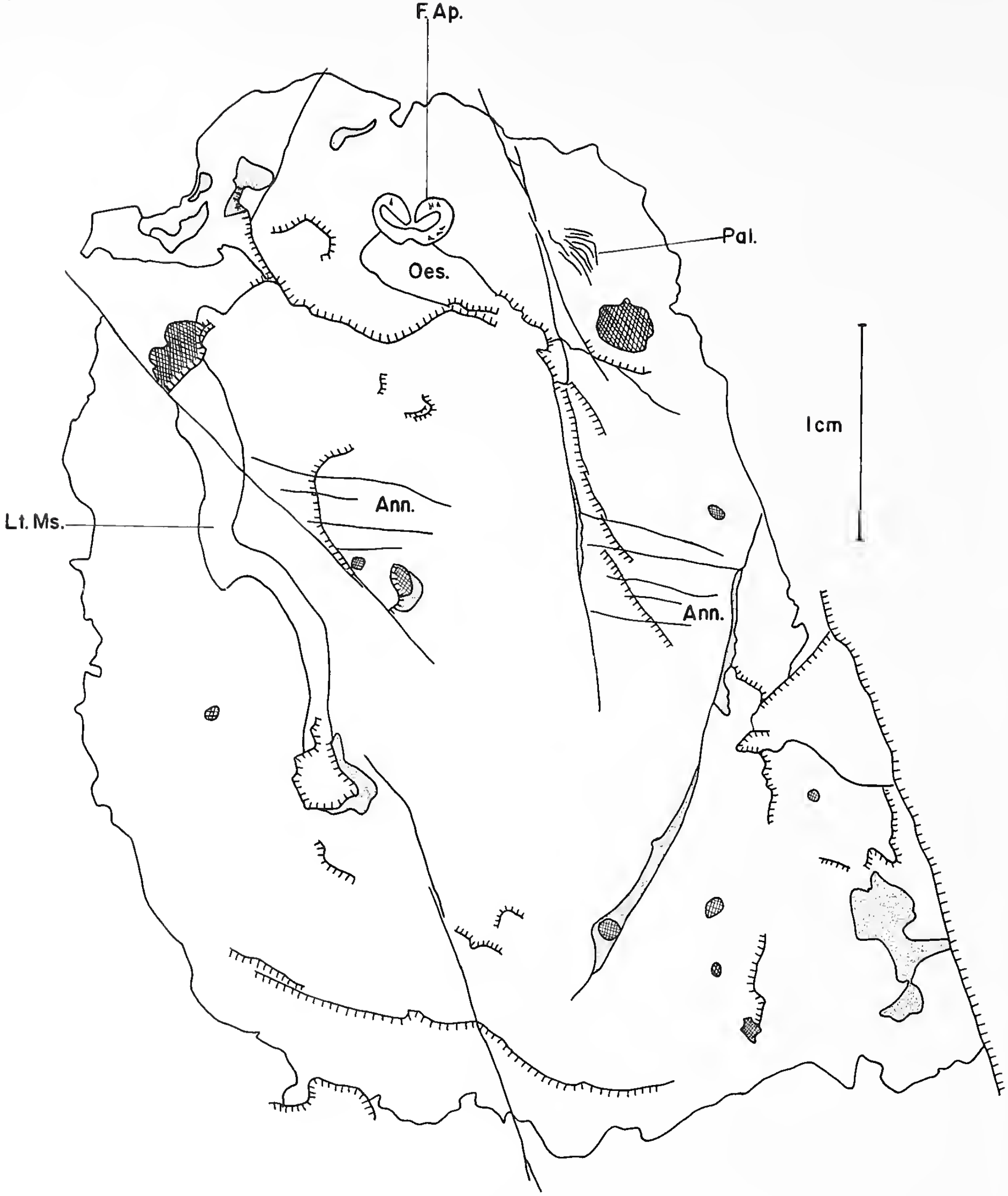
Preservation and morphology

The surface of the shale is slightly weathered, and there are scattered browny-yellow spots of iron oxide that presumably derive from iron pyrites. The specimen itself is poorly preserved and has been disrupted by compaction scarps. The fossil consists of a thin film that is darker than the surrounding rock. The anterior apparatus and palps are preserved in slight relief. Partial decay prior to fossilization is probably responsible for the poorly defined margins of the specimen. The processes of decay may have been instrumental in allowing details of internal anatomy to become more easily visible (Pls. 30–32). In a later paper evidence derived from study of the priapulid *Ottoia prolifica* will be presented to show that varying degrees of decay resulted in different anatomical features becoming visible.

The probable appearance of *Odontogriphus omalus* in life is shown in text-fig. 3. The anterior end was not clearly delimited from the trunk as a definite head. The body was about 6 cm long and some two and a half times longer than broad. It appears to have been dorso-ventrally compressed. The composition of the body may have been predominantly gelatinous. Although the edges of the body are indistinctly preserved the general outline is clear. The anterior margin was slightly convex, and the smooth lateral margins were more or less parallel to one another. The posterior part of the specimen is twisted so as to lie at right angles to the anterior part, and behind the locus of twisting the width of the body decreases (Pl. 31; text-fig. 2). This decrease is believed to be an original feature. The twisting of the body may have occurred when gentle currents disturbed the specimen on the sea-floor. If the twisting had taken place during transport in a mudflow the two parts of the body might be expected to be separated by a layer of sediment, as has been noted by the author in twisted specimens of the laterally flattened worm *Pikaia gracilens* Walcott, 1911*b*. The distortion was presumably purely passive rather than a death reaction.

The fine transverse lines (*c*. 1 mm apart) crossing part of the specimen are taken to represent annulations rather than true segmentation (Pl. 30, fig. 2; Pl. 31, fig. 2; Pl. 32, fig. 2; text-figs. 1, 2) as discussed below. Although only about ten of the annuli are preserved there is no reason to doubt that they originally occurred over most of the body. They may have totalled about fifty. The only other external details that have been preserved are the anterior apparatus and the palps (Pls. 30–34; text-figs. 1, 2, and 4).

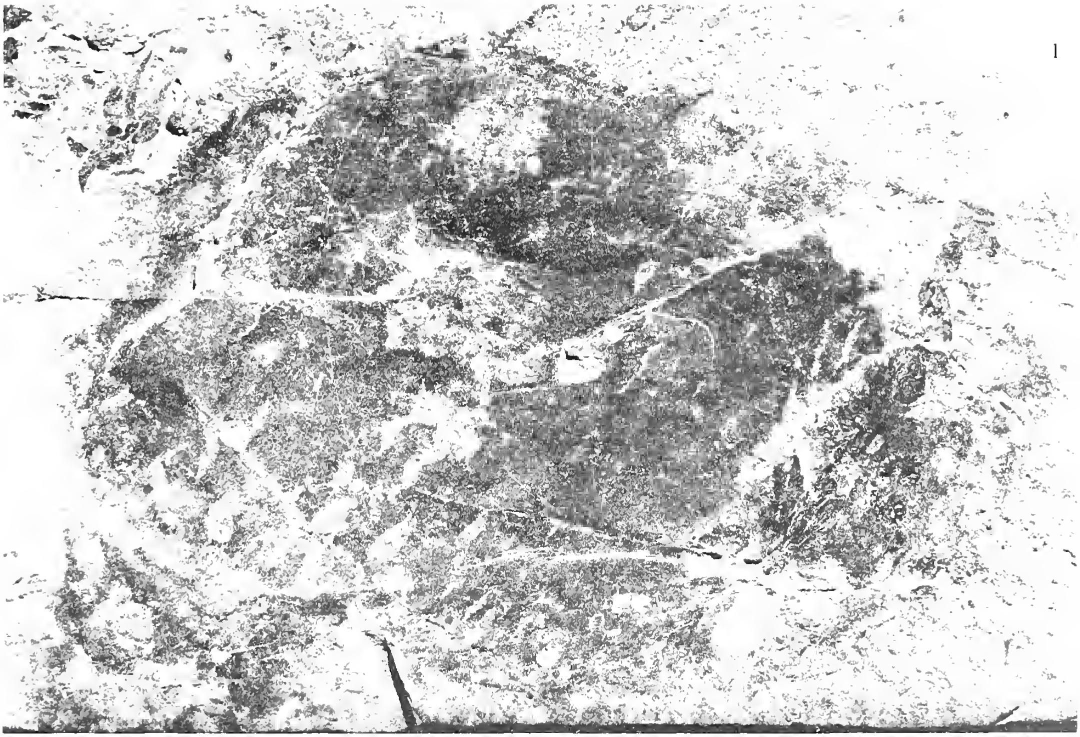
The anterior apparatus is taken to be a feeding apparatus. Its suitability for this purpose is plain. The apparatus is situated at the end of a broad medial tube that was almost certainly the gut, judging by its similarity to the fossilized gut of other specimens from the Burgess Shale. The apparatus is bilaterally symmetrical and is sited on the midline of the animal. It most probably lay on the ventral surface of the body. Its form is that of a shallow U opening forward with the closure gently flexed anteriorward, and the ends tending to coil inward (Pls. 33, 34; text-fig. 4). The ends do not appear to fuse. The apparatus as now preserved is about 4 mm across and 2 mm long. It carries the remains of about twenty-five ‘teeth’ (Pl. 33; text-fig. 4) (the reasons



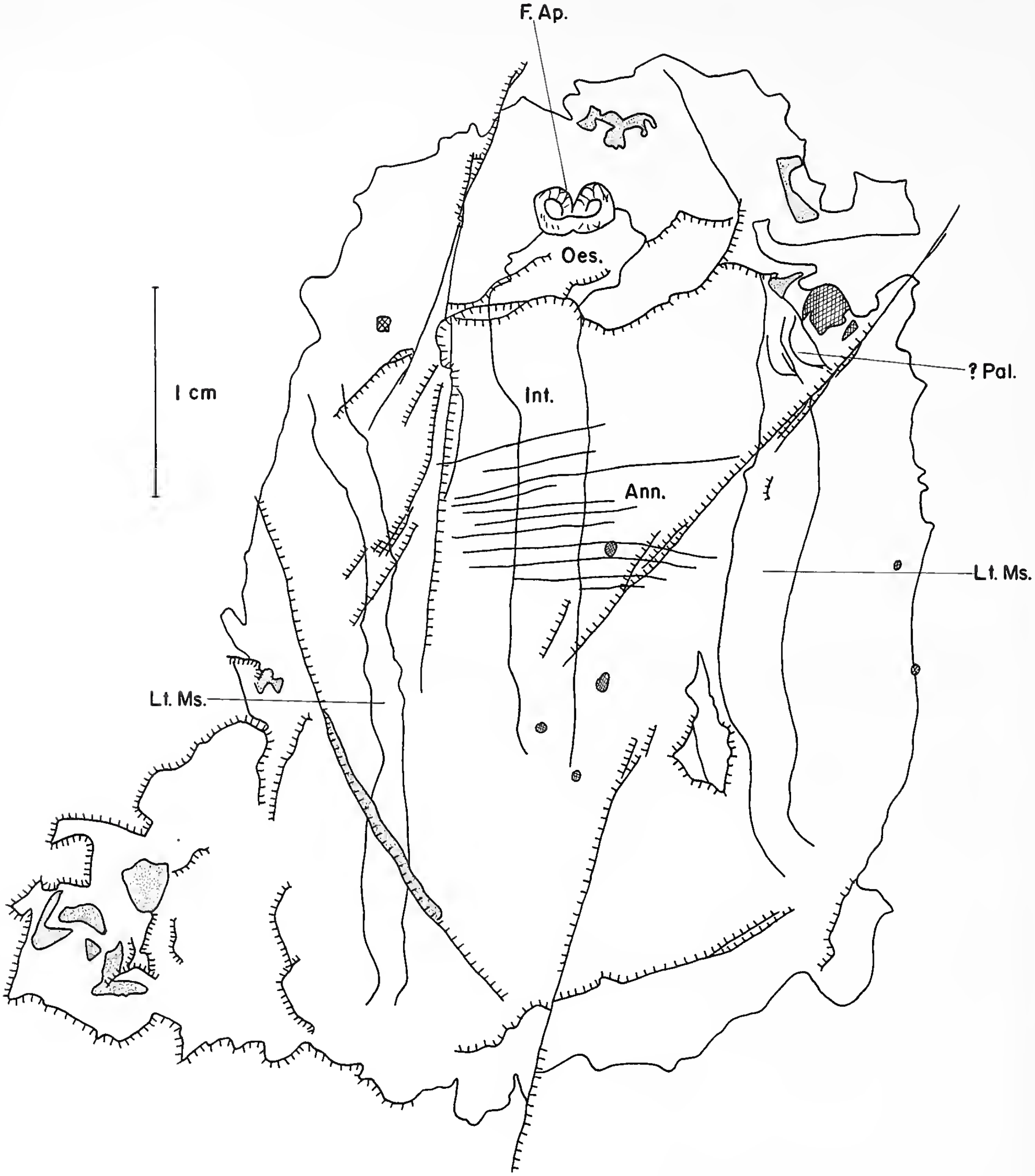
TEXT-FIG. 1. Camera-lucida drawing of the part (USNM 196169). With the exception of labelled features, all the lines crossing the specimen are the products of compression. Lines with hachures indicate definite breaks in slope, the hachures being directed downslope. Stippled areas represent rock, cross-hatched areas those parts rich in iron oxide and coloured browny-yellow. Ann., Annulations; F. Ap., Feeding apparatus; Lt. Ms., Lateral muscle; Oes., Oesophagus; Pal., Palp.

EXPLANATION OF PLATE 30

Figs. 1–2. *Odontogriphus omalus* gen. et sp. nov. Part of holotype (USNM 196169). Whole specimen in ordinary light from south-west, ×2·8. 1, in air. 2, under alcohol.



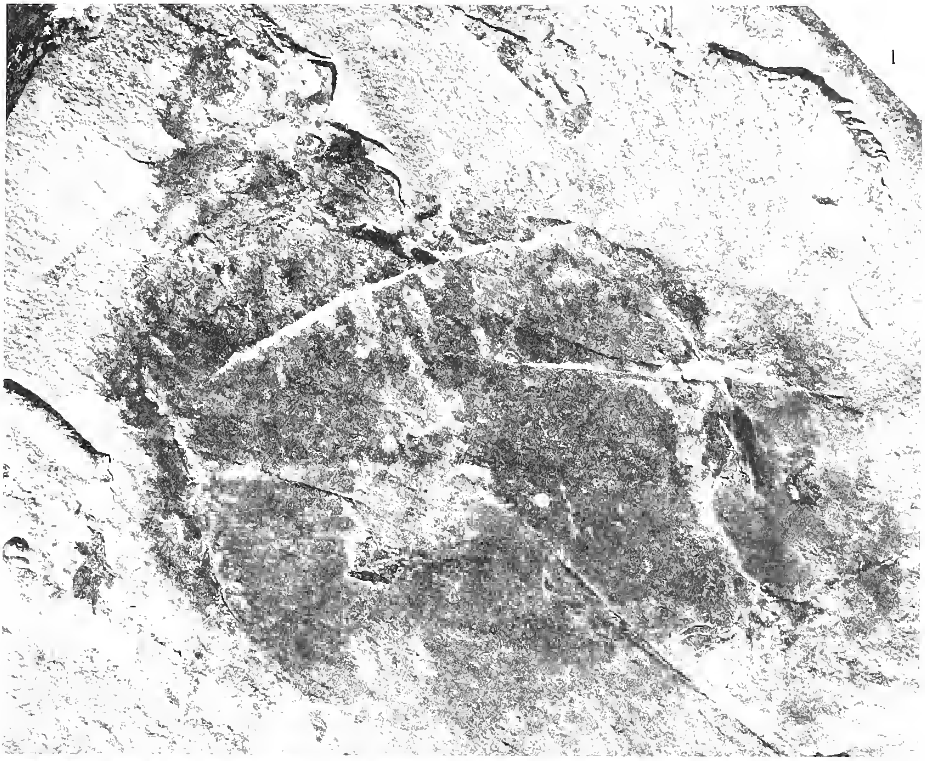
CONWAY MORRIS, Cambrian lophophorate

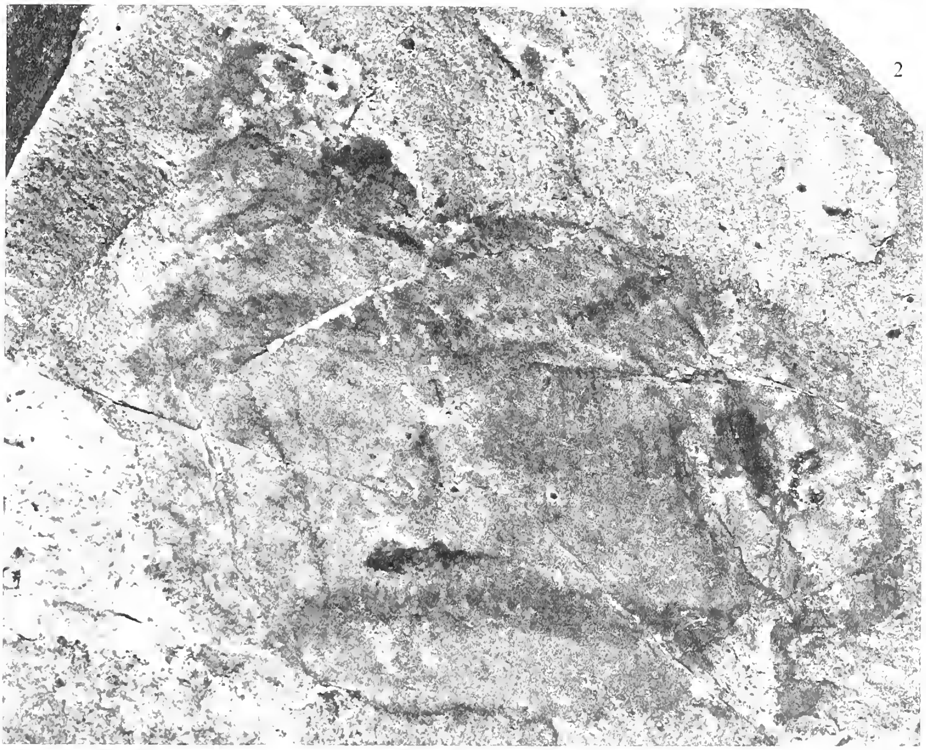


TEXT-FIG. 2. Camera-lucida drawing of the counterpart (USNM 196169a). See explanatory notes for text-fig. 1. Int., Intestine.

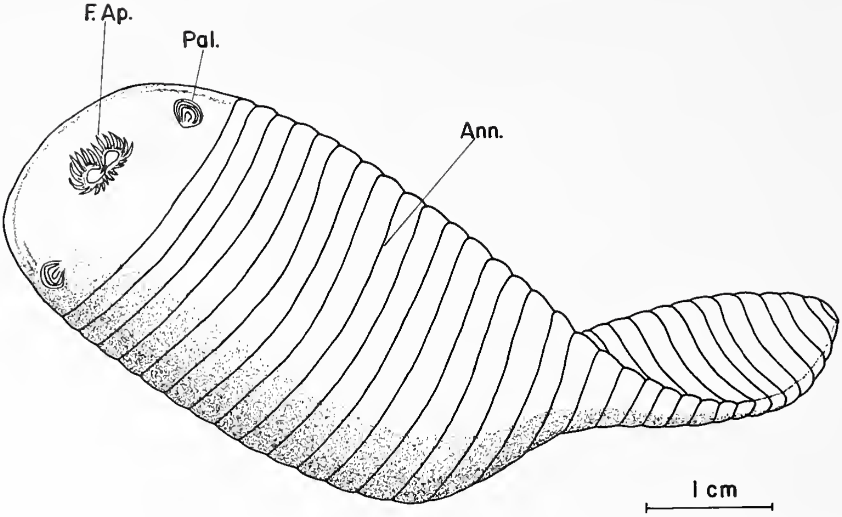
EXPLANATION OF PLATE 31

Figs. 1–2. *Odontogriphus omalus* gen. et sp. nov. Counterpart of holotype (USNM 196169a). Whole specimen in ordinary light from north-north-east, ×2·1. 1, in air. 2, under alcohol.





CONWAY MORRIS, Cambrian lophophorate



TEXT-FIG. 3. Reconstruction of appearance of *Odontogriphus omalus* gen. et sp. nov. in life. Anterior shows the ventral surface carrying the feeding apparatus and palps. The narrower posterior part of the trunk is twisted so as to reveal the dorsal surface. Abbreviations as for text-fig. 1.

for considering them to be other than true biting or rasping teeth are given below). With one possible exception the 'teeth' themselves have been leached away during diagenesis leaving external moulds or flattened, reflectively preserved impressions. Leaching of calcareous components of other members of the fauna, such as articulate brachiopods, has been noted by Whittington (1971). One 'tooth' (D in text-figs. 4A and 8), however, is preserved as a structureless whitish mineral. This mineral may be the original material, or a degraded remnant of the 'tooth', or a subsequent infilling of the mould. Three 'teeth' in the posterior part of the apparatus, including the 'tooth' preserved in the white mineral, are preserved sufficiently well and in such an orientation for much of their detail to be apparent (text-fig. 4B). They consist of a distinct expanded base (or root) that gives rise to a long thin cusp, the cusp itself being about six times longer than wide. These 'teeth' are about 0·4 mm long. The cusp is between 0·02 and 0·07 mm (maximum) wide and the expanded base is about 0·2 mm broad. In outline the basal edge is convex upward beneath the cusp, which suggests that the basal surface of each mould is domed upwards. This implies that there was a shallow central cavity, but it does not appear to have any pre-sedimentary filling. Furthermore, in the 'tooth' nearest the midline the expanded base is almost equally

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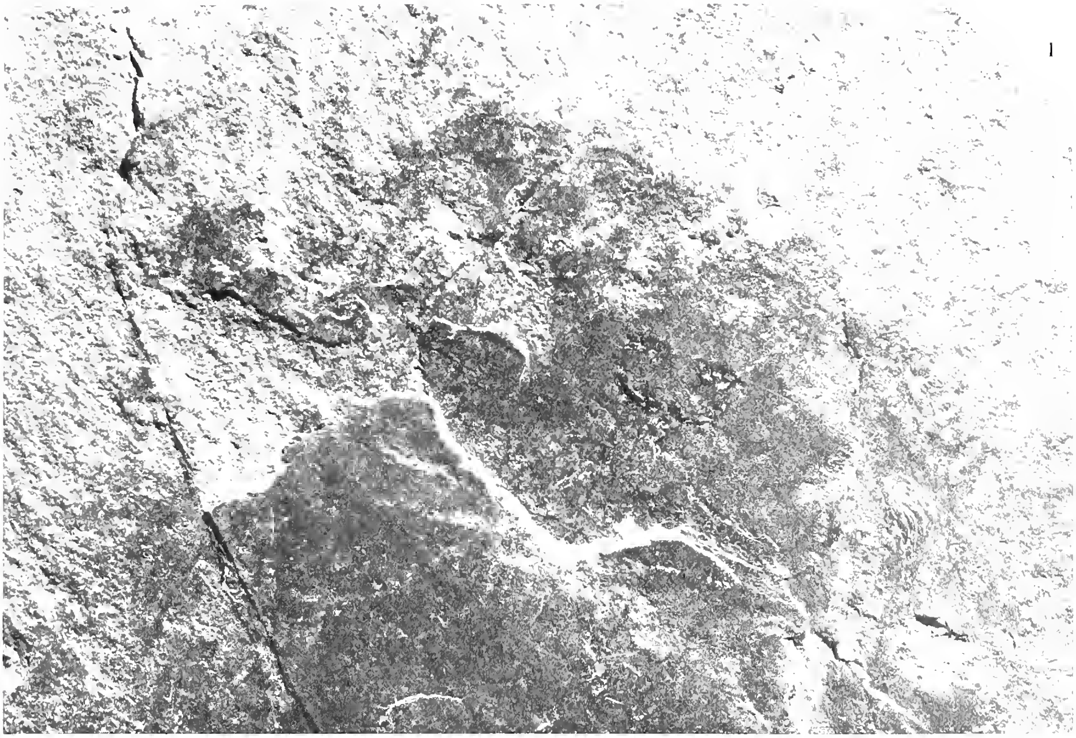
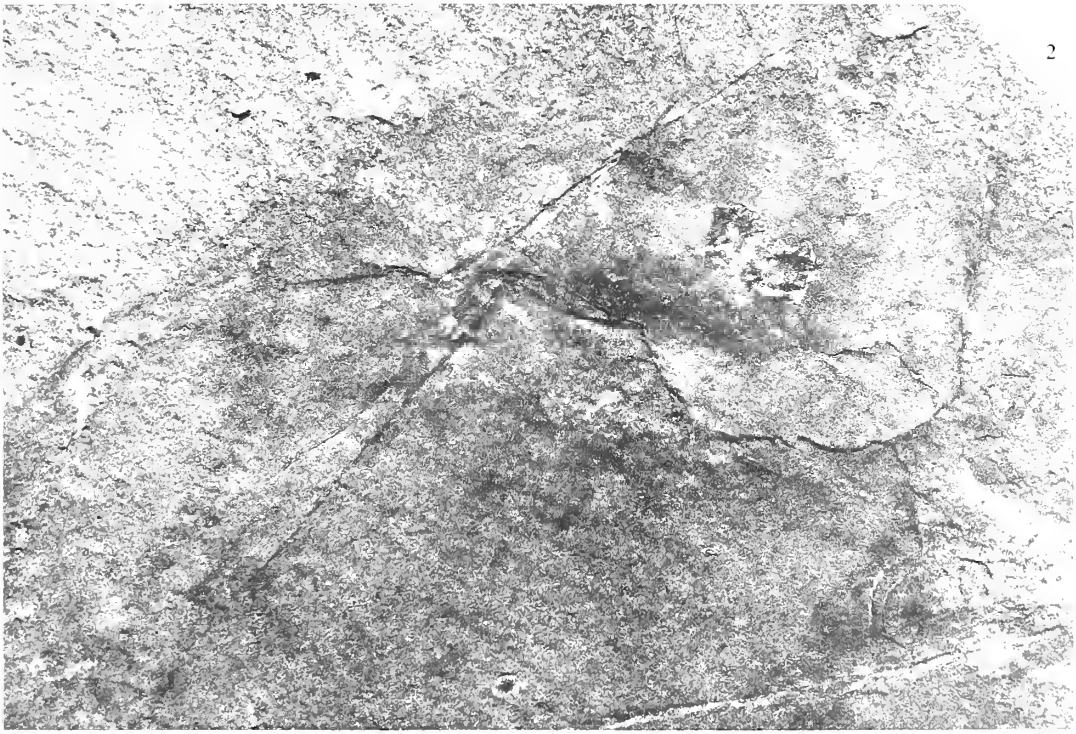
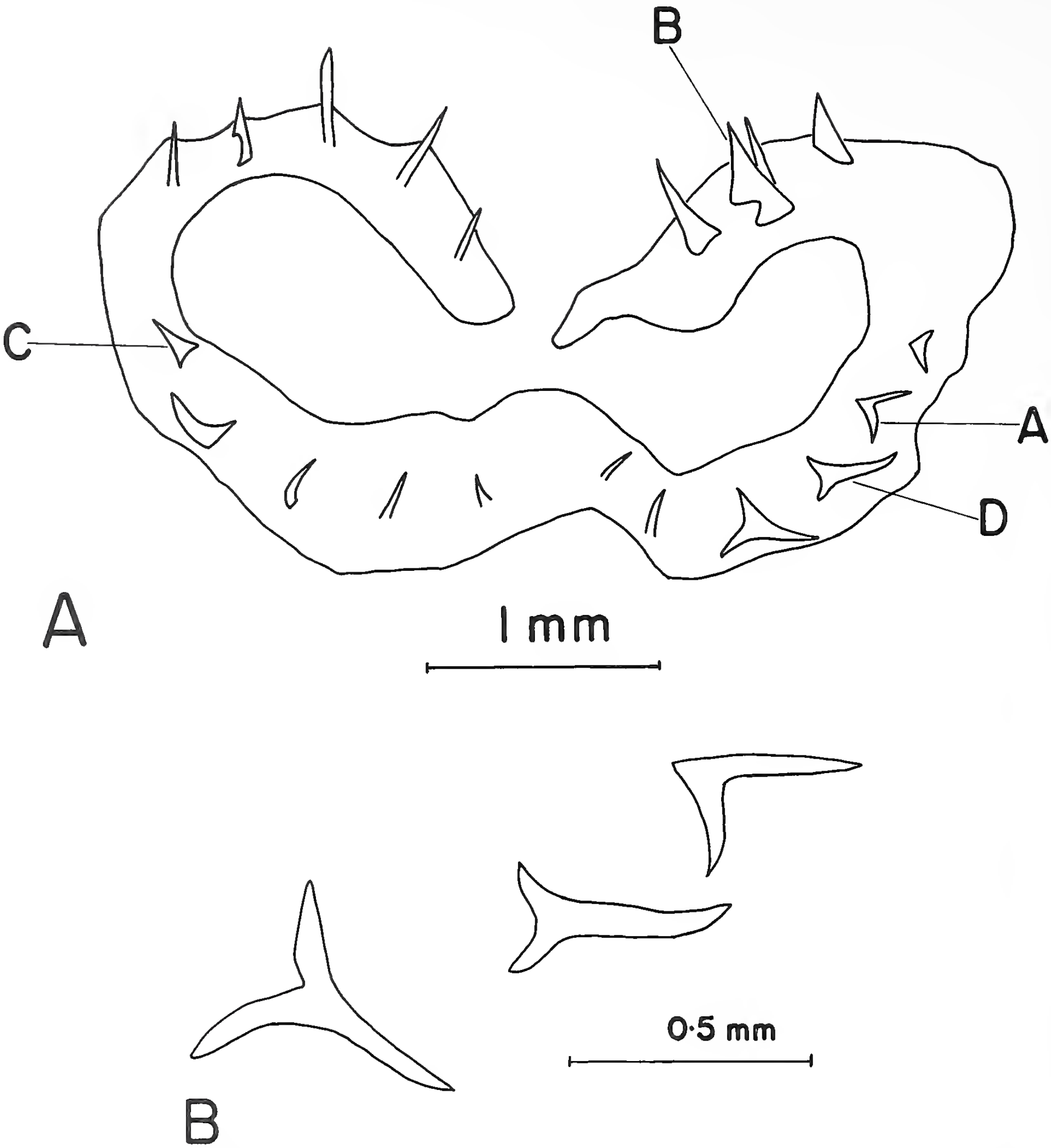
EXPLANATION OF PLATE 32

Figs. 1–2. *Odontogriphus omalus* gen. et sp. nov. Enlargement of anterior end in ordinary light from north-east. 1, part of holotype (USNM 196169) in air, ×4·7. 2, counterpart of holotype (USNM 196169a) under alcohol, ×4·2.





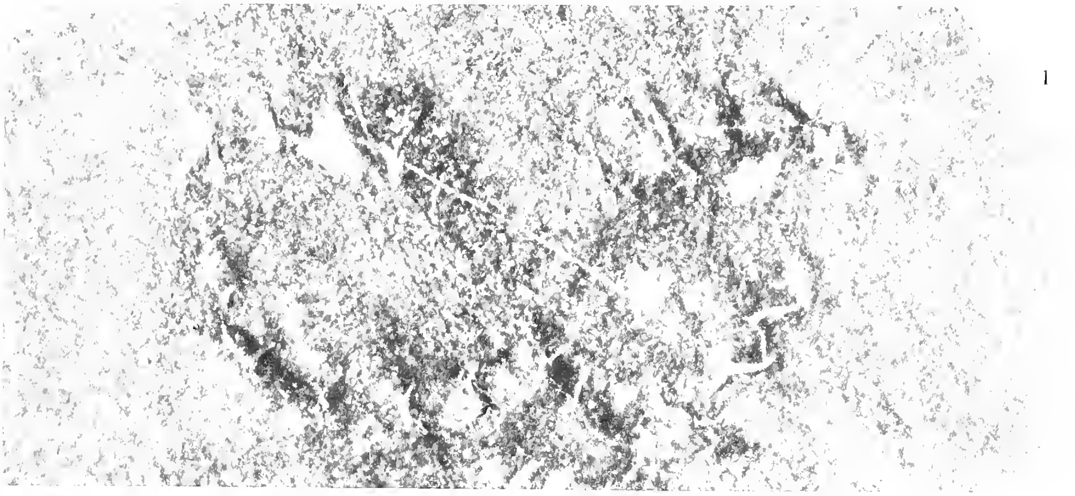
CONWAY MORRIS, Cambrian lophophorate



TEXT-FIG. 4. A, camera-lucida drawing of the feeding apparatus of the part (USNM 196169). The letters A–D refer to four well-preserved 'teeth', see text-fig. 8. Anterior of apparatus towards the top of page. B, enlargement of three 'teeth' including A and D from the posterior loop of the apparatus to show possible symmetry transition. Midline on left-hand edge.

EXPLANATION OF PLATE 33

Figs. 1–3. *Odontogriphus omalus* gen. et sp. nov. Enlargement of the feeding apparatus of part of holotype (USNM 196169) in ultraviolet light, ×23·5. 1, light from east. 2, light from north-east. 3, light from south-west.



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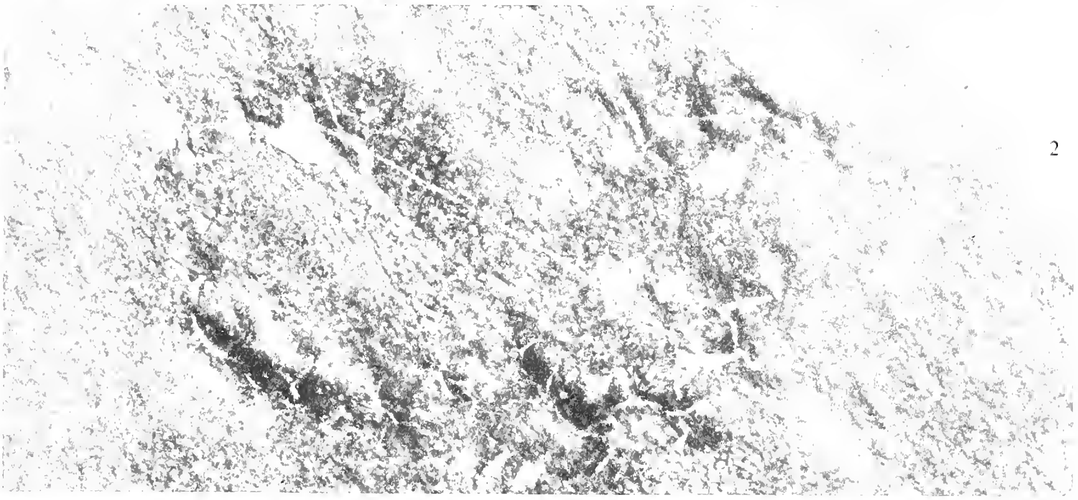

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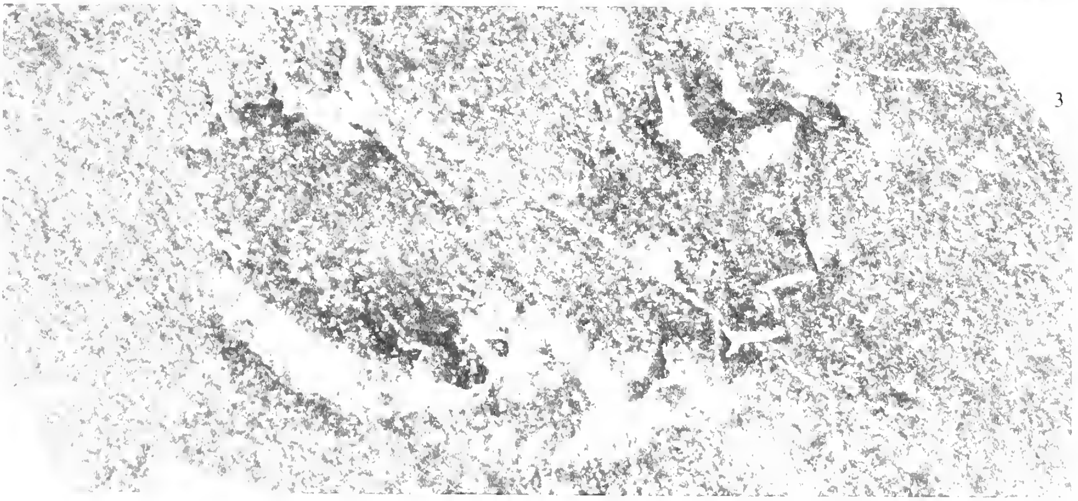

3

CONWAY MORRIS, Cambrian lophophorate

well developed on either side of the cusp, whereas the two more abaxial ones appear to have the base on the inner side of the apparatus reduced in size. Other 'teeth' within the anterior loop of the apparatus appear as simple cones (text-fig. 4A). Two explanations of the variations in shape are possible:

1. The suppression of one side of the expanded base may represent an original symmetry transition—from almost symmetrical 'teeth' beside the midline to increasingly asymmetrical 'teeth' abaxially.
2. The 'teeth' may lie at slightly different angles to the bedding plane so that different sections through one 'tooth' type are now seen. The 'teeth' may not originally have had the same orientation along the length of the apparatus, and it is possible that they were rotated by a regular amount along the length of each loop of the apparatus. Alternatively, during decay the 'teeth' may have fallen at different angles to the bedding plane.

These two explanations are not mutually exclusive. The author prefers to consider that the 'teeth' within the anterior and posterior parts of the apparatus represent two aspects, at right angles to one another, of one 'tooth' type. The aspects were determined by the way the 'teeth' came to lie with respect to the loop. Thus, the 'teeth' in the posterior part of the apparatus lie parallel to the loop, whereas the 'teeth' in the anterior are at right angles to the loop. It is not possible to determine whether the apparent symmetry transition of the three well-preserved 'teeth' is an original feature. The exact degree of variation among the 'teeth' cannot be established, but it is evident that they were in all cases relatively simple cones.

In the counterpart evidence of 'teeth' is almost entirely lacking. This is probably because the specimen split more or less through the middle, with the more ventral part of the apparatus coming away with the counterpart. The apparatus of the counterpart does, however, bear regularly spaced (four per 1 cm) depressed areas (0·4 mm across) (Pl. 34) which are faintly visible as raised areas in the part (Pl. 33, fig. 1). They are believed to represent decayed, and possibly retracted, remains of tentacles. The retracted tentacles of some entoprocts (Atkins 1932, fig. 3), for instance, are similar in appearance. The exact position and extent of the mouth cannot be determined, but it was almost certainly located within the loops of the apparatus. The probable appearance of the feeding apparatus in life is shown in text-fig. 5.

Slightly posterior to the apparatus and near one side of the ventral surface there is a palp (3 mm long, 2 mm across) consisting of about six layers that apparently were originally plates of tissue disposed parallel to the surface and fused adaxially in a common base. The layer closest to the surface of the animal is the largest and the size of the layers decreases away from the body (Pl. 30; Pl. 32, fig. 1; text-fig. 1). It is possible that this palp was formed by rock compression, but its regularity suggests that it is some genuine feature of the anatomy. On the counterpart the palp is much

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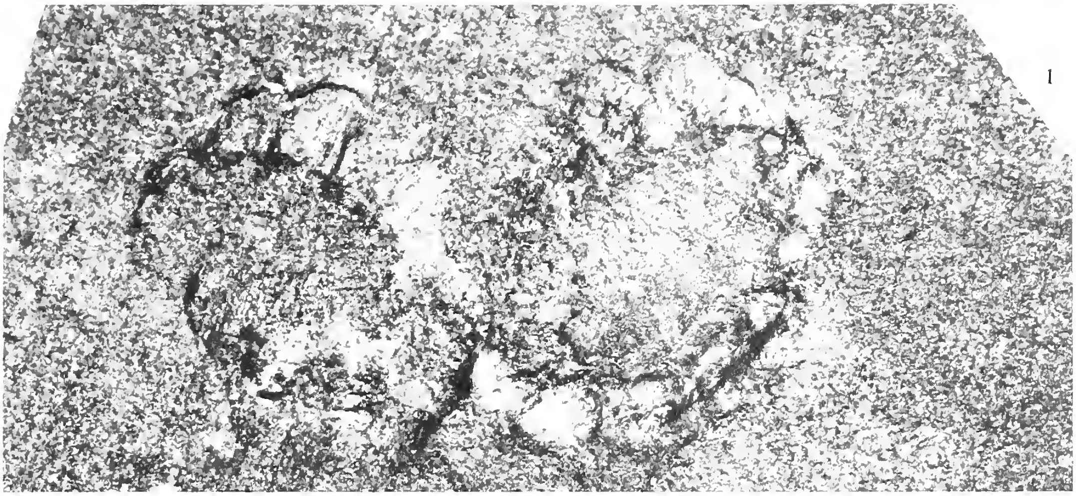
EXPLANATION OF PLATE 34

Figs. 1–3. *Odontogriphus omalus* gen. et sp. nov. 1, 2, enlargement of the feeding apparatus of counterpart of holotype (USNM 196169a) in ultraviolet light, × 21·8. 1, light from north. 2, light from east. 3, camera-lucida drawing of above figures. Lines with hachures indicate definite breaks in slope, the hachures being directed downslope. Tt., rounded areas which probably represent tentacles.

PLATE 34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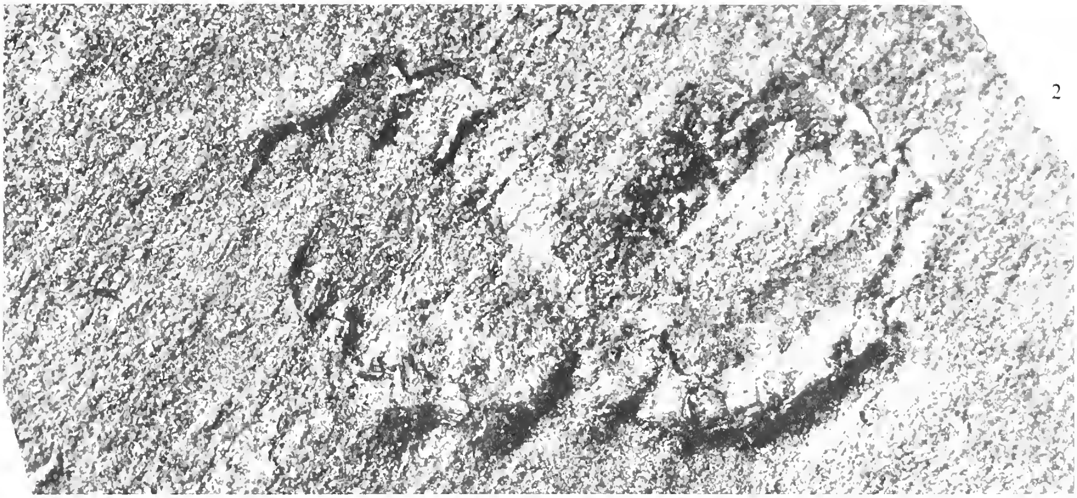
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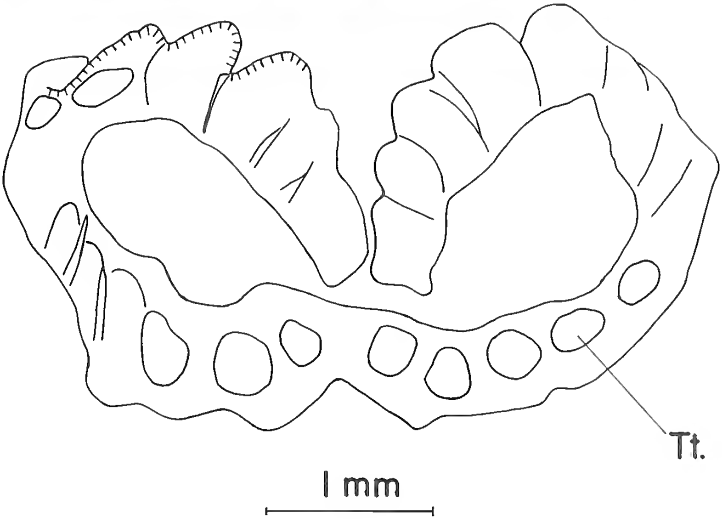
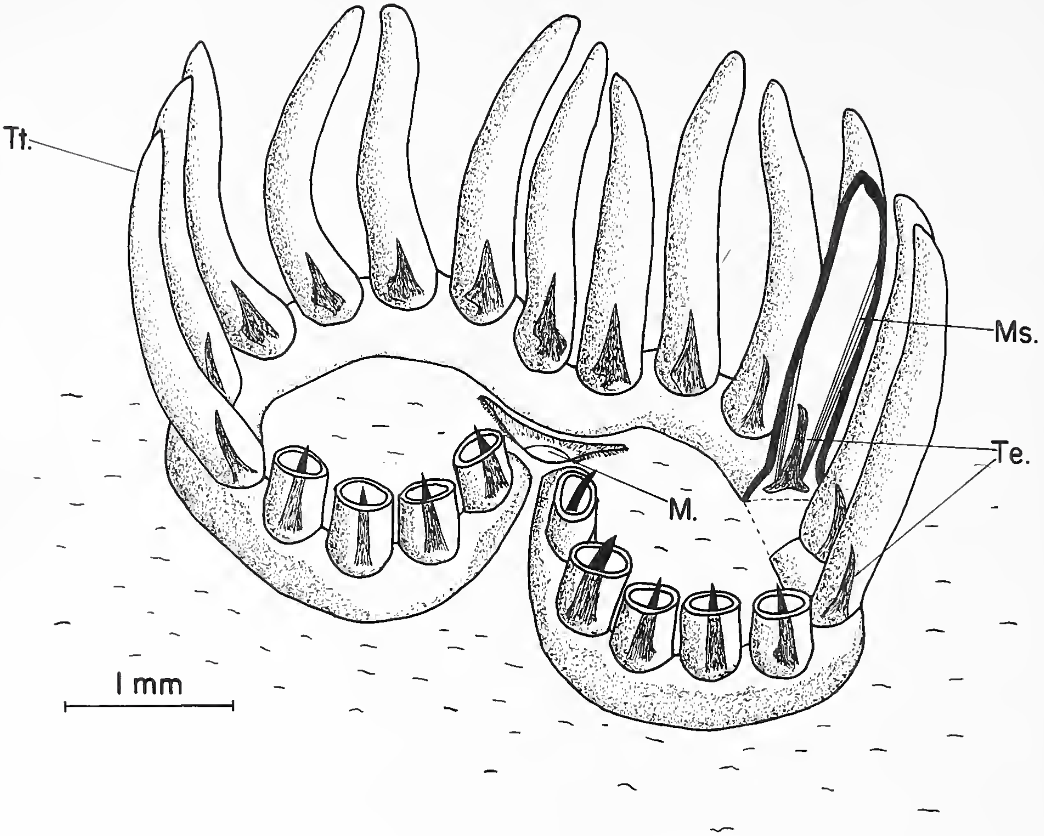


CONWAY MORRIS, Cambrian lophophorate



TEXT-FIG. 5. Reconstruction of appearance of the feeding apparatus in life from the anterior. The anterior tentacles have been cut away near the base to avoid obscuring detail. A section of the loop including part of a tentacle has also been removed to reveal hypothetical internal details. M., Mouth; Ms., Muscle; Te., 'Teeth'; Tt., Tentacles. The exact position of the mouth and presence of muscles is hypothetical.

less well preserved and its identification remains uncertain (Pl. 31; Pl. 32, fig. 2; text-fig. 2). When the counterpart is combined, by reversal, with the part the specimen can be seen to have possessed a pair of ventro-lateral palps.

A few details only of the internal anatomy have survived. Immediately behind the feeding apparatus there is a swollen, slightly reflective area which continued as a narrow parallel sided band (3 mm across) running down the middle of the trunk. After about 2·5 cm it fades away posteriorly (Pl. 31, fig. 2; text-fig. 2). These features are interpreted as an oesophagus and a narrower intestine. The anus is assumed to have been terminal. There is no evidence that the gut was recurved. No gut contents have been noted. Along each side of the body there is a dark longitudinal band (1·5–3 mm wide) which probably represents lateral longitudinal muscles (Pl. 30, fig. 2; Pl. 31, fig. 2; text-figs. 1, 2). The annulations could reflect underlying circular muscles.

DISCUSSION

Mode of life

The animal appears to have been dorso-ventrally compressed. This, together with its possibly gelatinous composition, suggests that it was pelagic. Its extreme rarity within the Burgess Shale indicates that, being pelagic, its chances of becoming involved in the mudflows that went to form the Phyllopod bed were slight. The absence of fins and the poor streamlining imply that it floated or else swam only sluggishly. Alternating contractions of the lateral longitudinal muscles on each side could have produced a wave-like rippling of the body edges that would have aided locomotion. The body may have been capable of more general undulations as well. A modern analogue of this animal might be seen in the bathypelagic nemertines (see e.g. Coe 1926, 1935, 1945, 1954). They have been found at depths of 200 m, but generally occupy depths of about 1000 m. Their distribution tends to be stratified with particular species occurring in greatest numbers at definite depths. The population density is, however, very low. Their dorso-ventrally compressed bodies are mostly composed of firm gelatinous tissues and many of the species are similar in shape to *O. omalus*. The majority of species appear to float or swim poorly by slow undulations.

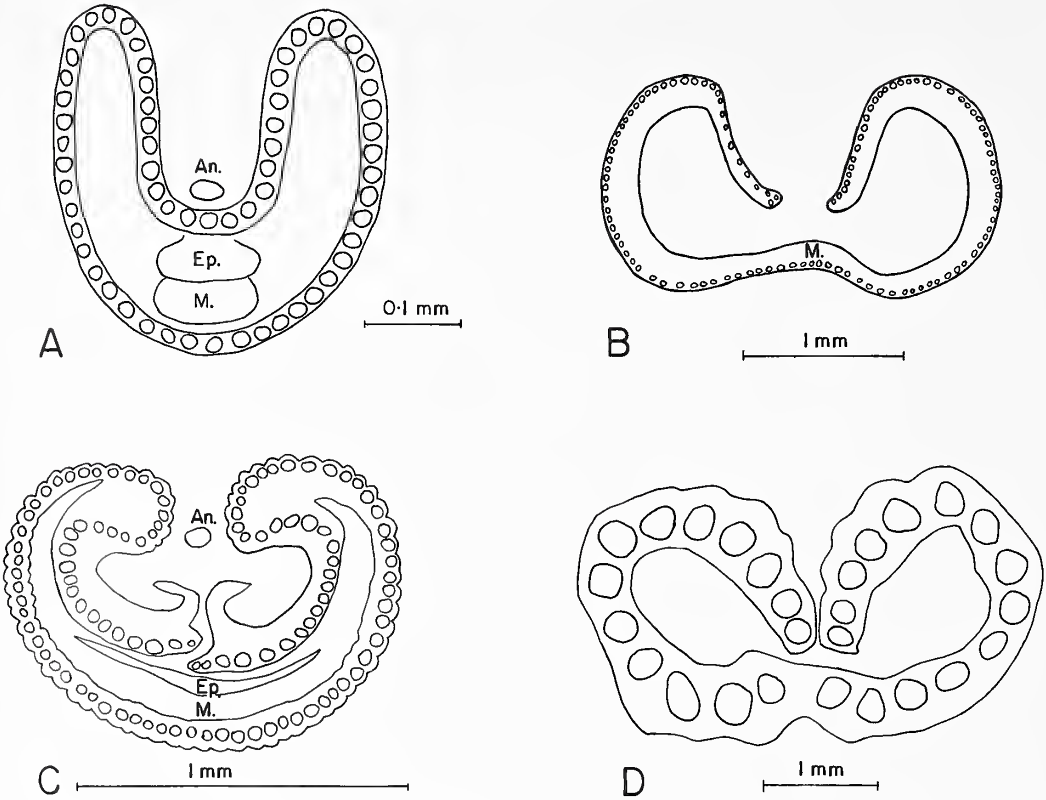
It is unlikely that the apparatus was used as a rasping tool. In the molluscan radula the teeth are uniformly directed posteriad and are sited on an elongate pad of tissue. The shape of the apparatus, on the other hand, is such that some of the 'teeth' could not have effectively contributed to rasping activities. Furthermore, the slenderness of the 'teeth' with their consequent fragility makes their use in rasping or biting improbable. The apparatus instead appears to have affinities with the tentacular lophophore of the lophophorates. It is suggested that the apparatus bore food-gathering tentacles that were supported internally by the 'teeth' (text-fig. 5). *O. omalus* probably fed in a similar manner to the modern lophophorates. Water currents may have been promoted by cilia that covered the tentacles. The looped shape of the apparatus could have induced water vortices which channelled food towards the mouth.

The palps are rather small to have acted as efficient respiratory organs, and they were probably sensory. Respiration may have been carried out over the entire body, with gases diffusing through all parts of the body wall.

Zoological affinities

The relationships of *O. omalus* are not easy to determine. It can be excluded from most groups of worms on various grounds. The flattened nature of the body does not compel reference to the platyhelminthes (the flat worms) or to pelagic nemertines, because none of the representatives of these phyla has a comparable feeding apparatus. The apparatus is not a radula, so that there is no indication of any affinity with the Mollusca. Comparisons with annelid jaws or with armed mouths of other invertebrate phyla such as the Gnathostomulida (Riedl 1969) achieve equally little.

The shape of the apparatus is, however, very much reminiscent of the tentacular lophophore that characterizes the lophophorate phyla, i.e. the Brachiopoda, Phoronida, and Ectoprocta or Bryozoa (text-fig. 6A–C). A valuable general account of the

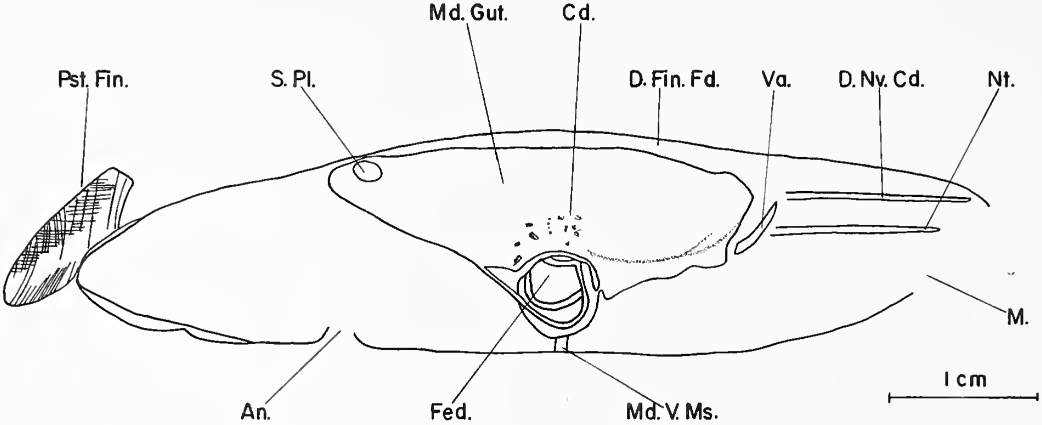


TEXT-FIG. 6. Comparison of the lophophores of A, phylactolaemate ectoproct (from Harmer 1896, fig. 236.3). B, articulate brachiopod (adapted from Atkins 1958, fig. 9). C, phoronid worm (from Benham 1889, pl. 10, fig. 12). D, the feeding apparatus of *Odontogriphus omalus* gen. et sp. nov. Circles indicate tentacles. An., Anus; Ep., Epistome; M., Mouth. The likely position of the mouth in D is given in text-fig. 5.

Lophophorata is given by Hyman (1959), and much of the following information is derived from her work. These three phyla differ in many respects, but the lophophore common to all remains a remarkably constant structure. The phoronids and ectoprocts have a recurved gut with the anus opening close to, but outside, the lophophore. The gut of the articulate brachiopods is blind, and that of the inarticulates is generally recurved. The phoronids are sessile worms occupying chitinous tubes, whereas the brachiopods and ectoprocts have well-developed calcareous, phosphatic, or chitinous exoskeletons. The lophophore in these animals is composed of one or two ridges bearing rows of tentacles and it partly or entirely encircles the mouth. The mouth is usually partially covered by a flap of tissue, the epistome. The lophophore of the phoronids and phylactolaemate (freshwater) ectoprocts consists of two parallel ridges bearing tentacles, with the mouth located between the two ridges. In the brachiopods and gymnolaemate (marine) ectoprocts there is a single ridge, which is basically circular and embraces the mouth. The ciliated tentacles are used to trap food. The primitive shape of the lophophore was probably that of a horseshoe, although circular and crescentic shapes are also known (Hyman 1959). The lophophores of some of the modern phoronids, brachiopods, and phylactolaemate ectoprocts are sometimes modified by inturning or even multiple coiling of the ends. The single-ridged apparatus of *O. omalus* compares well (text-fig. 6D), suggesting that this organ is indeed a lophophore. Further, there is evidence that it may have borne short tentacles. Apart from the presence of the lophophore, however, *O. omalus* has no significant feature in common with the known lophophorates. An important difference between the modern lophophore and that of *O. omalus* is that no present-day examples have internal 'teeth' for support of the tentacles. The entire lophophore in the articulate brachiopods is, however, often supported by a brachidium and the lophophoral tentacles or filaments of some of the terebratulids (brachiopods) carry numerous minute perforated calcareous plates (Steinich 1963*a*, *b*; Rowell and Rundle 1967; Williams 1968). Such cases are rare, and as the tentacles of recent lophophorates are almost without exception supported by coelomic fluid, it is pertinent to inquire why supporting 'teeth', if that was their function, were necessary in *O. omalus*. One possible explanation is that the coelom was greatly reduced or even obliterated by the dorsal-ventral compression and perhaps by ingrowth of occluding gelatinous tissue as well. The 'teeth' could have supplemented or even replaced fluid support of the tentacles. The body cavity of the terebratulids, however, does not appear to be reduced and their lophophoral spicules must impart some rigidity to tentacles. The exact function of these spicules is obscure however. They may represent a response to excess $CaCO_3$ secretion. Little direct comparison of the 'teeth' and spicules is possible, because the latter are much more numerous, asymmetric in distribution, more or less random in shape, and are also usually to be found in the mantle tissues (A. Williams pers. comm.). In contrast, each tentacle of *O. omalus* appears to have been supported by a single 'tooth' and the distal ends of the tentacles may have been flexible. An additional function of the 'teeth' might have been to act as insertion points for tentacular muscles (text-fig. 5).

In this context the views of Lindström (1973, 1974) on the nature of the conodont animal or conodontophorid are of particular relevance. Conodonts are minute teeth-like objects whose maximum dimension is usually of the order of a few millimetres. They are composed principally of calcium phosphate. Their range runs from late Precambrian to Triassic, and possibly to the Cretaceous (Diebel 1956; Müller and Mosher 1971). Cambrian conodonts are mostly simple cones, and such forms continue to occur through most of the Palaeozoic. Many more highly diversified conodonts appear in post-Cambrian rocks. The soft parts that held the conodonts have not been definitely identified, and their affinities have been the subject of much speculation. Lindström (1973) has argued in favour of relating the conodontophorid to the lophophorates, but he did not suggest firm reference to any of the three extant phyla. He proposed that the conodonts supported tentacles which formed a lophophoral ring around the mouth. This hypothesis of Lindström's is only one of several advanced in recent decades, although it is the most cogently argued. Reviews of the problem of affinity are available in Rhodes (1954), Hass (*in* Moore 1962), Lindström (1964), and Globensky (1970). The affinities are often thought to lie with the annelids or chordates, especially fish. Further recent hypotheses have suggested an alliance with the chaetognaths (Rietschel 1973), the conulariids (Bischoff 1973), the gnathostomulids (Ochietti and Cailleux 1969; Rodgers 1969), and the aschelminthes, in particular the kinorhynchs and rotifers (Hofker 1974). None of these proposals is especially appealing and some workers have suggested that the conodonts belong to a new group. The only generally accepted features of the conodontophorid are that it was 'soft-bodied, bilaterally symmetrical, marine and pelagic' (Hass 1962, p. W33). Whether it was entirely pelagic is not completely certain. Distribution of Ordovician conodonts suggest that, with the exception of simple cones, they may have belonged to nekto-benthonic animals. The Cambrian conoidal conodonts, however, probably derive from pelagic conodontophorids (Barnes and Fåhraeus 1975).

There is one record of supposed fossilized soft parts of a conodont animal. This is the soft-bodied chordate-like material, containing conodonts, discovered in the Namurian of Montana (Melton and Scott 1973; Scott 1973) (text-fig. 7). The few specimens found are not very well preserved, but the soft-part morphology appears to be almost invariable among these specimens. The slight differences that exist can be attributed to preservational factors. They have, however, been divided into three genera on the basis of the enclosed conodonts. The over-all shape was elongate. The mouth appears to have been sub-terminal, and although the connection cannot be traced it must have joined the expanded midgut, the deltaenteron, where the conodonts are found. The anus appears to have been ventral, and there was a large finned post-anal tail. A complex organ, the ferrodiscus, was located beneath the deltaenteron and may have been involved with circulatory and respiratory activities. These authors also presented evidence for an anterior notostyle and dorsal nerve cord. Lindström (1974) discussed these findings and suggested that there must be some doubt as to whether the animals were conodontophorids rather than conodontophages. In these fossils the conodont assemblages are variable in composition, although hindeodellids are always the commonest (Table 1). Also, the conodonts are rather scattered within each specimen. This suggests that the conodonts were ingested,



TEXT-FIG. 7. Slightly simplified interpretation of the chordate-like fossils (conodontochordates) from the Bear Gulch Limestone, Montana (from Scott 1973, fig. 6). An., Anus; Cd., Conodonts; D. Fin. Fd., Dorsal fin fold; D. Nv. Cd., Dorsal nerve cord; Fed., Ferrodiscus; M., Mouth; Md. Gut., Midgut (deltaenteron); Md. V. Ms., Midventral muscle; Nt., Notostyle?; Pst. Fin., Posterior fin; S. Pl., Sieve plate?; Va., Valve to midgut?

TABLE 1. Distribution of various conodont elements within the conodontochordate specimens from the Bear Gulch Limestone (Namurian), Montana. Each vertical column refers to one specimen. Data from Melton and Scott (1973) and Scott (1973).

Element type	*Lewistownella lowerae*	*Lochriea wellsi*			*Scottognathus elizabethi*	
Hindeodellids	12	10	9+	12	10+	12
Ozarkodinids	2	1	0	0	3	3
Synprioniodinids	0	0	0	0	2	0
Neoprionoidinids	3	3	1	3	0	0
Platforms	4	3	0	1	4	3

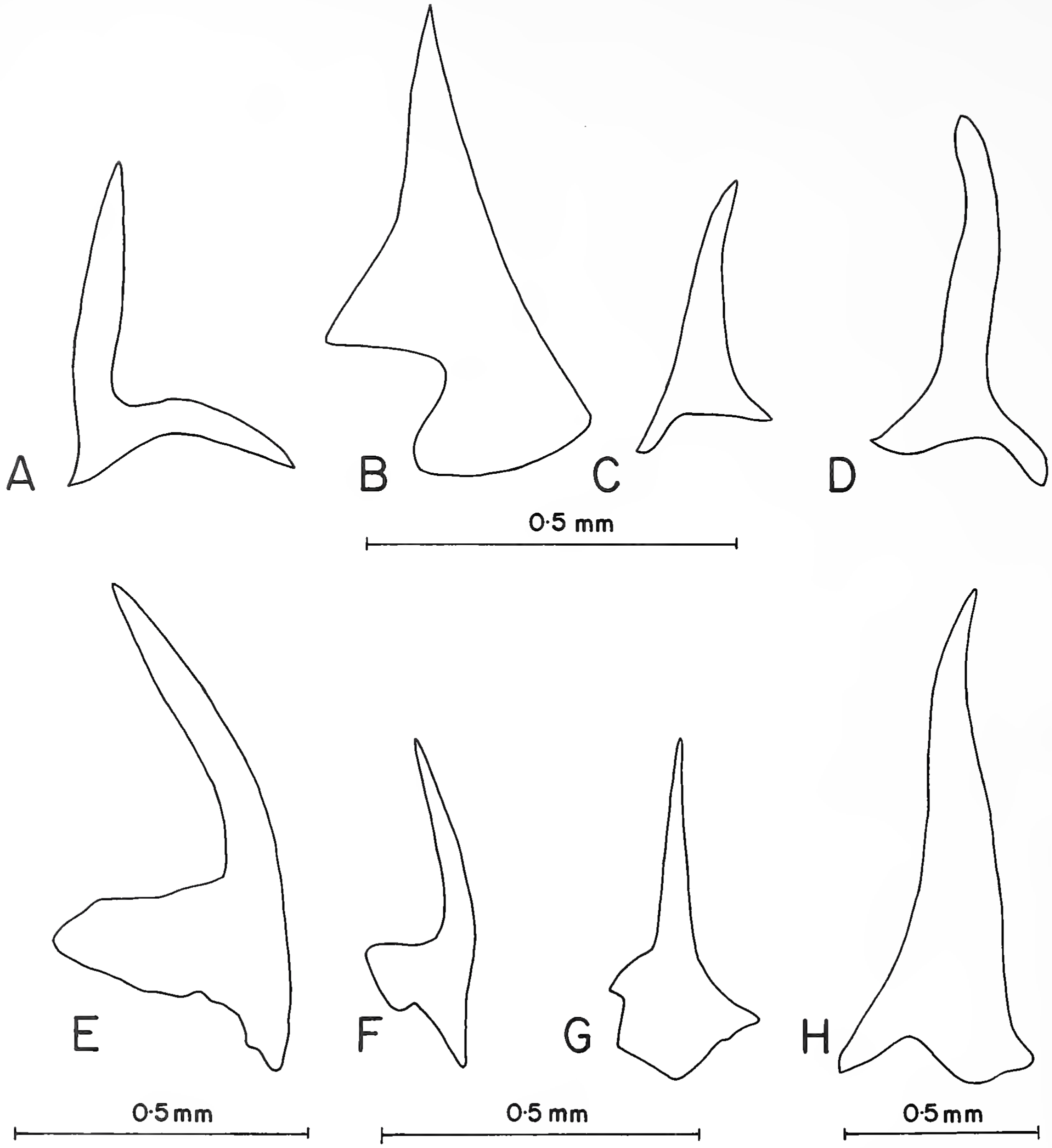
because in other cases, in which there are no associated soft parts, assemblages with a more regular and coherent arrangement have been identified.

It may be suggested that *O. omalus* is an example of a conodont animal. This conclusion is based on two principal lines of reasoning.

1. The 'teeth' of the feeding apparatus have a strong resemblance to some Cambrian conodonts (text-fig. 8). The earliest conodont-like fossils are found in late Precambrian and early Cambrian rocks (Poulsen 1966; Missarzhevsky 1973; Landing 1974; Matthews and Missarzhevsky 1975). Reviews of the record of Cambrian (especially upper Cambrian) conodonts have been produced by Müller (1971) and Barnes *et al.* (1973). Certain other Cambrian phosphatic microfossils, called paraconodonts, are perhaps related to the true conodonts (Müller 1971; Müller and Nogami 1971). Although some of the Cambrian conodonts have bizarre shapes, e.g. *Westergaardodina*, the majority are more or less conical. Conoidal conodonts continue to occur into the Devonian and perhaps the Carboniferous (Ellison 1972). The great predominance of cones in the Cambrian strongly suggests that the apparatuses of most of the Cambrian conodontophorids bore only this type of conodont. Such monoconoidal apparatuses probably continued into the Ordovician (Sweet and Bergström 1972) and perhaps to the Devonian (Klapper and Philip 1972), although some of the conoidal forms found in the Devonian may only have been one constituent of an apparatus (type 4 apparatus in Klapper and Philip 1971) that contained other, more complex, elements. Most examples of conical conodonts in natural assemblages are as fused clusters (Barnes 1967; Pollock 1969), but Miller and Rushton (1973) have noted a bilaterally symmetrical assemblage of approximately twelve elements from the Cambrian of Warwickshire.

Given the state of preservation of the 'teeth' of *O. omalus*, it is impossible to obtain information on the full shape and extent of the basal cavity or on the presence of carinae or striations, i.e. on any of the characters by which the majority of the genera and species of Cambrian conodonts are defined. Hence, no exact comparisons with known forms can be suggested. There is, nevertheless, a clear general resemblance to distacodontids such as *Scandodus* Lindström, 1955, emend. Lindström, 1971 (text-fig. 8), and the two are in much the same order of size.

It is not possible to establish whether the 'teeth' resemble paraconodonts rather than conodonts because no histological information is obtainable. The leaching of the 'teeth', with resultant moulds, raises questions concerning their composition. It may be noted that cases are known in which conodonts, originally phosphatic,



TEXT-FIG. 8. Comparison between 'teeth' of the feeding apparatus (A–D, for location in apparatus see text-fig. 4A) and three specimens (E, F and G, H) in various aspects of the upper Cambrian conodont *Scandodus tortilis* Müller (from Müller 1959, pl. 12, figs. 10, 7a and b, and 8 respectively).

have been leached during diagenesis, leaving either moulds or else a white or brown degradation product (Matthews 1969*a*, *b*; Matthews *et al.* 1972). It may be significant that these cases noted by Matthews are from dark siliceous shale (Lower Carboniferous) that is comparable to the Phyllopod bed in sedimentary character. Considering possible vulnerability during diagenesis, it is worth remembering that the ratio of organic material to phosphate is believed to have been relatively high in Cambrian conodonts (Clark and Miller 1969; Müller and Nogami 1971). The presence of appreciable amounts of organic matter may have helped to promote destructive leaching of the 'teeth' of *O. omalus*.

2. A second reason for regarding *O. omalus* as a possible conodontophorid lies in the fact that the lophophore apparatus shows considerable agreement with the hypothetical conodont apparatus proposed by Lindström (1974). The appearance of Lindström's hypothetical animal does not, however, tally closely with *O. omalus*. In the animal he envisaged almost the entire surface is occupied by the lophophore. In criticism of this proposal it may be pointed out that it would be unusual for an animal to devote a major part of its outer surface to the activities of feeding. Further, Lindström's animal is too large to have floated (judging by the behaviour of similarly sized aquatic creatures today) and some sort of post-lophophoral body to be used in propulsion is presumably necessary. There are few animals which manage to make use of one organ system for locomotion and simultaneously for feeding. Although the free-living crinoid, *Antedon*, for instance, employs its flexible arms in both feeding and locomotion, it feeds only when stationary (Hyman 1955). It is, therefore, unlikely that the tentacles of Lindström's animal served, at any one time, for both feeding and swimming. There is also a difference in size between *O. omalus* (length 6 cm) and Lindström's hypothetical animal (length 1 cm). Lindström (1974) came to this value by supposing that the 7 cm long conodontochordates described by Melton and Scott would have been unable to ingest animals of any size larger than about 1 cm. However, some animals are known to be capable of eating prey of their own size.

These apparent differences of size may not be very significant. It is quite possible that post-Cambrian conodontophorids were smaller than late Precambrian and Cambrian forms in which the conodonts could on occasion be relatively large (see lengths of the order of 2 mm reported in Poulsen 1966). The number of conodonts in the apparatus may also have varied, but the 'teeth' total about twenty-five in *O. omalus* and it may be significant that the largest number of conodonts recorded in an assemblage is twenty-two (Rhodes 1962). Presumably, with increasing diversity of conodont form in post-Cambrian time, increasingly complex configurations of the lophophore arose. The lophophore as portrayed by Lindström (1974), for example, is much more elaborate than noted in *O. omalus*. It is likely that this diversification of the conodonts led to looped and branched lophophores, in a way analagous to the development in increasingly complex lophophores in many brachiopods (Hyman 1959; Rudwick 1970, fig. 79), thus greatly increasing the surface area available for feeding.

The systematic position of O. omalus

In attempting to establish the systematic position of *O. omalus* the following points should be borne in mind:

1. In his 1973 paper Lindström regarded the conodontophorid as being distantly related to other lophophorates, in particular the brachiopods. He drew attention to a similar development of pitted microstructure in conodonts and in the inarticulate calcareous brachiopod *Crania*. He suggested that the polygonal pattern, known to be characteristic of muscle insertion areas in *Crania* (Williams and Wright 1970),

had the same significance in conodonts. It has been suggested above that the 'teeth' too may have had muscles inserted on them (text-fig. 5). It may be significant, moreover, that *Crania* is regarded as one of the most primitive brachiopods and could have retained features lost in other more advanced members of this phylum (Hyman 1959).

2. Although other groups such as the endoprocts and sipunculids have a lophophore-like organ, the author prefers to regard the lophophore of *O. omalus* as indicating an affinity with the superphylum Lophophorata. This new form cannot readily be accommodated in any of the three constituent phyla, and nor is it easy to indicate to which of the three *O. omalus* is most closely related. It may be marginally closer to the vermiform phoronids, which Hyman (1959, p. 603) noted 'seem to come nearer a presumed type plan' and are believed to have some 'characteristics of the common lophophorate ancestor' (Hyman 1959, p. 604) than to the brachiopods or ectoprocts. None of the modern lophophorates have multiple segmentation such as the annelids possess. If *O. omalus* is genuinely related to the lophophorates, its annulations are most probably superficial rather than a reflection of true segmentation.

3. If *O. omalus* is taken to belong within the Lophophorata brief speculation on the ancestral form of this superphylum is relevant. The stock that produced *O. omalus* is unlikely to be ancestral to the other lophophorates, because it has specialized features such as the lophophoral 'teeth'. One would presume also that the common ancestor must have existed before the appearance of the late Precambrian conodonts. *O. omalus* might, nevertheless, have primitive features now obscured or lost in the other lophophorates. Hyman (1959, p. 229) stated that 'Presumably the ancestral type of Lophophorata was a vermiform animal with body regionated into head, lophophoral region, and trunk, but the head appears to have undergone practically complete degeneration, probably as a consequence of a sessile or sedentary mode of life'. It is tempting to suggest that the area anterior to the lophophore represents the ancestral head, retained in this animal because of its active way of life. It is impossible to determine whether the pre-lophophoral area was the protosome containing the protocoel, being separated from the lophophoral region by a distinct septum. The protocoel is considered by some authors (e.g. Hyman 1959) to be absent from the modern lophophorates, but more recent evidence suggests that it exists as the greatly reduced cavity within the epistome (e.g. Ryland 1970; Zimmer *in* Larwood 1973). It is very probable that the feeding apparatus of *O. omalus* was ventral rather than dorsal. If the pre-lophophoral area became so reduced that the feeding apparatus was located at the anterior end, the apparatus would then have the orientation the lophophore has in modern forms, with the convex side ventral to the mouth. The straight gut with apparently terminal anus of *O. omalus* may also be primitive. Hyman (1959, p. 230) noted that the 'median posterior position of the anus is seen only in the brachiopod genus *Crania*, where it may be primitive'. The recurved gut of the ectoprocts and phoronids may be an adaptation to a sedentary way of life. The shape of the apparatus deviates only slightly from the primitive horseshoe shape of the basic lophophore (Hyman 1959).

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EARLY CAMBRIAN INTERGROWTHS OF ARCHAEOCYATHIDS, *RENALCIS*, AND PSEUDOSTROMATOLITES FROM SOUTH AUSTRALIA

by M. D. BRASIER

ABSTRACT. Lower Cambrian life and death assemblages of late Atdabanian–Botomian age are described from the Wilkawillina Limestone of South Australia. The biota, sedimentology, and diagenesis are analysed to reveal an ecological succession in which archaeocyathids grew one upon another, and were overgrown by the problematic organism *Renalcis*, with the cavities later filled by pseudostromatolites (coniatolites). A low-latitude, littoral habitat is inferred. Examination of the unusually well-preserved archaeocyathid intergrowths suggests that their individuality was strongly expressed, with an organization at least of sponge or coelenterate grade. Settlement and growth of archaeocyathid juveniles was apparently controlled by substrate type, space, and light. The life assemblage provides one of the oldest examples of competitive interreactions between animals.

THIS paper investigates some early Cambrian algal-archaeocyathid–*Renalcis* associations collected from the Wilkawillina Limestone of South Australia. During the early Cambrian these associations flourished widely and our present understanding of them owes much to the work of Russian geologists such as I. T. Zhuravleva and A. Yu. Rozanov (see Hill 1972). Nevertheless, for a proper understanding of both palaeoecology and biological affinities, more needs to be known about the growth relationships, microstructure, and diagenesis of the problematica involved and it is hoped that this study will stimulate discussion in these areas.

Archaeocyathids are generally associated with areas of carbonate sedimentation, whether as extensive blankets or as localized bioherms and biostromes within clastic strata. Although often quoted as the 'reef-builders' of the early Cambrian, they usually played a role subordinate to the lime-secreting and trapping algae with which they are commonly associated (Hill 1972). Few of these 'reefs' show any signs of wave-resistant structures or other attributes associated with that term and so the word 'bioherm' is preferred (Debrenne 1959). The Cambrian algae have been reviewed by Johnson (1966). The mound-building types are of uncertain affinities but are usually placed amongst either the Schizophyta or the Rhodophyta and include *Epiphyton* (possibly an arborescent red alga), *Girvanella* (possibly a tubular blue-green alga), and *Renalcis*. The algal affinities of *Renalcis* have been questioned by Riding and Brasier (1975) who suggest that it may have been an early form of calcareous foraminifer. Algal-archaeocyathid bioherms of the *Epiphyton–Renalcis* dominated type have been recorded from the early Cambrian of Siberia, southern Europe, Morocco, North America, Antarctica, and Australia (Debrenne 1959, 1964; Zhuravleva 1960, 1972, 1974; Hill 1972; Balsam 1973). The extensive archaeocyathid developments of South Australia have received little attention as yet but may also be largely algal (Professor D. Hill, written communication); they include *Epiphyton* and *Girvanella* (Walter 1967).

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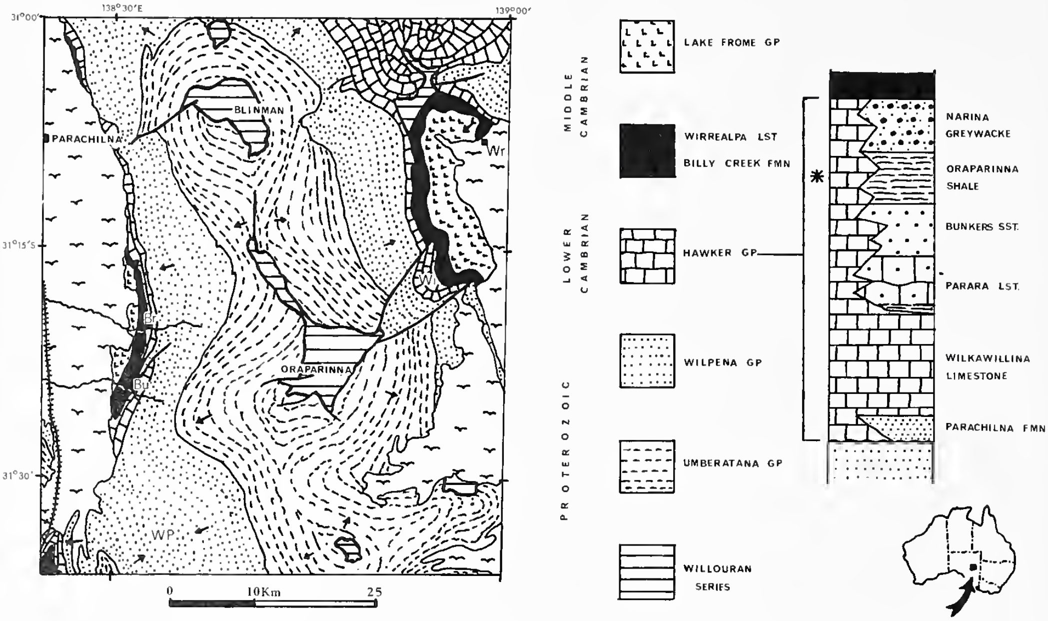
In contrast, algal-archaeocyathid communities of stromatolitic type do not appear to have been so extensive. Debrenne (1964) has figured stromatolitic laminae enclosing possibly contemporaneous archaeocyathid cups from Morocco. More examples of 'stromatolite'-*Renalcis*-archaeocyathid intergrowths have been collected from the early Cambrian Wilkawillina Limestone of the Flinders Range, South Australia and are examined in this paper (text-fig. 1).



TEXT-FIG. 1. Geological map of the Parachilna to Wirrealpa area, Flinders Range, with detail of the Hawker Group succession. Br = Brachina Gorge; Bu = Bunyeroo Gorge; Wi = Wilkawillina Gorge; Wr = Wirrealpa; WP = Wilpena Pound. Based on Dalgarno and Johnson (1966).

Stratigraphy and palaeogeography

Much has yet to be learnt about the stratigraphic and palaeogeographic setting of the Cambrian in the Flinders Ranges. Goldring and Curnow (1967) and Wade (1970) have studied the conditions of deposition of the preceding Pound Quartzite which contains the soft-bodied Ediacara fauna. At that time the area formed part of a marine bay, with a north-south trending shoreline to the west, sheltered from the open sea to the east by shoals, possibly controlled by diapiric movements. The overlying sandstones and shales of the Uratanna and Parachilna Formations represent considerable transgressions over bioturbated, and in places much-eroded, surfaces. The trace fossils *Rusophycus* and *Curvolithus* are found in the Uratanna and *Diplocraterion*, *Plagiogmus*, and *Phycodes* in the Parachilna Formation. These may be taken to indicate a Cambrian age for the transgression (Glaessner 1969; Wade 1970; Webby 1973) and represent shallow-water conditions within the *Cruziana* facies.

On the western side of the anticlines about the Oraparinna and Blinman diapirs, at Brachina and Bunyeroo Gorge, the Parachilna Formation is succeeded conformably by the Wilkawillina Limestone, but on the eastern side it appears to rest directly on the Pound Quartzite (Walter 1967). There, the Wilkawillina Limestone comprises a biohermal bank rich in archaeocyathids, which passes up into the more argillaceous Parara Limestone with fewer archaeocyathids, the Bunkers Sandstone with none, the Oraparinna Shale with some, and the Narina Greywacke with none. This succession is absent in the Brachina–Parachilna area to the west, where a continuation of the Wilkawillina Limestone forms a lateral, biohermal equivalent (Dalgarno 1964; Walter 1967). This lower Cambrian Hawker Group was succeeded by the middle Cambrian sandstones and tuffaceous shales of the Billy Creek Formation and the nodular Wirrealpa Limestone, both lacking archaeocyathids.

The pseudostromatolitic-archaeocyathid limestones of Brachina Gorge described in this paper occur also at Bunyeroo Gorge, about 8 km to the south (Walter 1967, pl. 7, fig. 5*a*). Both probably formed in a relatively sheltered bay devoid of terrigenous influx and subject only to periodic episodes of current or wave action. The biohermal banks and shoals to the east may have resembled barrier reefs, behind which were deposited these lime muds and *Renalcis*-archaeocyathid biomicrites. Collections by Walter from near the top of the Wilkawillina Limestone at Bunyeroo Gorge included *Robustocyathus* sp., *Spirillicyathus pigmentum* Bedford and Bedford, *Coscinocyathus* sp., *Coscinoptycta* sp., *Flindersicyathus* sp., ?*Protopharetra*, and a colonial nochoroicyathid. These Walter considered to be of middle early Cambrian age, as were those from the Ajax Limestone to the north-west of the range (Debrenne 1969), both workers arriving at their conclusions by comparison with the well-known successions of Siberia. A variety of early Cambrian trilobites, brachiopods, molluscs, hyolithids, sponge spicules, and tubular organisms have also been recorded from the Wilkawillina Limestone (Daily 1956). This paper updates the faunal list, the following archaeocyathid genera being identified in collections from near the top of the Wilkawillina Limestone at Brachina Gorge (asterisks denote a new record for Australia): '*Aldanocyathus*'*, *Ajacicyathellus**, *Coscinoptycta*, *Dentatocyathus**, *Dokidocyathus*, *Erugatocythus*, ?*Flindersicyathus*, *Gordonicyathus*, *Graphoscyphia**, *Mennericyathus*, ?*Metaldetes*, *Polycoscinus*, *Pretiocyathus**, *Protopharetra*, *Robertocyathus**, and *Tumulocoscinus**. Other organisms include brachiopods, spicular structures, *Chancelloria* rosettes, and *Renalcis* sp. This fauna indicates a late Atdabanian (Kameshki) to early Lenian (Botomian) age for the Wilkawillina Limestone, as already suggested by Rozanov and Debrenne (1974).

Material and methods

The assemblages described below were collected as loose blocks from Brachina Gorge by Dr. R. Goldring during a study of the late Pre-Cambrian of the region. It was not possible at that time to determine their field relationships or precise stratigraphic horizon, but as this paper concentrates on organism interrelationships these problems are diminished. Two assemblages can be recognized in the collections: a life assemblage, or taphocoenosis and a death assemblage, or thanatocoenosis. The former consists of organisms preserved *in situ* (in growth position) and is represented by rock specimens Wilk. 1/1–1/30 and Wilk. 4 and 5, weighing altogether about $3\frac{1}{2}$ lb. The death assemblage comprises organisms which have suffered uprooting, transport, abrasion, and breakage, presumably the result of current or wave action. This is represented by rock specimens Wilk. 2/1–2/3, of similar weight to the former. The rock specimens are deposited in the Geology Department of Reading University, whilst the thin sections are in the author's collection. The relatively complex intergrowths in the rocks were revealed by serial sectioning both normal to and co-axial with the predominant direction of archaeocyathid growth. In the life assemblage these were made at measured intervals of about 10 mm. The slabs were then polished, etched, and stained ready for taking acetate peels using the technique of Davies and Till (1968). Additional thin sections were prepared for electron probe analysis and photography. Although archaeocyathids are invariably associated with bioherms or biostromes, their original life orientations have only rarely been preserved. The *in situ* life assemblage is therefore of particular interest because of the light it throws on the palaeobiology of these problematic organisms and their associates. Special issues relating to these problems are discussed in a later section.

DEATH ASSEMBLAGE

Biota. The bulk of the rock consists of broken and more-or-less prostrate adult archaeocyathids and less-damaged juvenile cups within a fibrous calcite matrix, interspersed with 'stromatolitic' structures of similar fabric (Pl. 35, figs. 1–5 and Pl. 37, figs. 1–2). The archaeocyathids include species (many undescribed) of the following genera: *Erugatocyathus*, *Mennericyathus*, *Gordonicyathus*, *Dokidocyathus*, *Dentatocyathus*, *Robertocyathus*, *Pretiocyathus*, *Tumulocoscinus*, *Graphoscyphia*, and *Protopharetra*. Their skeletal elements are usually preserved as dense, almost porcellaneous, microgranular calcite, often differentiated into lighter and dark layers. Some of this layering results from archaeocyathid 'secondary thickening' (see Hill 1972). The death assemblage also includes *Chancelloria* rosettes (Pl. 37, fig. 2) possibly part of the epidermal skeleton of an echinoderm (Goriansky 1973), together with indeterminate brachiopods, spicular structures, and other bioclastic debris. *Renalcis* concentrations occur rarely as overgrowths on the skeletal fragments or scattered through the matrix. All these broken skeletal elements indicate strong currents or turbulence at the time of deposition.

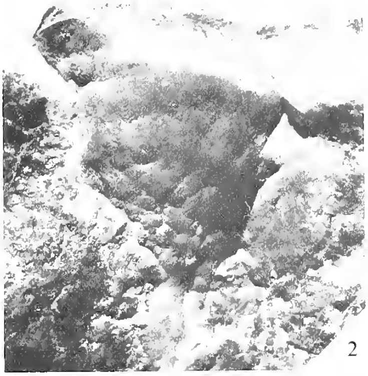
The origin of the 'stromatolites' in this assemblage (and in the life assemblage where they are similar) is not entirely clear. Laminae of fibrous calcite occur throughout as a matrix and in some places appear to have originated through recrystallization of lime mud. However, extensive 'stromatolite' structures also occur, many having the appearance of inverted *Conophyton* or oncolites. Despite the considerable diagenesis, possible organic structures can be discerned in the outermost laminae, represented by rows of discrete ovoid blebs (algal thalli?) composed of dark-grey or brown microgranular calcite. These either 'float' in a clearer calcite mosaic or are joined basally by a thin, dark lamella of similar microgranular composition (text-fig. 2 and Pl. 35, fig. 4). In several cases these 'thalli' are replaced by an equigranular brown dolomite

TEXT-FIG. 2. Mode of occurrence of the 'algal thalli' within the 'stromatolites'. A = micritic or equigranular calcite of outer layers; B = 'algal thallus'; C = dark lamella; D = drusy cavity, left by decomposed thalli?; E = radiaxial fibrous calcite lamella of inner laminae (× 10).

EXPLANATION OF PLATE 35

Figs. 1–5. Death assemblage. 1, weathered section through rock showing many broken cups and 'stromatolitic' intergrowths, × 1. 2, side view of mammillated outer surface of a 'stromatolite'-coniatolite, × 1·6. 3, detail of 'algal thalli' growing towards right, × 128. 4, cluster of 'thalli', growing to bottom left, × 50·4. 5, numerous 'thalli' underlain by fibrous calcite laminae, × 8.


1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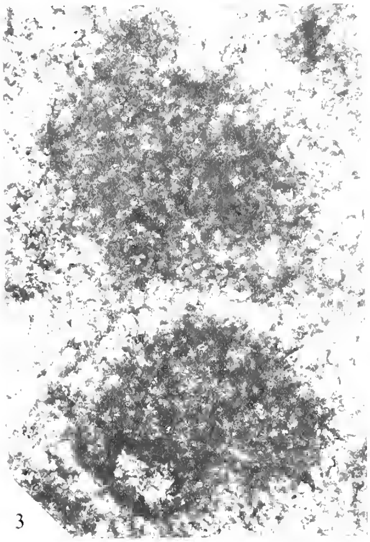
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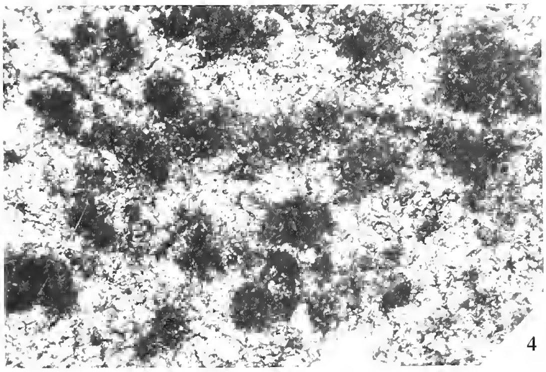
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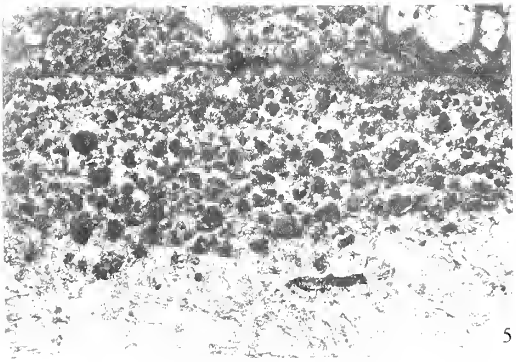

5

BRASIER, early Cambrian communities (archaeocyathids)

mosaic of larger crystal size than the surrounding matrix, or by voids, suggestive of organic decomposition.

The size of these 'thalli' ranges from less than 0·075 × 0·100 mm to at least 0·300 × 0·500 mm. The dark lamellae can be seen in places to pass from the outer layer into the core of the 'stromatolite', where they attenuate. Each dark lamella is usually less than one-quarter of the total laminar thickness (which varies from less than 0·2–1·0 mm or more) and is underlain by a lighter, thicker lamella of radiaxial fibrous calcite (Pl. 37, fig. 8). Towards the 'stromatolite' core these fibrous calcite crystals become larger and may cross the dark lamellar boundaries. X-ray analyses indicate these crystals to be largely low magnesium calcite, with $MgCO_3$ probably less than 1 mol %, together with subordinate quantities of dolomite. Stained peels and electron-probe analysis of similar laminae in the 'life assemblage' indicate that the dolomite was concentrated as minute crystals in the dark lamellae, as noted in many stromatolites. Discussion of the significance and interpretation of these 'stromatolites' follows in a later section.

Sedimentology and diagenesis. Within certain layers in the rock are patches of grey clotted micrite, commonly infilling brachipods or other shells. These patches have indistinct margins, for they grade from micrite to silt-sized equigranular calcite to fibrous calcite. The stromatolitic laminae are also of fibrous calcite (see later), but differ in the possession of dark lamellae and distinct lamination. The micritic patches may represent less pure detritus, for small opaque minerals are present. Recrystallization may therefore have been inhibited by this lesser purity.

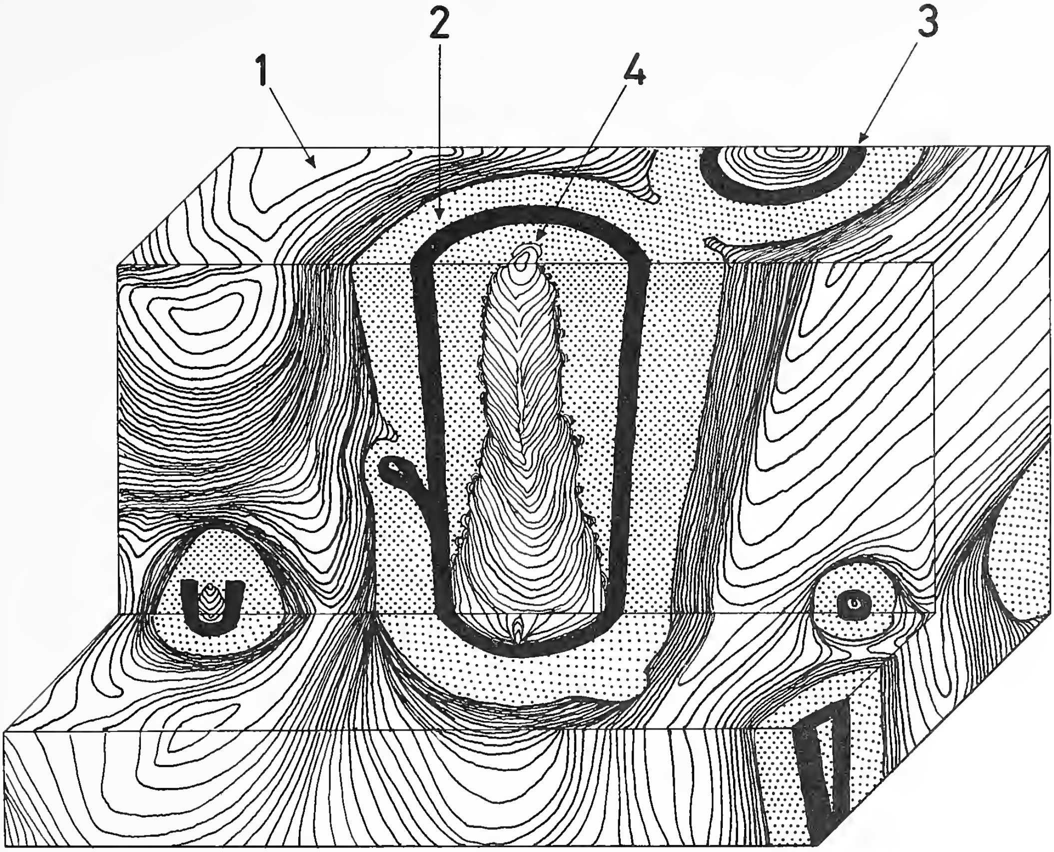
A mosaic of iron-stained quartz crystals occurs locally as a 'skin' at the contact between archaeocyathid outer walls and the peripheral layers of adjacent 'stromatolites'. The loculi are filled with a radiaxial fibrous calcite, which is probably a replacement of an acicular carbonate cavity infilling (Kendall and Tucker 1973).

LIFE ASSEMBLAGE

The constituents of this interesting assemblage are essentially the same as in the death assemblage. There are four major components (text-fig. 3) to be discussed: (*a*) archaeocyathid cups, (*b*) a 'perithecal' zone around the cups, containing *Renalcis*, (*c*) 'stromatolites' external to the archaeocyathid cups, and (*d*) 'stromatolites' within the central cavity of the archaeocyathid cups.

(*a*) *Archaeocyathid cups.* Most of the cups are Regulares, especially of the genera *Mennericyathus*, *Erugatocyathus*, *Robertocyathus*, *Coscinoptycta*, *Ajacicyathellus*, ?*Polycoscinus*, and '*Aldanocyathus*'. The Irregulares are volumetrically less abundant but include *Protopharetra*, ?*Flindersicyathus*, and ?*Metaldetes*, the first being by far the commonest. Both classes of archaeocyathid have been preserved as dense, often layered microgranular calcite cups, with white radiaxial fibrous calcite or yellow ferruginous micritic calcite filling the intervallar spaces. Stylolites often occur along the walls, the skeletal elements having dissolved away locally.

It is significant that nearly all the Regulares share the same general growth direction

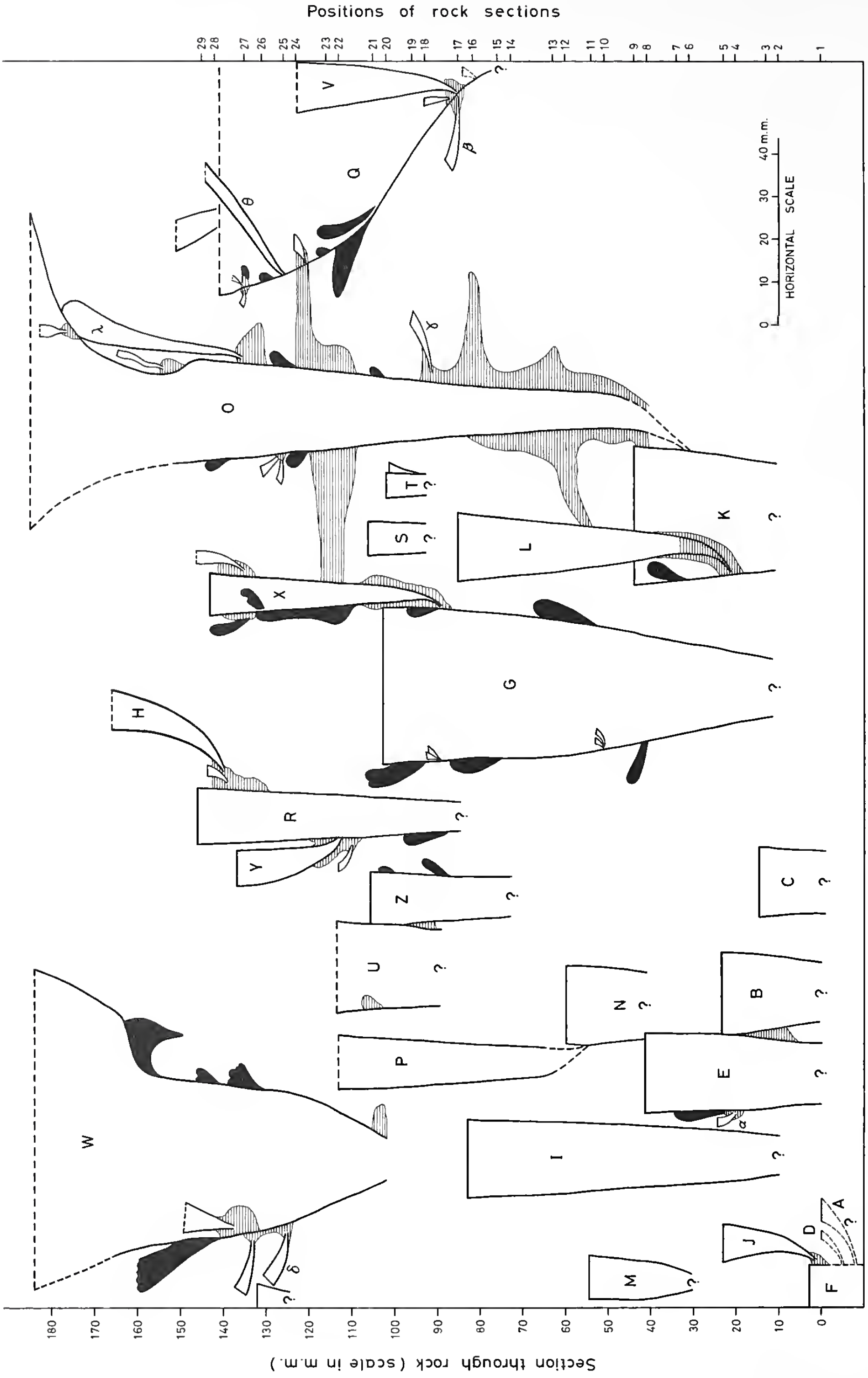


TEXT-FIG. 3. Cut-away diagram of the observed relationships of components in the life assemblage; 1 = 'stromatolites' external to archaeocyathid cups; 2 = perithecal zone; 3 = archaeocyathid cup; 4 = 'stromatolite' within archaeocyathid central cavity (× 2·5).

and several reach heights of over 90 mm (see text-fig. 4). These cups often bear complex and delicate exothecal outgrowths (tersiae), invariably associated with the attachment of a regular juvenile or with the close growth of two or more 'adult' cups. None of the archaeocyathids examined throughout the 200 mm height of the rock specimen were attached initially to anything other than archaeocyathid cups. These factors rule out the possibility that the assemblage is allochthonous.

The small adherent *Protopharetra* are more common in the upper part of the specimen where they attach directly to regular cups without the prior development of tersiae or exothecal lamellae. All of these lack a central cavity and are largely non-porous, in contrast to the Regulares.

(*b*) '*Perithecal*' *zone*. A 'perithecal' zone of micritic calcite occurs as a band of almost uniform width around each archaeocyathid, separating it from the various intergrowths of 'stromatolites' (text-fig. 5). This zone appears near-black in hand specimens (Pl. 36). A similar zone is seen marginal to the upper part of the central cavity,


Positions of rock sections
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29
Section through rock (scale in m.m.)
0 10 20 30 40 50 60 70 80 90 100 110 120 130 140 150 160 170 180
HORIZONTAL SCALE
0 10 20 30 40 m.m.
A B C D E F G H I J K L M N O P Q R S T U V W X Y Z
α β γ δ θ λ
?

again separating the archaeocyathid from the inner 'stromatolites'. In this case, however, the dark perithecal zone is not of uniform width but decreases down the central cavity until the 'stromatolite' comes directly into contract with the inner wall of the archaeocyathid cup. Thin sections and stained acetate peels reveal that the perithecal zone is packed with the small irregular chambers of *Renalcis*, probably *R. jacuticus* Korde, which is generally found rather earlier in Siberia (Zhuravleva, pers. comm. 1975). This organism appears to have attached to the outer and inner walls of the archaeocyathids and to have grown out from them at right angles, or nearly so. *Renalcis* appears to have grown freely, perhaps by settling on the mud of the perithecal zone, or growing attached to other individuals or pellets, as observed by Riding and Toomey (1972). Unfortunately, recrystallization of the rock is such that it is not possible to recognize any true pellets within the matrix. No *Epiphyton* has been recognized in these sections.

The areas between the chambers of *Renalcis* may consist of either clotted micrite, equigranular calcite mosaic, or radiaxial fibrous calcite mosaic, the latter often adjacent to the fibrous calcite of the 'stromatolites'. Again, it is possible that these mosaics are diagenetic replacements of lime mud. Few biogenic components other than *Renalcis* occur in the perithecal zone, except near the top of the rock specimen, where the matrix is relatively shelly, with tubular organisms, sponge spicules, trilobite fragments, and inarticulate brachiopod valves. This more shelly material was presumably washed in from above at a period post-dating much of the *Renalcis*, for the material occurs as an infilling between clumps of the latter but never within the central cavity of the archaeocyathids.

(*c*) '*Stromatolites*' *external to the archaeocyathids*. These 'stromatolite'-like structures comprise 50% or more by volume of the rock. In this assemblage the growth form consists of successive, usually vertical and convex-downwards, laminae reminiscent of stalactites (text-fig. 3). The laminae are interconnected throughout the rock in such a way that it might be thought to comprise a large, downward-growing overhang of a stromatolite, the structure being at least 185 mm long and 120 mm wide at the broadest point. Asymmetry of the growth form is marked, with laminae thinning and dying out in the vicinity of the perithecal zone. Thin sections reveal rows of ovoid 'thalli' and dark lamellae in the outer laminae, much as in the death assemblage. Each 'thallus' is separated from its neighbour by small hemispherical stacks of relatively thin laminae ('microstromatolites') which give the outer surface of the 'stromatolite' a mammillate appearance (Pl. 35, fig. 2). As in the death

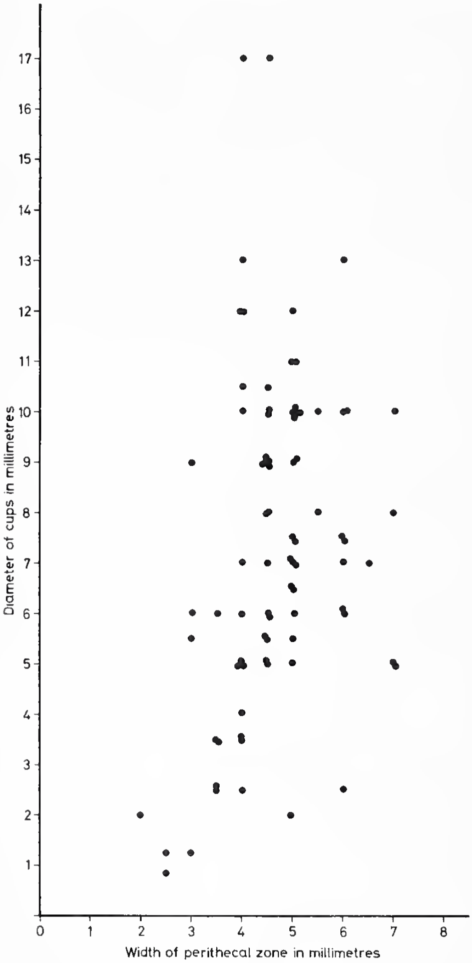
TEXT-FIG. 4. Archaeocyathid relationships in the life assemblage as revealed by serial sections. Horizontal distances between cups have been changed for graphic representation: O, X, and Q should be much closer, as should W and R.

Horizontal hatching = exothecal outgrowths; white 'cones' = Regulares; black shapes = Irregulares (mostly *Protopharetra*); question marks and dashed lines refer to uncertain origins or terminations.

'*Aldanocyathus*' sp. = cups C and R; *Ajacicyathellus* sp. = cups D, H, U, X; *Mennericyathus* sp. = cups P, S, U, W, Z; *Robertocyathus* = cups G, O, Q; *Coscinoptycta* = cup N; *Polycoscinus* = cup T; *Erugatocyathus* = cup E; indet. coscinocyathids = cups B, I, L; others uncertain or not represented. The cup letter symbols correspond with those used in the text and other figures.

C

assemblage the radiaxial fibrous calcite structure of the laminae becomes coarser and the crystals may cross the lamina boundaries. X-ray and electron-probe analyses revealed that the mineralogy is low magnesium calcite except in the region of the dark lamellae where higher MgO concentrations probably relate to small dolomite crystals. It is important to note that in no portion of the rock are the archaeocyathids and these external travertinous 'stromatolites' in contact. Instead, they appear to observe a mutual distance of separation which is remarkably constant (text-figs. 5 and 6A). This unusual relationship has not been described previously and its significance will be discussed in some detail later.



TEXT-FIG. 5. Graph illustrating the relatively constant thickness of the perithecal zone.

(*d*) '*Stromatolites*' *within the archaeocyathid central cavity.* Almost without exception and regardless of size, the regular cups contain a 'stromatolite' growth within the central cavity, indistinguishable in microstructure from those surrounding the archaeocyathids in the death assemblages. Significantly, a few of them show signs of having originally been formed of clotted micrite, the radiaxial fibrous calcite forming diagenetically. There are two observable origins for these internal 'stromatolites'. Firstly, they can represent downgrowth into the central cavity from the surrounding, often overhanging, external 'stromatolite'. Alternatively, they may comprise completely independent growths which were apparently hanging in mid-water without an obvious origin (text-fig. 3 lower left). In all cases, however, the lower part of the central cavity is totally filled by the downward-curving laminae, frequently with the growth core to one side. These inner 'stromatolites' are the only instances in this assemblage where they and the archaeocyathid cups are demonstrably in contact. However, towards the upper part of the cups the algal laminae observe the mutual distance exhibited by the external 'stromatolites', and the growth core is usually central. The interpretation of these curious growths is discussed later.

SPECIAL ISSUES

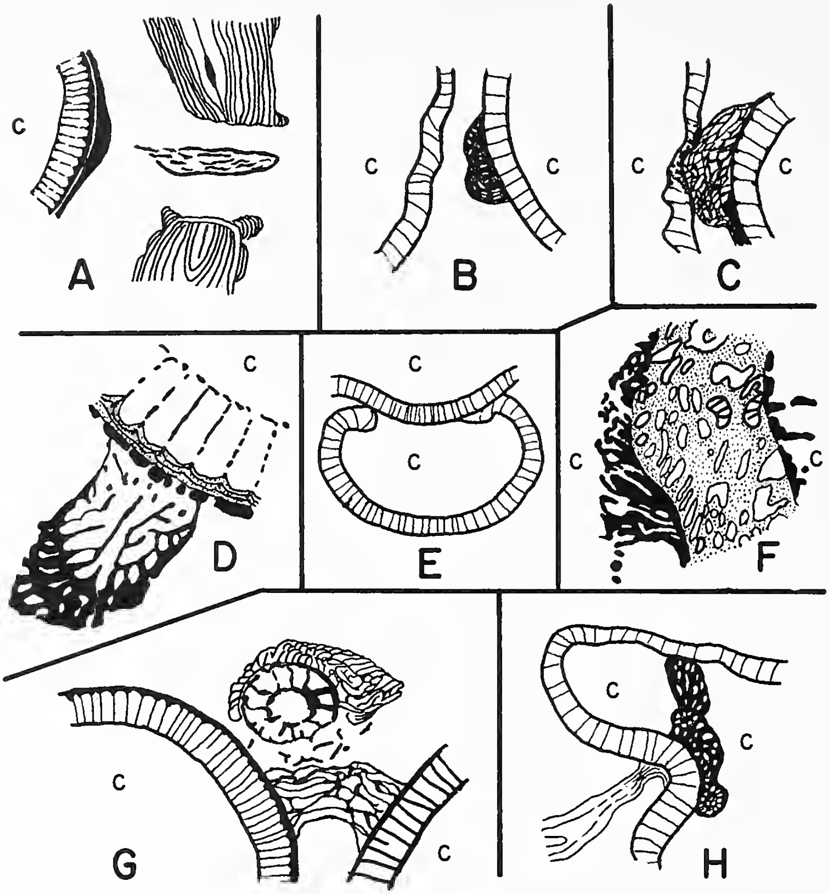
The intergrowths described briefly in the foregoing assemblages prompt a number of questions concerning the biological affinities and palaeoecological relationships of the different organisms at such an early period in the fossil record. Points at issue dealt with below include archaeocyathid relationships, the nature of the 'stromatolites', and *Renalcis* and the nature of the perithecal zone.

Archaeocyathid relationships

Growth relationships. As mentioned previously, all the archaeocyathids in the life assemblage appear to be in their positions of growth. The relative sizes of the individuals and their relationships are plotted in text-fig. 4. This illustrates that all growth stages are present and intimately interconnected, some cups reaching heights of almost 150 mm. Several trends can be elucidated from these data. Firstly at the top of the sequence (150 mm+) where the 'stromatolitic' growth is virtually lacking, the cups appear to have grown more haphazardly, suggesting that 'stromatolites' were exercising some control over their growth further down. Conversely, in the lower part, several 'adult' cups (E/B and U/Z) have been squashed together because of overcrowding or accidental dislodgement. This resulted in growth distortion along with the production of tersiae (calcified exothecal tissue?). In cup B, for example, the skeletal elements appear to have been disrupted adjacent to the tersiae produced from cup E (text-fig. 6B, C, and F). Likewise in cup Z, the intervallum is missing adjacent to cup U (text-fig. 6E). Both U and Z and E and B are different genera so that no sexual interaction can be inferred. In cup O localized distortion of septa and walls is seen in association with tersiae.

Another case of distortion occurs in cup W. This was apparently due to the settlement of juveniles on both outer and inner walls (text-fig. 6H). The distortion is again associated with the formation of tersiae but it is not clear whether these were produced by the host (cup W) or the juveniles. However, these and several other cases are indicative of the sensitivity of the growth form of archaeocyathids. It would seem to indicate the existence of initially non-calcified soft parts in the region of growth, presumably at the top of the cup. The remarkable tersiae surrounding cup O appear to have been produced by that organism and may have served some function of support. Again they are most pronounced where other cups are close but not usually in contact. Here also, the interreaction took place between cups of different genera. Some kind of sensory mechanism might therefore be indicated.

The attachment of juveniles by tersiae or exothecal lamellae was predominantly to the outer wall of larger cups. There is no significant correlation between the taxa of juvenile and host. Many of these juveniles were apparently prevented from growing to a large size because of confined conditions. For example, those which settled on cups which were growing close to the external 'stromatolites' rarely reached adult size (e.g. cups A, D, J, O, and B). Others, especially those which grew laterally or low down on the host cup were impeded by the outer wall of adjacent cups (e.g. λ). Conversely, juveniles which settled either near the top of an old (dead?) cup (e.g. X, H, and O) or on the inner wall or a relatively wide cup (e.g. L, V) were able to thrive because there was plenty of room for growth. It is interesting to note here that settlement on the inner wall was rare, unless the cup was wide. Those on the inner wall of G appear to lack tersiae and arise directly from the wall but close inspection shows that pressure solution has cut out the contact between them. Even so none of these reached lengths of more than a few millimetres.



TEXT-FIG. 6. Camera-lucida drawings of some growth relationships from the life assemblage. A, mutual distance observed between 'stromatolic laminae' (top and bottom) and cup O with tersia, ×4; B, tersiae from the cup on the right (cup E), with mirrored distortion in the cup on the left (cup B), ×3; C, a later stage of the above, with disruption of septa and walls in cup B, ×3; D, tersiae and secondary thickening in *Robertocyathus* sp. (cup O), ×12; E, breakdown of skeleton of cup Z adjacent to wall of cup U, ×2; F, detail of C, showing distortion of the skeletal elements (black) adjacent to tersiae (stippled), ×11; G, tersiae produced by a juvenile (cup X) attaching to two larger cups (O and G), ×4; H, distortion of walls of larger cup (W) in region of juvenile attachment to outer wall (bottom left). Tersiae in black. c = side of central cavity.

The scarcity of settlements on the inner walls may be explained in a number of ways. The strong upward water currents presumed to have been set up in the central cavity (Balsam and Vogel 1973) might have prevented settlement there, even after the death of the host, if the currents were passive as these authors have suggested. However, as already noted, *Renalcis* settled at some stage in the central cavity. If the inner 'stromatolites' developed during the life of the archaeocyathid then the central cavity would have been unattractive or impossible for post-mortem settlement of juveniles. More likely is the possibility that the development of juveniles was relatively substrate-specific and required well-lit, well-circulated conditions which the narrow central cavities would not have provided. Similar phenomena are observed with respect to the small adherent irregular archaeocyathids, mostly species of *Protopharetra*. There is a tendency for these to be larger and more abundant away from the lower part of a cup, again perhaps due to the less confined conditions. Although they may attach to tersiae they do not appear to form any of their own, growing directly on to the outer or inner wall of the host cup. Their generally upward growth expansion does not seem consistent with a parasitic mode of life and is perhaps more reminiscent of the habit adopted by recent coral-encrusting foraminifera such as *Homotrema*, i.e. suspension or deposit feeding. It seems likely from these observations that the settlement of both regular and irregular archaeocyathids upon other cups did not take place until those cups were dead, with the possible exception of γ upon W, for they would otherwise have been more uniformly colonized. This may imply either that these colonizations took place in cycles, or perhaps more likely, that the living archaeocyathids had some means of preventing the settlement of epibionts. The existence of a thin 'ectoplasmic' layer (like that of the perforate foraminifera), which was ciliate, flagellate, or pseudopodial, or the cleaning activities of mobile symbionts around the outer wall (as with the imperforate foraminifera, see Loeblich and Tappan 1964, p. C70) might be inferred.

The terminations of most of the larger cups have been simplified in text-fig. 4. In many cases the top of the cup is not normal to the growth axis (as illustrated) but at an angle of up to 45 degrees. The reason for this appears to be inhibition of growth due to close proximity of 'stromatolites' or other archaeocyathids. The skeletal elements of the upper parts of the cup also exhibit greater diagenesis, with much solution of calcite. Stained peels reveal a change there from normal to ferruginous calcite. Why these effects should have been localized to the top of the cup is not clear. It may be that downward percolations after burial preferentially affected the relatively open upper regions of the intervallum, there being no closure observed in these cups.

Biological implications of growth relationships. The affinities of the archaeocyathids may eventually be evinced by studies of their palaeobiology. Zhuravleva, in her definitive study of the group (1960), regarded them as multicellular organisms consisting of uniform, largely undifferentiated cells which filled the intervallar loculi. Feeding currents were considered to pass through the pores of the outer wall to those of the inner wall and thence up the central cavity (1960), or down the central cavity and out through the outer wall and terminal region of the intervallum (1974). She concludes that archaeocyathids possess a degree of differentiation higher than that of the Protozoa but lower than that of the Porifera, inferring that Archaeocyatha were representatives of the first Metazoa and ancestral to all others (1970). A new kingdom, the Archaeata, has even been suggested for archaeocyathids, aphrosalpingoids, soanitids, and receptaculitids (Zhuravleva 1974).

There are, nevertheless, grounds for believing that the archaeocyathids were at least of sponge grade and possibly higher. Their separation from the calcisponges has recently been contested by Ziegler and Rietschel (1970) on the grounds that they share a similar skeletal morphology, a criterion which has always been central to the debate. They do not mention, however, that the skeletal elements of many archaeocyathids have such a strong symmetry that measurements like intervallum or interseptal width, pore size, pore spacing, and the number of septa relative to cup size are used as viable specific and generic characters. This regular symmetry infers regular and well-coordinated mitoses of the calcifying cells, a degree of somatic integration at least equivalent to, if not greater than, that found in the Porifera.

Tissue restoration. The biological affinities of any group may be evinced by their observable faculties of tissue restoration subsequent to injury and by their tissue compatibility with organisms of the same or different species. In the sponges, for instance, Korotkova (1970) has shown that the more highly integrated unioscular sponges (which have relatively distinct body symmetry) restore their injuries by regeneration proper, so that the lost parts are completely and harmoniously replaced. The less well-integrated multioscular sponges, however (which have an irregular body outline), tend to develop whole new organisms at the injury site, the former tissues being completely reorganized. In these there is a resultant change in growth polarity. It is important to note that observations on the restoration of damage in archaeocyathid cups (Zhuravleva 1960) resemble those of the more highly organized unioscular sponges, so that the group cannot fairly be regarded as having been more lowly than the Porifera.

The ability of living sponges to redevelop from aggregates of cells or fragments of the body is well known and has often been cited as evidence that sponges are colonies rather than individuals. Despite the many observations on archaeocyathids, though, there is little to suggest that they were capable of these faculties of regeneration. One might expect to find, for instance, new cups arising from broken fragments if they were of such lowly organization. The evidence from the assemblages studied here suggests rather that archaeocyathid tissues were not very plastic. Overcrowding with other cups resulted not so much in dramatic changes of symmetry, or the budding of individuals, as in the cessation of growth in the trauma region, so far as can be ascertained.

Tissue compatibility. The interreactions observed between archaeocyathids are also relevant to an understanding of their biological status. It is now known that immunity or compatibility reactions between cells of different individuals become more sophisticated as one ascends the animal kingdom. In sponges, mixtures of cells from two different species will aggregate to form mixed clumps which only separate out with time (Humphreys 1970). There are no reports of cell damage or killing of incompatible cells in sponge interreactions (Hildemann 1974), attesting to the loose organization of the Porifera. Nevertheless, fusion between incompatible sponge colonies does not take place (Ivker 1972). In the coelenterates, incompatibility between allogeneic individuals is more the rule, for example contact between incompatible colonies of the same or different species of *Acropora* (staghorn coral) results in a zone of destruction of the soft tissues (Hildemann 1974), and allogeneic colonies

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EXPLANATION OF PLATE 36

Figs. 1–9. Horizontal serial sections through a portion of the life assemblage showing the archaeocyathids, perithecal zone (dark), and 'stromatolites' (laminated or white infillings of cups), ×1.


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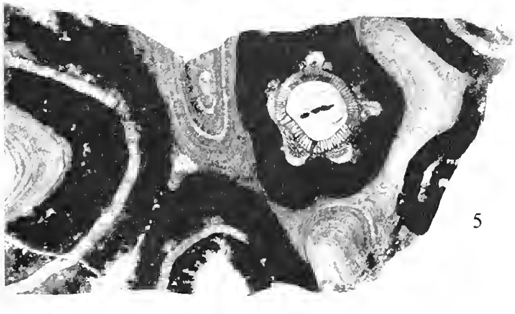
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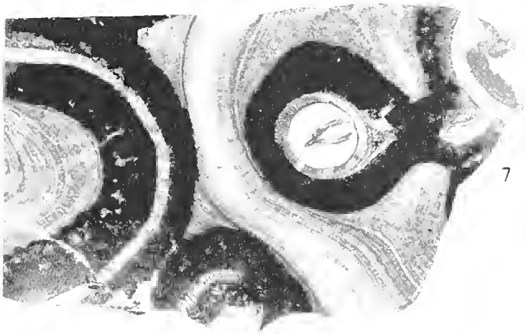
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BRASIER, early Cambrian communities (archaeocyathids)

of the hydroid *Hydractinia echinata* fail to fuse when grown in contact, with hyperplastic growth rather than tissue destruction taking place at the contact zone (Ivker 1972). In this species a hierarchy of incompatibility exists between different colonies. The stronger strains produce dense fringes of intertwined stolons by hyperplastic growth which serve to smother some of the weaker strains.

The observed archaeocyathid interreactions are similar to the above. The exothecal outgrowths produced by proximity or contact of two individuals of the same or different species may be analogous to the hyperplastic growth of hydroids. That is, it represented a proliferative response of ectodermal cells to contact with foreign-cell surfaces. In some instances (e.g. text-fig. 6C and F) the skeletal elements of the recipient were distorted by tersiae from a neighbouring cup. The fact that in nearly every case only one individual seems to have produced tersiae in an encounter is in accord with the observations on hydroids, and likewise indicates a hierarchy of incompatibility.

There is, furthermore, no evidence of any harmonious fusion of elements between apparently compatible archaeocyathids such as one might expect from primordial metazoans. The recorded lack of tersiae in Irregulares and certain Regulares could be considered the result of a lesser porosity of the outer wall, providing protection from external interference. The phenomenon of secondary thickening sometimes observed on the inner surfaces of the outer wall (see text-fig. 6D) is frequently associated with exothecal outgrowths and may likewise have been a defensive mechanism. One concludes that the individuality of these archaeocyathids was strongly expressed. If it was general then it is suggestive of an organization higher than sponges.

Feeding. Although it has long been recognized that archaeocyathids were filter feeders, it has recently been suggested by Balsam and Vogel (1973) that the filter-feeding currents were not actively pumped, but rather, set in motion passively by the conical perforate structure of the cup. But it is unlikely that those which lacked a central cavity operated in this manner; furthermore, in those with feebly porous to non-porous walls, the low ratio of pore to wall-surface area would have caused the establishment of vertically successive vortices within the central cavity in the absence of a pumping mechanism. Such vortices would have limited the exchange of nutrients on which the organism would have passively depended. In addition, it is not clear why Balsam and Vogel consider that early Metazoa had lost the ability

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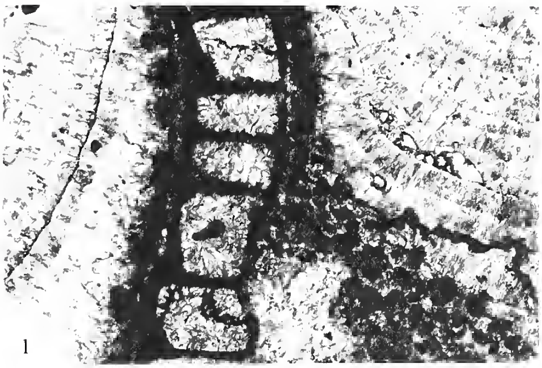
EXPLANATION OF PLATE 37

Figs. 1–2. Death assemblage. 1, 'stromatolitic' laminae and 'algal thalli' abutting against an archaeocyathid (centre), ×8. 2, *Chancelloria* rosette, with adherent *Protopharetra* in recrystallized micrite, ×8.

Figs. 3–8. Life assemblage. 3, *Protopharetra* adhering to regular archaeocyathid wall, overgrown by *Renalcis*. Horizontal section, ×8. 4, *Protopharetra* with fibrous and equigranular cavity-fill cement, overgrown by *Renalcis*. Vertical section, ×8. 5, regular archaeocyathids overgrown by *Renalcis*. Horizontal section, ×8. 6, inner wall of cup O with adherent *Renalcis* and *Protopharetra*. Laminae of inner 'stromatolite' (coniatolite) visible in central cavity to the right, ×8. 7, outer wall of cup O (top) encrusted by *Renalcis*. ? 'algal thalli' (bottom) surrounded by rims of fibrous calcite, on the margins of a 'stromatolite'. Horizontal section, ×8. 8, 'stromatolitic' laminae of coniatolite with dark dolomitic and paler fibrous calcite lamellae. Horizontal peel, ×20.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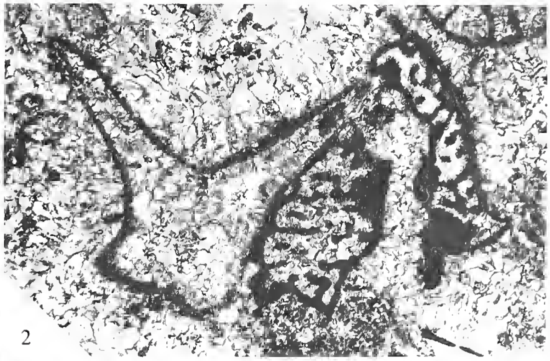
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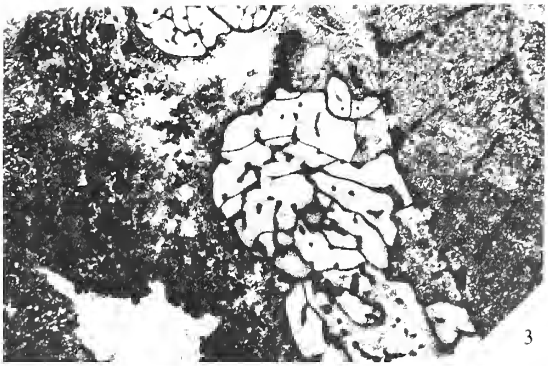
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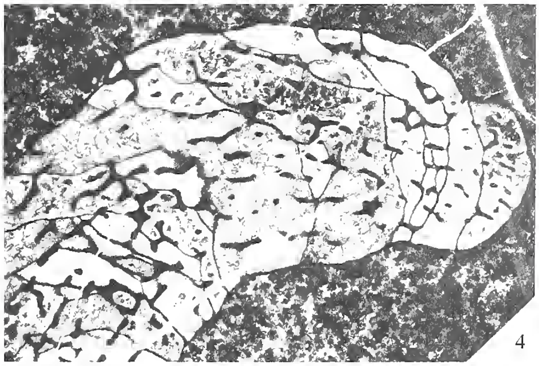
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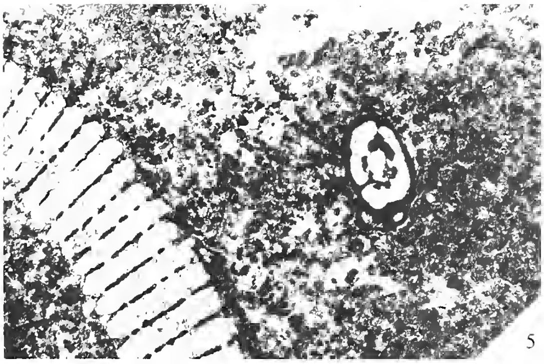
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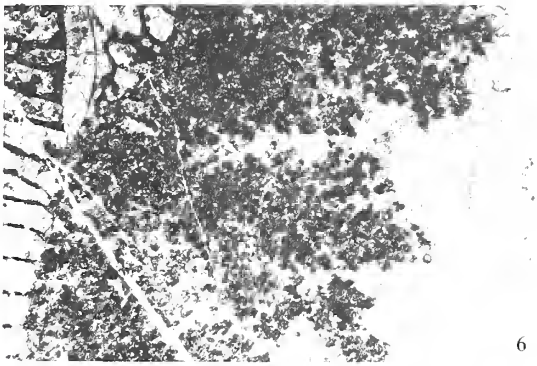
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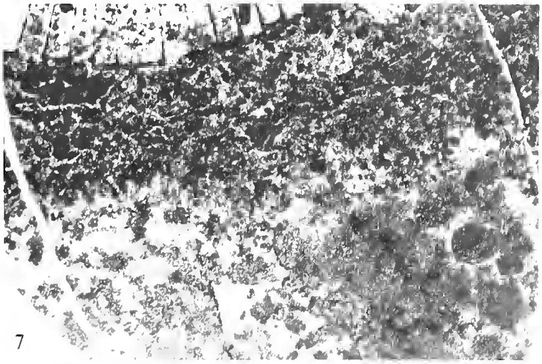
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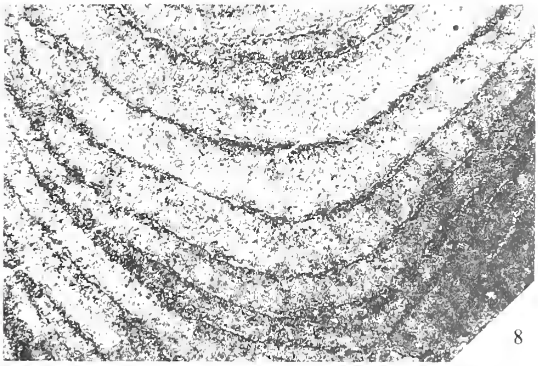
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BRASIER, early Cambrian communities (archaeocyathids)

to move water actively, arising as they probably did from ciliate or flagellate ancestors, especially when such a faculty would have had strong selective advantages.

Zhuravleva (1974) justifiably pointed out that the diversity of skeletal structure found in archaeocyathid genera does not permit a single, cogent explanation of current flow. However, she speculated that flowage in cup-like forms was active, coming in through the central cavity and out via the outer wall or intervallar terminations or vice versa. This pattern would contradict Balsam and Vogel's flume experiments and it is difficult to envisage active currents developing in opposition to the natural, passive tendencies. The suggestion that these animals fed on bacteria and dissolved organic matter (Balsam 1973) is reasonable. However, the feeding mode of the non-porous *Protopharetra* must have been different. Apart from their degenerate appearance there is nothing else to suggest that they were parasitic on the Regulares. Whether they were sessile microcarnivores, bacteriophages, or general suspension feeders is as yet uncertain. Debrenne (1975) suggests that placement of archaeocyathids in a distinct Kingdom may be premature. More work is required on microstructure, on exothecal outgrowth, and on analogies with other organisms before any statement about affinities can be upheld.

THE 'STROMATOLITES'

The 'stromatolitic' structures described from both assemblages are unusual both in their mode of growth and preservation. Their interpretation affects interpretation and inferences about the other organisms and hence it is necessary to examine the origin of these structures. Four origins are plausible: (i) stromatolite, (ii) sediment recrystallization, (iii) rim-cement cavity fill, and (iv) tufa cavity fill ('coniatolite').

(*i*) *Stromatolitic origin*. The outer layers of the 'stromatolites' frequently bear ovid thallus-like structures with 'microstromatolitic' laminae between them (text-fig. 2) giving the outer surface a mammillate appearance (Pl. 35, fig. 2). These 'thalli' resemble recent clumps of Chroococcales cells which are known to form non-laminated clotted fabrics on the lateral (often vertical) selvages of stromatolites (Gebelein 1974). The occurrence of 'thalli' in clotted, unlaminated patches in both assemblages could confirm this analogy. However, the laminae are defined by thin dark lamellae and these would more resemble those produced by recent thin sheathed Oscillatoriacea, which can construct vertical and overhanging structures in association with Chroococcales (ibid.). A fibrous calcite, travertine-like appearance may result from recrystallization of trapped or precipitated $CaCO_3$ material, perhaps the result of the activities of denitrifying bacteria. The latter often concentrate below the surface of algal mats, leading to the crystallization of fibrous high magnesium calcite or aragonite (Milliman 1974, pp. 49–50 and 188) which may in turn convert to radiaxial fibrous low magnesium calcite (Kendall and Tucker 1973). Such subsurface bacterial diagenesis would, for instance, account for the progressive loss of the 'organic' structures towards the centres of the 'stromatolites'. Similar fabric is known in the Cambrian stromatolite *Actinophycus* Korde from Siberia. However, the 'thalli' more closely resemble those of the stromatolitic alga *Stereophycus* Korde (Zhuravleva, pers. comm. 1975). Despite these similarities there are a number of important objections to the stromatolitic hypothesis. The downward and outward growth of nearly all laminae has been mentioned, as has the observed connection between certain internal and external 'stromatolites'. Even accepting this, it is difficult to envisage how stromatolitic algae could grow downwards into the central cavity, bounded on all sides by archaeocyathid walls or *Renalcis* encrustations. Some of these internal structures formed after the central cavity was totally 'roofed over' by *Renalcis*. Another objection is that the gross growth structures are totally unlike those of any described stromatolites, with many thin 'tubes', 'limbs', and isolated 'eyes' developed by largely encapsulating laminae. Such structures could hardly have been self-supporting in space. Furthermore, there are no indications of the desiccation structures which characterize many true stromatolites.

(*ii*) *Sediment recrystallization origin*. Cullis (1904) and Orme and Brown (1963) have described the development of acicular carbonate from lime mud. Certainly, transitions from lime mud, through silt-sized equant grains to elongate calcite fibres have been observed in the Wilkawillina Limestone. However, the large multilaminar structures formed in these 'stromatolites' are far removed from the small rims or irregular patches noted elsewhere and by the above authors. Successive generations of fibrous calcite with straight crystal boundaries, and of more or less uniform size are more typical of cavity-fill cements (Wolf 1965). It is therefore unlikely that the complex structures arose from simple recrystallization of a micrite matrix.

(*iii*) *Rim cement-cavity fill origin*. Such cements form around the rims of cavities (e.g. skeletal structures, sheet cracks, etc.) as early diagenetic inward-growing fibrous sparite layers and are typical of reef-associated sediments (Wolf 1965). They are usually associated with drusy or granular calcite infilling of the cavity, internal sediment layers, and other geopetal structures such as stromatactis. None of these is seen in the 'stromatolites'. A further objection to this hypothesis is the over-all complexity of the outward-growing mammillate structures. These are much more consistent with the following origin.

(*iv*) *Tufa* ('*Coniatolite*')-*cavity fill origin*. In all respects other than in the presence of organic (?) thalli, the 'stromatolites' resemble tufa (e.g. stalactites), especially with regard to the distal drip-tips seen in those forms within archaeocyathid central cavities (text-fig. 3). Aragonitic travertines, known as 'coniatolites', are found forming today in the intertidal and supratidal regions of the Persian Gulf (Purser and Loreau 1973). These are usually found on beach rock or other hard surfaces, and may develop stalactitic form at overhangs or in cavities. Whilst coniatolites may morphologically resemble stromatolites, they differ from them in their dripstone micromorphology (superimposed laminae of honey-coloured fibrous calcite), their downward growth around the edges, their lack of desiccation features, or bird's-eye structures and scarcity or lack of detrital sediment. All these features correspond with the 'stromatolites' discussed above.

Discussion. The structures are interpreted as coniatolites formed by downward dripping of marine brines into cavities, during a period of subaerial exposure (tidal?), as in the recent Persian Gulf and the Bathonian limestones of Bourgogne. The *Renalcis* encrustations helped to bind the archaeocyathid cups together, leaving cavities between or within. In the death assemblages, cavities were left by the sudden deposition of large cups and coarse biogenic detritus and these were infilled by the tufas. Early diagenetic alteration of the aragonite to calcite, without evidence of leaching, may indicate an arid environment.

If one accepts the marine tufa (coniatolite) origin, then the algal 'thalli' and lamellae must be explained. There are several possibilities. Firstly, the most distinctive 'thalli' are seen only in the outer laminae and in few sections. These may have grown on or within the tufa at a late stage, where there was sufficient light. Secondly, the cruder blebs more commonly seen could represent diagenetic alteration of *Renalcis* and pelletoids of the perithecal zone into which the tufa has grown. Thirdly, the organic structures may be those of bacteria, blue-green algae or fungi responsible for, or associated with, the formation of tufas. Similar downgrowing 'cryptalgal' mats and heads have been described from the undersides of sheet cracks in the late Palaeozoic of Algeria (Bertrand-Sarfati and Fabre 1972), whilst others have been seen by the writer in the Triassic of Glamorganshire. In both cases fibrous calcite has developed in the downgrowing laminae under lagoonal conditions. As flexibacteria can form siliceous stromatolites in the absence of light (Brock 1969) it is possible that similar organisms may be involved in the formation of tufas in such unlit spaces (e.g. see Krumbein 1968).

RENALCIS AND THE PERITHECAL ZONE

The 'mutual distance' observed between archaeocyathids and the 'stromatolites' relates to a more or less constant thickness of *Renalcis* encrustations around the outer walls. Similar perithecal zones of *Renalcis* have been observed by the writer in other assemblages from the Wilkawillina Limestone and from elsewhere around the world. These overgrowths will form the subject of a later study but several points are worth noting here. Firstly, the absence of *Renalcis* from the intervallum and lower central cavity requires explanation. Whilst the intervallum may have been closed off by an organic membrane or filled with tissue, the central cavity almost certainly was not. The *Renalcis* zone gets thicker as the central cavity widens, which could suggest that a dependence upon light or well-circulated water kept the organism out of the lower central cavity.

A second point concerns the role played by *Renalcis* as a binding organism strong enough to prevent the disruption of a delicate archaeocyathid community in a littoral habitat. This kind of encrusting-binding habit seems generally inconsistent with blue-green affinities, as are certain other points about the organism (Riding and Brasier 1975).

CONCLUSIONS

1. The archaeocyathids were growing in warm, shallow sublittoral waters in a geographic setting resembling a wide backreef lagoon. Their faunal associates included trilobites, brachiopods, echinoderms, hyolithids, *Chancelloria*, and various problematica.

2. Juvenile archaeocyathids mostly attached to the upper, outer wall of an older, probably dead cup. Inner-wall settlements took place only where the central cavity

was wide. Regulares commonly formed exothecal outgrowths at the attachment site whilst Irregulares attached directly. Those juveniles which grew upright from near the top of the host cups attained a larger size than those which grew laterally and lower down on a cup, for the latter were overcrowded by other individuals.

3. Growth distortions occurred where two archaeocyathid cups came into contact, indicating the existence of non- or poorly calcified parts in the region of growth at the top of the cup. Exothecal outgrowths are associated with these overcrowding phenomena and may have represented a proliferative response of the ectoderm to the presence of foreign cells. They also served for adherence. Considerations of the level of cellular integration indicated by archaeocyathid skeletal structure, especially consequent to damage or contact with other individuals, suggest that they had an organization as high and possibly higher than that of the Porifera.

4. In the life assemblage the outer walls of the cups were encrusted by colonies of the calcareous-chambered organism *Renalcis.* These encrustations were probably post-mortem and were substantial enough to bind the delicate archaeocyathid intergrowths together. *Renalcis* is usually lacking from the lower part of the central cavity and all of the intervallum of the archaeocyathid hosts. In the death assemblage, the cups were mostly uprooted and transported before *Renalcis* encrustation was able to take place.

5. Structures resembling stromatolites surround the archaeocyathids in many places. These are interpreted as early post-mortem tufas ('coniatolites'), formed by brines percolating downwards into cavities, perhaps during low tides. These tufas encouraged the recrystallization of some lime mud matrix into radiaxial fibrous carbonates.

Much further work needs to be done on the sedimentological relationships and the mode of preservation of these problematic early Cambrian organisms before their palaeoecology and palaeobiology will come to light. With the above and many other studies one hopes eventually to build up a clearer picture of one of the most important periods in the history of life, the Cryptozoic-Phanerozoic transition.

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LATE CAMBRIAN BRACHIOPODA, MOLLUSCA, AND TRILOBITA FROM NORTHERN VICTORIA LAND, ANTARCTICA

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ABSTRACT. The discovery of late Cambrian fossils in the Bowers Group of Northern Victoria Land, Antarctica, provides the first reliable evidence for the age of basement sedimentary rocks in the region. Together with a previously reported fauna of generally similar over-all composition and age, from the Heritage Range of the Ellsworth Mountains on the opposite side of the continent, they are the only late Cambrian fossils known in Antarctica and the youngest yet reported from the pre-Devonian basement.

Seventeen taxa of trilobites (including representatives of *Pseudagnostus*, *Stigmatoa*, *Pedinocephalus*, *Prochuangia*, and *Proceratopyge*), four of molluscs (*Contitheca webersi*, sp. nov., *Hyolithes*, *Pelagiella*, *Scaevogyra*), and three of brachiopods (*Schizambon reticulatus*, sp. nov., *Billingsella*, *Prototreta*) are described; they represent a single fauna of late Idamean (*Erixanium sentum* Zone; late Dresbachian, late Tuorian) age.

The fauna bears affinity with faunas of Australia, China, and Kazakhstan, in agreement with affinities indicated by previously described early and middle Cambrian trilobite faunas of Antarctica.

THE Antarctic continent has yielded very few fossils from its pre-Devonian rocks. Early and mid-Cambrian trilobite faunas, described by Palmer and Gatehouse (1972), are known only from the Pensacola Mountains (Argentina and Neptune Ranges) and the Harold Byrd Mountains of the Transantarctic Mountain Range (text-fig. 1). Ten faunules were recognized in morainic boulders, ranging in age from late in the early Cambrian (late Aldanian to Botomian Stages and their equivalents) to late in the middle Cambrian (mid-Mayan Stage). Late Cambrian trilobites have been previously reported from the Heritage Range of the Ellsworth Mountains (Webers 1970), where they are associated with Monoplacophora, Gastropoda, Brachiopoda, and other forms (Webers 1970, 1972; Yochelson *et al.* 1973). Early Cambrian Archaeocyatha are known from several localities in or near the Transantarctic Mountains, including Southern Victoria Land (Laird 1962, 1963; *in* Laird *et al.* 1971; Hill 1964*a*, 1964*b*, 1965).

All previously known Cambrian fossils thus come from that sector of Antarctica containing the Ellsworth Mountains and the Transantarctic Mountains, from the south-west edge of the Ross Ice Shelf to the Weddell Sea. The discovery of a late Cambrian fauna containing trilobites, brachiopods, and molluscs in Northern Victoria Land (Laird *et al.* 1972), over 1500 km away on the other side of the continent, and over 2500 km from the Heritage Range upper Cambrian locality, is thus of considerable interest. It represents the youngest fossils from the basement of East Antarctica, and the only definite fossils in Northern Victoria Land, thus establishing for the first time the precise age of part of the sedimentary basement in the region. The Ross Orogeny (Laird *et al.* 1972) which deformed the basement before the basal, Devonian, beds of the platform-cover sequence were deposited, is shown to be post late Cambrian.

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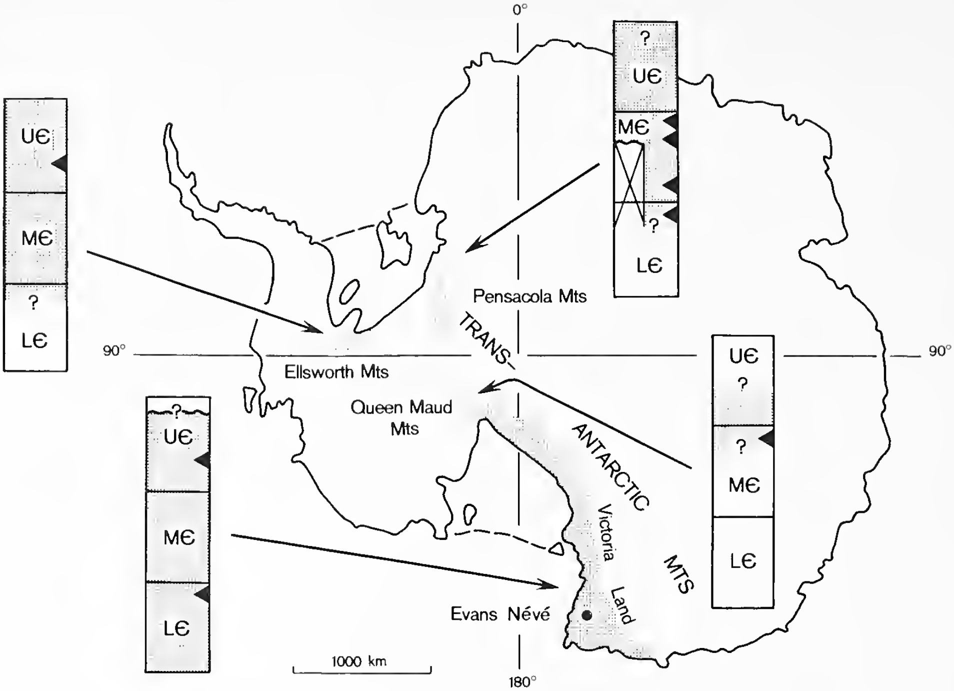

TEXT-FIG. 1. Locality diagram indicating regions with fossiliferous Cambrian rocks; the known or inferred range of Cambrian sedimentation (light stipple) and general horizon from which fossils have been obtained (solid triangles) are shown in diagrammatic form for each region. The lower Cambrian fossiliferous horizon indicated for the Victoria Land region refers to archaeocyathids from Southern Victoria Land. Evans Névé, from which were obtained the fossils described in this report, is also shown.

The geographic affinities of the new fauna are of particular interest in view of its postulated proximity to the fossiliferous Cambrian beds of South-east Australia and New Zealand in reconstructions of Gondwanaland in the Lower Palaeozoic (Crawford and Campbell 1973; Harrington *et al.* 1973; Cooper 1975).

Stratigraphy

The fossils described here represent the entire recognizable fauna collected by Dr. M. G. Laird, New Zealand Geological Survey, and his field party during the southern summer of 1971/2. They are from 'the southernmost known outcrops of the Bowers Group, where it flanks the eastern side of the Evans Névé' (Laird *et al.* 1972; see also Gair *et al.* 1969; text-fig. 1). A stratigraphic section 1600 m thick is given by Laird *et al.* 1972; the lower 900 m comprises predominantly dark fissile mudstones with scattered thin sandy beds and horizons with trilobites and brachiopods. The succeeding 650 m is composed mainly of grey, green-grey, or red well-bedded quartz sandstone with scattered fossiliferous horizons, and one muddy band containing lenses of oolitic hyolithid limestone. All rocks to this level are regarded by Laird *et al.* 1972, as probably equivalent in stratigraphic position to part of the Sledgers Formation of Crowder (1968), mapped 150 km to the north-east; they have been named Mariner Formation by Andrews and Laird (1976). Overlying beds consist of about 100 m of light yellow-grey cross-bedded unfossiliferous quartzose conglomerate and pebbly sandstone referred to the Camp Ridge Quartzite (Le Couteur and Leitch 1964). Sedimentology and general geology of the Bowers Group rocks in the region are described by Andrews and Laird (in press) and Laird *et al.* (1974).

Lithology of the fossiliferous beds ranges from fissile non-calcareous siltstone with poorly preserved complete trilobite impressions (collections from locality MS/f270) to fine sandstone, calcilutite, and calcarenite containing much broken brachiopod shell material and, in some beds, complete but separated *Billingsella* valves (collections from locality MS/f267). Petrographically, sediments containing the best-preserved material, the float slabs of locality MS/f266, are richly fossiliferous, oolite-bearing, packed biomicrite, and calcilutite. Trilobite parts are disarticulated but not noticeably abraded, and brachiopod valves are separated. Delicate orthothecoids are generally undamaged and the sediments are likely to have been deposited in conditions of some current agitation but not strong current activity. Ooliths up to 0·8 m diameter are present in shelly calcilutite at localities MS/f267 and MS/f266.

The trilobites and molluscs of this study are from two float slabs of shelly calcilutite (locality MS/f266) derived from a horizon 400 m above the base of the measured section of Laird *et al.* (1972), all outcrop material being too poorly preserved for identification. The brachiopods are from localities MS/f266, MS/f271, and MS/f272, at the 400-m, 900-m, and 1100-m levels respectively in the stratigraphic column of Laird *et al.* 1972. In addition, brachiopods collected by Cooper, Jago, and Simes in 1974 from a new locality, MS/f274, representing a horizon approximately equivalent to that of MS/f271, are included. The quantity of trilobite and mollusc material available for study is small, but because of the inaccessibility of the locality and difficulty in obtaining further material, and the importance of the fauna, both groups are described fully here. The brachiopod *Billingsella* is less sparsely represented. Although quality of preservation is generally good, much material, particularly the trilobites, is fragmentary and a conservative attitude towards nomenclature has been adopted. Only two new species are erected, *Schizambon reticulatus* MacKinnon and *Contitheca webersi* Yochelson; however, several of the trilobites are likely to represent new species.

All fossils are held in the collection of the New Zealand Geological Survey, Lower Hutt; specimen numbers prefixed with AR, TM, and BR being catalogued in the Trilobite, Mollusc, and Brachiopod registers respectively. Locality numbers are listed in the New Zealand Fossil Record File. In Plates 38–42, all specimens except those examined under the Scanning Electron Microscope have been coated with ammonium chloride.

Authorship

For convenience of reference new taxa are erected under the name of the author responsible rather than under the names of all four joint authors. Responsibility is as follows: Shergold, trilobites; Yochelson, molluscs; MacKinnon, brachiopods. Work was organized by Cooper who wrote the introduction, and Shergold compiled the final manuscript from individual authors' contributions.

FAUNAL COMPOSITION: AFFINITIES AND AGE

Composition of the fauna is:

Brachiopoda: *Schizambon reticulatus* MacKinnon, sp. nov., *Prototreta* sp., *Billingsella* sp.

Mollusca: *Contitheca webersi* Yochelson, sp. nov., *Hyolithes* sp., *Pelagiella* sp., *Scaevogyra* sp.

Trilobita: *Pseudagnostus* sp., *Stigmatoa* sp., *Olentella* cf. *olentensis* Ivshin, *Irvingella*? sp., *Pedinocephalus* sp. cf. *P. bublichenkoi* Ivshin, Aphelaspid sp. 1, Aphelaspid sp. 2, Aphelaspid sp. 3, *Talbotinella*? sp., Olenid sp., *Prochuangia* sp. aff. *P. granulosa* Lu, *Proceratopyge* sp. cf. *P. lata* Whitehouse, Trilobita sp. 1, Trilobita sp. 2, Trilobita sp. 3, Trilobita sp. 4, Trilobita sp. 5.

Data for assessing age and regional affinity of the trilobites are summarized in Table 1; each taxon is listed alongside the species or higher group with which it is most closely allied. The locality or general region of the allied form is shown together with its age or stratigraphic horizon.

Affinities are shown with trilobites previously described from Australia, China, and central Kazakhstan. Apart from the questionable presence of the cosmopolitan genus *Irvingella*, and the aphelaspidinids similar to '*Aphelaspis buttsi*', there is little affinity with North American faunas; and apart from the cosmopolitan *Pseudagnostus* and *Proceratopyge* there is nothing in common with European faunas.

TABLE 1. Affinities of Antarctic trilobites.

Antarctica taxa	Affinities
Pseudagnostus sp.	'*Pseudagnostus communis*' Lu *et al.* 1965; 'China'
Stigmatoa sp.	*Stigmatoa tysoni* Öpik, 1963; Idamean; *Erixanium sentum* Zone; western Queensland, Australia
Olentella cf. *olentensis*	*Olentella olentensis* Ivshin, 1956; Tuorian; *G. reticulatus* Zone; *Aphelaspis–Kujandaspis* fauna, Kazakhstan, U.S.S.R.
?*Irvingella* sp.	*Irvingella major* Ulrich and Resser, 1924; Franconian; *Elvinia* Zone; many localities, U.S.A.
Pedinocephalus cf. *bublichenkoi*	*Pedinocephalus bublichenkoi* Ivshin, 1956; Tuorian; *G. reticulatus* Zone; *Aphelaspis–Kujandaspis* fauna; Kazakhstan, U.S.S.R.
Aphelaspid 1	'*Aphelaspis buttsi* (Kobayashi, 1936)'; Dresbachian; *Aphelaspis* Zone; Ala, Nevada, U.S.A.
Aphelaspid 2	'*Aphelaspis buttsi* (Kobayashi, 1936)'; as above
Aphelaspid 3	'*Aphelaspis granulata* Kuo, 1963'; 'China'
?*Talbotinella* sp.	*Talbotinella notulata* Öpik, 1963; Mindyallan; *G. stolidotus* Zone; western Queensland, Australia.
Olenid 1	*Hancrania brevilimbata* Kobayashi, 1962; early Upper Cambrian; *Hancrania* Zone; South Korea
Prochuangia sp.	*Prochuangia granulosa* Lu, 1956; ?Paishanian; eastern Kueichou, China
Proceratopyge cf. *lata*	*Proceratopyge lata* Whitehouse, 1939; Idamean; *E. sentum–I. tropica* with *A. inconstans* Zones; western Queensland, Australia
Specimen 1	??*Pedinocephalus simplex* Ivshin, 1962; Tuorian; *G. reticulatus* Zone; Kazakhstan, U.S.S.R.
Specimen 2	??*Litocephalus*; late Dresbachian–early Franconian; *Dunderbergia–Elvinia* Zones; Nevada, U.S.A.
Specimen 4	??*Stigmatoa*; late Idamean; *E. sentum–I. tropica* with *A. inconstans*; western Queensland, Australia

The brachiopods and molluscs show less-pronounced regional affinity but generally agree with that shown by the trilobites. In particular, the gastropod *Scaevogyra* is a characteristic late Cambrian genus in North America and North-east Asia.

Interestingly, the trilobite affinities are similar to those of early and middle Cambrian Antarctic faunules (Palmer 1970, 1972; Palmer and Gatehouse 1972) that are most closely allied to faunas from Australia, China, and Siberia, and to those of the late Cambrian Antarctic fauna noted by Webers (1970, 1972), which also contains aphelaspidinid trilobites of Siberian affinity. The general composition of Webers's fauna is apparently similar to that described here; detailed comparison, however, must await the full description of his material.

The trilobites indicate a late Idamean age on the Australian biostratigraphic scale, equivalent to latest Tuorian or earliest Shidertan on the Siberian scale and latest Dresbachian or earliest Franconian on the North American scale. If the specimen described here as *Irvingella*? sp. is a true *Irvingella*, it suggests that the fauna may be of earliest Franconian age (*Elvinia* Zone), equivalent to early Shidertan: the lower boundaries of both stages are marked by the first appearance of *Irvingella*. In Australia *Irvingella* first appears in the youngest zone (*I. tropica* with *Agnostotes inconstans*) of the Idamean Stage. On the other hand, the genera *Olentella*, *Pedinocephalus*, *Stigmatoa*, and *Talbotinella* and the aphelaspidinids suggest a horizon no younger than the preceding *Erixanium sentum* Zone of the Australian Idamean, that is, late Dresbachian in North America and late Tuorian in Siberia. The Bowers Group fauna is here regarded as of probable late Idamean, *E. sentum* Zone, age, equivalent to latest Dresbachian (*Dunderbergia* Zone) and latest Tuorian.

SYSTEMATIC PALAEONTOLOGY

Phylum BRACHIOPODA (by D. I. MacKinnon)
Class INARTICULATA Huxley, 1869
Order ACROTRETIDA Kuhn, 1949
Superfamily SIPHONOTRETACEA Kutorga, 1848
Family SIPHONOTRETIDAE Kutorga, 1848
Genus SCHIZAMBON Walcott, 1884

Type species. Schizambon typicalis Walcott (1884, pp. 70–71, pl. 1, fig. 3*a–d*), early Ordovician, Goodwin Formation, Eureka district, Nevada; by original designation.

Other species. Species assigned to *Schizambon* are too numerous to list here. Cambrian to early Ordovician species described prior to 1938 by Walcott (1884, 1905, 1912, 1924*a*), Matthew (1901), Poulsen (1927), and Ulrich and Cooper (1936) have been listed by Ulrich and Cooper (1938, pp. 60–63), who added a further four new species. Subsequently, early and middle Ordovician *Schizambon* species, described by Hudson (1904) and Willard (1928), have been discussed by Cooper (1956) who described six more species and left two under open nomenclature. Also left under open nomenclature are specimens described by Termier and Termier (1950, p. 36, pl. 68) and Henderson (*in* Hill *et al.* 1971, p. Cm2, pl. Cm1, figs. 28–29) from the late Cambrian Gola Beds of western Queensland, Australia. With the erection of the genus *Multispinula* (Rowell 1962, p. 147) to embrace the majority of the large middle Ordovician species which have been referred to *Schizambon*, the species of *Schizambon sensu stricto* appear to range in age from late Cambrian to early Ordovician. Of all the species described to date the bulk are of North American provenance.

Schizambon reticulatus MacKinnon, sp. nov.

Plate 38, figs. 1–2

Name. Reticulatus (L.) refers to the reticulate pattern of intersecting growth lines and costellae of the external surface of the shell.

Types. Holotype, pedicle valve, BR 1902; measured paratypes, pedicle valves, BR 1903 (subsequently damaged), BR 1904.

Material. Available material consists of seven pedicle valve exteriors, three of which can be measured. The holotype, BR 1902, has a length of 4·7 mm and a width of 4·5 mm; BR 1903 is 4·5 mm long and 4·0 mm wide; and BR 1904 is 3·8 mm long and 3·5 mm wide.

Diagnosis. Average-sized *Schizambon* (up to approximately 5 mm in length) with finely reticulate micro-ornament. Median fold lacking in pedicle valve.

Description. The pedicle valve is gently convex and roughly subcircular in outline, slightly longer than wide. The pedicle foramen, which lies anterior to the beak, is moderate in size and widens anteriorly. It is bounded posteriorly by a sunken, elongate, triangular pedicle track. The beak is situated marginally.

The surface ornament is finely reticulate and consists of fine concentric growth lines and radial costellae; it is inconspicuous near the beak and pedicle foramen and becomes more distinctive toward the valve margin. At a distance of 2 mm from the umbo of the holotype, the radial costellae have a frequency of approximately 16 per mm.

The brachial valve is unknown.

Discussion. Of species described and figured in sufficient detail, the Argentinian early Ordovician *S. australis* Ulrich and Cooper (1936, p. 619; 1938, p. 60, pl. 4E, figs. 14–22) bears closest resemblance to the Antarctic specimens. This species differs principally from *S. reticulatus* because its exterior is dominated by fine, radiating costellae with minor concentric threads, whereas *S. reticulatus* is characterized by a much more even development of costellae and fine growth lines which produce a reticulate pattern. Also, the pedicle valve of *S. reticulatus* lacks a median fold,

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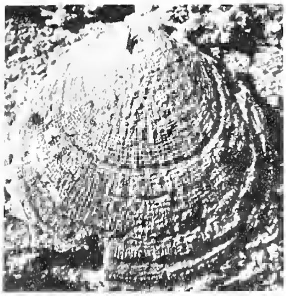
EXPLANATION OF PLATE 38

Figs. 1–2. *Schizambon reticulatus* MacKinnon, sp. nov. 1, BR 1902, holotype, external view of pedicle valve, ×8. 2, BR 1903, paratype, external view of pedicle valve, ×7.

Figs. 3–10. *Prototreta* sp. indet. All except fig. 10 are scanning electron micrographs. 3, BR 1912, external view of pedicle valve showing details of protegular region and pedicle foramen, ×200. 4, BR 1916, oblique lateral view of brachial valve interior, ×18. 5, BR 1546, external view of brachial valve, ×17. 6, BR 1911, pedicle valve in lateral profile, ×19. 7, BR 1911, external view of pedicle valve, ×19. 8, BR 1916, internal view of brachial valve, ×18. 9, BR 1911, oblique posterior view of pedicle valve showing pseudointerarea with intertrough, ×19. 10, BR 1913, external view of partly decorticated pedicle valve, ×16.

Figs. 11–19. *Billingsella* sp. indet. 11, BR 1555, internal mould of pedicle valve, ×2·5. 12–13, BR 1556, rubber-latex cast and internal mould of brachial valve, ×3. 14, BR 1556, internal mould of pedicle valve showing development of mantle canal system, ×4. 15–16, BR 1549, rubber-latex cast and internal mould of pedicle valve, ×3. 17–18, BR 1551, rubber-latex cast and internal mould of small brachial valve, ×3. 19, BR 1552, part of slab with several external moulds of brachial and pedicle valves, ×2.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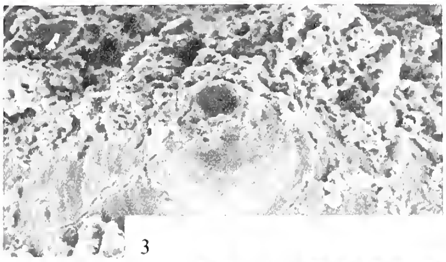
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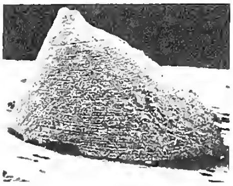
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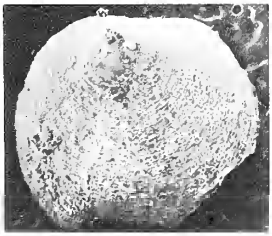
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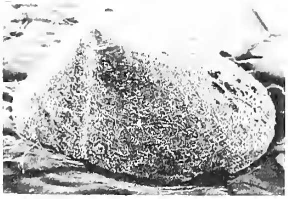
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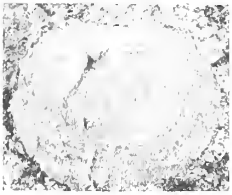
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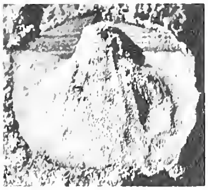
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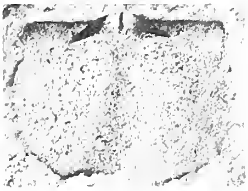
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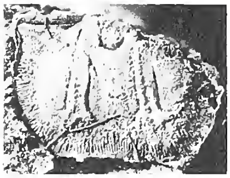
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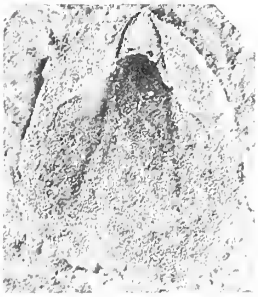
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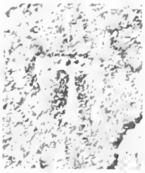
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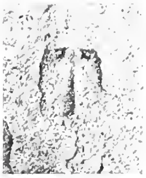
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SHERGOLD *et al.*, Antarctic Cambrian brachiopods a feature faintly discernible in *S. australis* and variably developed in many other species of *Schizambon*.

A single specimen of a small inarticulate brachiopod bearing a reticulate surface pattern was figured by Walcott (1912, p. 679, pl. 79, fig. 5, 5*a*) who named it *Acrotreta*? *cancellata*. Ulrich and Cooper (1938, p. 62) listed this specimen from the early Ordovician of Nevada as a *Schizambon* without adding further to Walcott's inconclusive description. Although similarities in micro-ornament suggest specific affinity, the development of angular cardinal extremities in *S. cancellata* (as observed in Walcott's fig. 5) serves to distinguish this species from *S. reticulatus* which has more evenly arcuate posterolateral margins.

Superfamily ACROTRETACEA Schuchert, 1893
Family ACROTRETIDAE Schuchert, 1893
Genus PROTOTRETA Bell, 1938

Type species. Prototreta trapeza Bell (1938, p. 405, pl. 1, figs. 1–6; 1941, pp. 229–230, pl. 31, figs. 34–38), middle Cambrian, *Bathyuriscus* Zone, Big Belt Mountains, Montana; by original designation.

Other species. A. attenuata Meek (1873, p. 463, footnote), middle Cambrian Meagher Limestone, Gallatin, Montana; also figured by Bell (1941, p. 223, pl. 31, figs. 20–23) and Robison (1964, p. 559, pl. 91, figs. 10–15) who give synonymies. *P. flabellata* Bell (1941, pp. 223–226, pl. 31, figs. 49–58), middle Cambrian, *Ehmania* Zone, Meagher Limestone, Wyoming and Montana. *Homotreta interrupta* Bell (1941, pp. 230–231, pl. 30, figs. 19–26), middle Cambrian, 'Pagoda' Limestone, Montana. *P. mimica* Bell (1941, pp. 226–228, pl. 31, figs. 24–33), middle Cambrian, Meagher Limestone, Big Belt Mountains, Montana. *P. subcircularis* Bell (1941, pp. 228–229, pl. 31, figs. 10–14), middle Cambrian, *Bathyuriscus* Zone, Meagher Limestone, Horseshoe Hills, Montana.

Comments. The concept of *Prototreta* has been discussed at length by Bell (1938, 1941). Robison (1964, p. 559) and Rowell (1965, p. 276) place *Homotreta* in junior synonymy with *Prototreta*. *Angulotreta* Palmer (1954, p. 769) has brachial valves indistinguishable from those assigned to *Homotreta*. The pedicle valve of *Angulotreta* has a deltoid interarea instead of the intertrough seen in *Prototreta*. Previously well-known species of *Prototreta* appear to be mainly from the middle Cambrian, *Bathyuriscus*-*Elrathina* Zone and *B. fimbriatus* and *Bolaspidella contracta* Subzones of the *Bolaspidella* Zone (Robison 1964, pp. 559–560). The occurrence here documented thus extends the upper range of the genus well into the late Cambrian.

Prototreta sp. indet.

Plate 38, figs. 3–10

Material. Five pedicle and three brachial valves which have the following dimensions (in mm):

		Length	Width	Height
Pedicle valves	BR 1911	1·5	1·7	0·9
	BR 1912	2·0	2·1	1·4
	BR 1913	1·8	2·0	0·8
	BR 1914	1·0	1·5	0·7
Brachial valves	BR 1916	1·7	1·8	
	BR 1546	1·1	1·3	

Description. Both valves are transversely suboval in outline. The pedicle valve is moderately high and proconical in lateral profile. Apart from a small apical protuberance, the curvature of the shell in lateral profile is gently and evenly convex. The maximum height of the pedicle valve, at the valve apex, is about one-third of the length from the posterior valve margin. The pedicle foramen is small, circular, apical, and directed ventrally, not posteriorly. The posterior sector of the valve forms a broadly triangular pseudointerarea which is planar in lateral profile. The pseudointerarea is interrupted medially by a well-defined intertrough which widens gradually from apex to commissure. Valve ornamentation consists of numerous distinct fila (approximately 40 fila per mm). Fila are absent on or very close to the apex of the valve. Almost no internal details are discernible owing to sediment infilling, but in one partly decorticated specimen (BR 1913) a pair of posterolaterally situated cardinal muscle scars could be distinguished when viewed from the exterior. At the apex of this specimen there is a small depression which may have accommodated skeletal material in the form of a short apical process.

The brachial valve possesses a low, gently convex profile. Anacline dorsal propareas are separated by a triangular, concave, median groove. A pair of subelliptical cardinal muscle scars diverge anterolaterally in front of the propareas. Lateral to the apex of the median septum are two small, faintly impressed anterior muscle scars. The median septum is blade-like and subtriangular in profile, with its maximum height of about 0·25 valve length occurring at about 0·6 of valve length. In all three specimens the median septum is damaged to some extent so that the possibility of some digitation of the anterior edge cannot be excluded. At its posterior extremity the septum buttresses the concave median groove.

Discussion. The lack of sufficiently clean and undamaged pedicle and brachial valve interiors renders an identification to species level difficult. In the possession of a protoconical lateral profile, a relatively planar pseudointerarea with well-marked intertrough, finely concentric ornament, and a high, blade-like subtriangular medium septum, this Antarctic acrotretid closely resembles *P. interrupta* (Bell) (1941, p. 230, pl. 30, figs. 19–26).

Class ARTICULATA Huxley, 1869
Order ORTHIDA Schuchert and Cooper, 1932
Suborder ORTHIDINA Schuchert and Cooper, 1932
Superfamily BILLINGSELLACEA Schuchert, 1893
Family BILLINGSELLIDAE Schuchert, 1893
Genus BILLINGSELLA Hall and Clarke, 1892

Type species. Orthis pepina Hall (1863, p. 134, pl. 6, figs. 23–27), late Cambrian, Franconia Formation, Wisconsin; designated by Hall and Clarke (1892, p. 230).

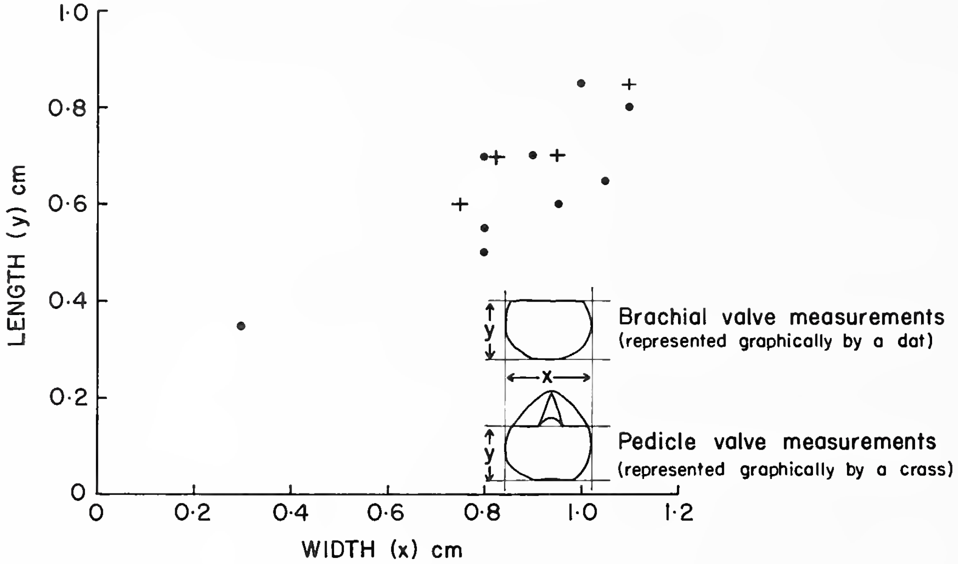
Other species. Other species of *Billingsella* are too numerous to list here: to date fifty species and subspecies can be assigned to the genus whose concept has been reviewed by Schuchert and Cooper (1932), Ulrich and Cooper (1938), Bell (1941), and Nikitin (1956). The last lists twenty-four species definitely assigned to *Billingsella*, and nine possible ones (1956, pp. 25–26), but this listing is incomplete.

Comment. Billingsella is a cosmopolitan genus of middle Cambrian to early Ordovician age, which occurs in Europe, U.S.S.R., China, Korea, Vietnam, Iran, U.S.A., Canada, Argentina, and Australia. It has been recorded previously from Antarctica by Webers (1972, p. 237). The majority of *Billingsella* species are from the late Cambrian of North America.

Billingsella sp. indet.

Plate 38, figs. 11–19

Material. Except for a few, rather worn pedicle valve exteriors, all material consists of internal and external moulds. Twenty-one disarticulated internal moulds were recorded from two slabs of very calcareous muddy fine sandstone (MS/f272). Several disarticulated internal and external moulds were recorded from small fragments of fissile wavy laminated siltstone (MS/f266). One internal and one external mould, both brachial valves, were recorded from fragments of a massive, very fine sandstone (MS/f271). A number of internal and external moulds were recorded from a calcareous siltstone (MS/f274). Figured specimens have measurements as follows: BR 1549 has a length of 13 mm and a width of 11 mm; BR 1551 is 3·5 mm long and 3 mm wide; BR 1553 is 8 mm long and 11 mm wide; BR 1555 is 9·2 mm long and 9·5 mm wide. Length/width parameters for nine brachial and four pedicle valves are illustrated in text-fig. 2.



TEXT-FIG. 2. Graph showing the relationship of brachial and pedicle valve length to width in *Billingsella* sp. indet.

Description. The outline of the pedicle valve is subquadrate or elongate subrectangular, with the width of the hinge line slightly more than, equal to, or slightly less than, the width at about mid valve. The interarea, which is orthocline to slightly apsacline, is generally one-third to one-half as long as wide. The posterolateral margins of the interarea are slightly convex outward. The delthyrium, whose sides subtend angles of 27–30°, is restricted for about half its length by a convex pseudodeltidium. No pedicle foramen is apparent within the pseudodeltidium. The cardinal extremities are sharply angular and range from obtuse to right angled. In lateral profile, valve convexity is slight, with greatest curvature at the umbo. The posterolateral flanks are flat or slightly concave. In some valves a slight median fold may be developed. The external ornamentation is variable, being unequally parvicostellate with fila distinct and numerous. Concentric growth lines are variably developed. On the pedicle valve interior, the central muscle field is narrow and anteriorly arcuate, and extends anteriorly for about 0·4 of the valve length. Posteriorly the muscle field is slightly bilobed. The mantle canal system is saccate, with the anterior extremities of the *vascula media* divergent. Around the periphery of some pedicle valves the *vascula media* are seen to be finely branched. The teeth are small and lacking in any support.

The brachial valve is transversely subrectangular in outline, with the width of the hinge approximately equal to the width about the mid valve. The cardinal extremities are roughly rectangular. Valve convexity is the same as or slightly greater than in the pedicle valve. Close to the hinge line a median sulcus is developed but this dies out toward the anterior valve margin. The interarea is short and vertical or slightly anacline. No chilidium is visible. The external ornamentation is unequally parvicostellate, with costellae most prominent on the flanks of the sulcus. Concentric growth lamellae are variably developed. Socket ridges are present on the brachial valve interior as widely divergent, unsupported blades which extend no further than the anterolateral edges of the cup-like sockets. A notothyrial platform is well developed and extends forward as a median ridge toward the centre of the valve. A simple ridge-like cardinal process is located posteromedially on the notothyrial platform. Adductor muscle scars are not discernible.

Discussion. As noted by Bell (1941, p. 245), the general form and ornamentation within many species of *Billingsella* vary widely, and it is often difficult to assign a small sample, such as the one under consideration, to any particular species with any degree of confidence. In addition, the problem is compounded by the lack of adequate published data on the form and variability of any southern-hemisphere species of *Billingsella*. With a substantial number of species of *Billingsella* recorded from the North American continent alone, it is evident that genetic variability was high both temporally and spatially. Morphologic characteristics of the Antarctic species are reflected in several North American species of *Billingsella* described by Ulrich and Cooper (1938), Bell (1941), and Bell and Ellinwood (1962). In particular, there is resemblance to *B. perfecta* Ulrich and Cooper (1936, p. 619; 1938, pp. 74–75, pl. 7, figs. 11–21) and *B. coloradoensis* (Shumard 1860) *sensu* Walcott (1912 (*pars.*), pp. 751–752, pl. 85, fig. 1, 1*c*, 1*e*, 1*f*, 1*i*, 1*k*, 1*s*, and 1*v*) (see also Bell and Ellinwood 1962, p. 410, pl. 62, figs. 1–10) in the nature of its valve profiles and, in part, external ornament. Some specimens, such as BR 1549, have a high interarea imparting an outline reminiscent of *B. perfecta pyriformis* Bell (1941, pp. 247–248, pl. 35, figs. 22–24). *B. texana*, a rather elongate form described by Bell and Ellinwood (1962, p. 413, pl. 62, figs. 11–21) from the late Cambrian of Texas, and considered gradational with *B. coloradoensis*, possesses a similar pedicle valve outline. However, until additional and better-preserved material from the Antarctic is forthcoming, further comparison cannot be made.

The discovery of a small brachial valve internal mould sheds some light on ontogenetic development. Whereas in gerontic forms the median ridge extending anteriorly from the notothyrial platform lies only in the posterior half of the valve, in the neanic form the ridge is much more strongly developed and extends to the valve margin. On the pedicle valve exterior this may well indicate the development of a pronounced median sulcus during the early stages of shell growth, a feature which diminishes progressively with maturity.

Phylum MOLLUSCA (by E. L. Yochelson)
Class HYOLITHA Marek, 1963
Order HYOLITHIDA Matthew, 1899
Family HYOLITHIDAE Nicholson, 1872
Genus HYOLITHES Eichwald, 1840

Type species. Hyolithus acutus Eichwald (1840, p. 97), early Ordovician, late Arenigian, Zone with *Asaphus eichwaldi* (see Öpik 1952, p. 6), Odensholm, Estonia.

Hyolithes sp. indet.

Plate 39, figs. 11–12, 21

Material. Several hyolithid conchs occur along with the more abundant specimens of orthothecoids. The following are figured: TM 5414, 5415, 5425.

Description. All specimens belong within the typical genus and all are conspecific. They are semilenticular in cross-section but the dorsal surface is significantly more inflated than the ventral (Pl. 39, fig. 11); there is no dorsal crest or even a change of curvature. The juncture of the dorsal and ventral surfaces at the lateral edge is relatively sharp and forms a small acute angle (Pl. 39, fig. 11). The apical area is unknown, but the angle of expansion is nearly 22°. Curvature of the ventral surface from apex to aperture is exceedingly slight, and, in the mature part of the conch preserved, is nearly imperceptible. The ligula is prominent and smoothly curved at the ventral apertural margin; this margin seems to occupy about one-sixth of the circumference of a circle (Pl. 39, fig. 12). Growth lines on the dorsal surface are straight from one edge to the other, indicating a simple orthogonal aperture. Except for the closely spaced growth lines there is no ornament. No operculum is known.

EXPLANATION OF PLATE 39

Figs. 1–9. *Contitheca webersi* Yochelson, sp. nov. 1–5, TM 5411, right side, left side, dorsal, ventral, and apical views of holotype, a steinkern, ×5. 6–7, TM 5413, a very slightly oblique natural cross-section of a small paratype, a steinkern and natural cross-section of the larger end, ×5. 8–9, TM 5410, dorsal views of paratype showing fine thread-like longitudinal lirae when illuminated from side and fine transverse growth lines when illuminated from the aperture, ×5.

Fig. 10. '*Pelagiella*' sp. indet. TM 5407, oblique view of steinkern tilted to show profile, ×5.

Figs. 11–12. *Hyolithes* sp. indet. 11, TM 5414, 12, TM 5415, side view of two specimens in profile and ventral view, the one in the lower centre slightly oblique. Fig. 12 also shows TM 5418, a paratype of *Contitheca webersi* with base exposed, ×5.

Figs. 13–20. '*Pelagiella*' sp. indet. 13–14, 20, TM 5406, side view, tilted, oblique basal view and basal view of specimen retaining patch of shell on basal surface, ×5. 15, TM 5407, top of steinkern showing markings which are not growth lines, ×5. 16–18, TM 5408, oblique top view, oblique side view reversed in orientation to show lenticular profile, and basal view of a steinkern, ×5. 19, TM 5409, top view of specimen retaining patch of shell, ×5.

Fig. 21. *Hyolithes* sp. indet. TM 5425, ventral view of a broken specimen with steinkern removed and growth lines of dorsal surface visible towards the apex, ×5.

Fig. 22. *Contitheca webersi* Yochelson, sp. nov. Slab with two incomplete paratypes, TM 5423, 5424, both showing the curvature of the ventral surface, ×5.

Figs. 23–24. *Scaevogyra* sp. indet. 23, TM 5417, side view of a steinkern showing two whorls, ×5. 24, TM 5416, oblique basal view of elongated steinkern; the sharp line to the left intersecting the specimen is a tool mark, ×5.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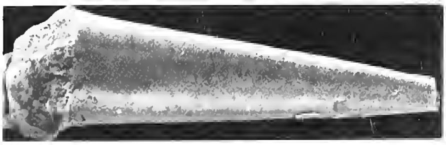
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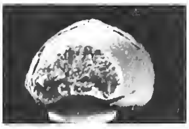
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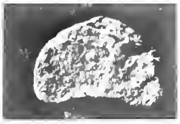
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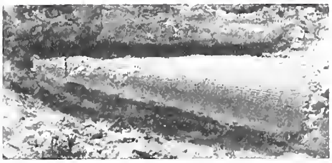
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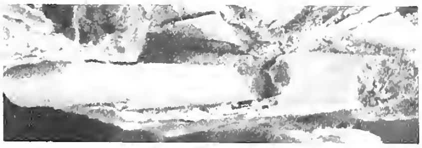
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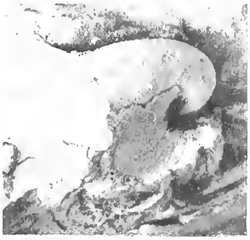
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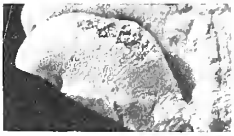
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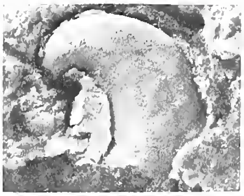
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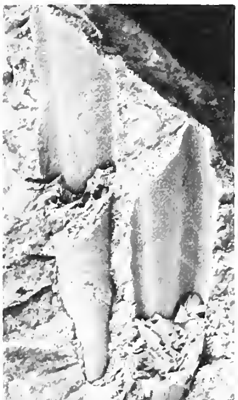
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Discussion. The hyolithids are wider and somewhat longer than associated orthothecoids but probably are not significantly different in terms of hydraulic equivalency. On one small rock slab, similar orientation of these two elongate forms is apparent (Pl. 39, fig. 12). No opercula are known from this assemblage.

Although the material may be well-enough preserved to name formally, it is left in open nomenclature. Literally hundreds of specific names have been applied to Cambrian hyolthids (Sinclair 1946). Many species are poorly understood and likely to be conspecific; it therefore seems inadvisable to add further names to the literature until some of the older named species are better known.

Order ORTHOTHECIDA Marek, 1966

Family ORTHOTHECIDAE Sysoiev, 1958

Genus CONTITHECA Sysoiev, 1972

Type species. Hyolithes cor Holm (1893, p. 58, pl. 1, figs. 60–62; pl. 6, fig. 10), from the middle Cambrian, *Paradoxides forchhammeri* Zone, Andrarum, Sweden; designated by Sysoiev (1972, p. 94).

Other species. Hyolithus (*Orthotheca*) *lineatulus* Holm (1893, p. 59, pl. 1, figs. 53–56; pl. 5, figs. 64–66), middle Cambrian, *P. forchhammeri* Zone, Andrarum, Skaane, Sweden. *H. kotoi* Saito (1936, p. 361, pl. III, figs. 20–23), middle Cambrian, Chunghwa, North Korea.

Contitheca webersi Yochelson, sp. nov.

Plate 39, figs. 1–9, 22

Name. The species is named for G. F. Webers, Macalister College, St. Paul, Minnesota, who initially reported late Cambrian fossils in Antarctica.

Types. Holotype, TM 5411, the steinkern illustrated on Plate 39, figs. 1–5; paratypes, TM 5410, 5412, 5413, 5423, 5424.

Dimensions. The holotype, the only complete specimen available, has a length of 10 mm.

Diagnosis. C. webersi sp. nov. is an orthothecoid with a concavo-convex profile, ornamented longitudinally by numerous fine lirae along the dorsum and sides, but not along the venter.

Description. The nucleus and earliest parts of the shell are unknown, the principal length of which is without septa. The shell is bilaterally symmetrical; the sides diverge at an angle close to 9°; dorsal and ventral surfaces diverge at a smaller angle. Though the dorsum is straight throughout growth, the ventral surface near the anterior margin expands slightly. In side view the mature shell curves downwards. The height to width ratio is 2:3. In cross-section the shell is concavo-convex, superficially resembling that of a kidney bean. The inner two-thirds of the ventral surface, in cross-section, is very gently curved downward from the median line to an abrupt angulated change in slope; the outer part of the ventral surface curves strongly downward, outward, and then upward for an extremely short distance following the arc of a small circle, so that there is a distinct change between the ventral and dorsal surfaces but no development of an angulated lateral edge. The dorsal surface joins the rounded edge smoothly and has a much more gentle curvature; the entire dorsum is nearly a semicircle in cross-section with flanks and median line differentiated, but with a greater degree of curvature than that shown on the inner part of the ventral side. The inner part of the ventral surface is covered with faint, fine, closely spaced growth lines, trending at right angles to the plane of symmetry. An ornament of fine thread-like lirae is present; more than 40 lirae cover the dorsum and rounded ventral margins, but lirae are absent on the gently curved inner face of the ventral surface. At maturity the interspaces between lirae are about twice the width of the threads. The shell is thin, composed of at least two layers.

The operculum is unknown.

Discussion. Presumably the unusual cross-section (Pl. 39, figs. 6–7) is a consequence of the need to keep the aperture above the sediment–water interface and free from sediment. The distinctly curved basal lateral edges (Pl. 39, fig. 4) are obvious; they effectively raise the main part of the shell above the substrate. Presumably the slight downward extension seen in the larger of the shells (Pl. 39, figs. 1–2) is a development of maturity to compensate for the increased weight of the growing animal. The well-rounded dorsum covered by fine ornament (Pl. 39, figs. 8–9) is not easily explained from the viewpoint of functional morphology, though ornament on the rounded lateral edges might serve to lower adhesion of the shell to fine-grained sediments.

Although hyolithids are widespread, the collections of the National Museum of Natural History (formerly U.S. National Museum) contain virtually no undoubted specimens of American orthothecids. Accordingly, comparison is limited to material described by Walcott (1905, 1913) from China. None of his middle Cambrian species show any traces of longitudinal ornament. His only late Cambrian species, *Orthotheca cyrene*, lacks ornament and has a flat ventral surface rather than one concave in outline.

Several dozen Cambrian species of *Orthotheca* (*sensu lato*) were erected before the Second World War (Sinclair 1946) and more have been named since. *C. webersi* is closest to *C. lineatulus* (Holm) from the middle Cambrian *Paradoxides forchhammeri* Zone of southern Sweden. The cross-section of that species is unknown, but the concave venter is more gently curved than in *C. webersi* and is ornamented by longitudinal threads.

The ornament of *C. webersi* is uncommon for the group, and the absence of these threads on the inner part of the ventral surface appears to be unique. I prefer to use a new name rather than to include this excellent material in any ill-defined older named species. For orthothecoids to become useful as stratigraphic tools, monographic treatment is needed. The recent work by Sysoiev (1972) provides an excellent model.

Class GASTROPODA Cuvier, 1797
Order ARCHAEOGASTROPODA Thiele, 1925
Family ONYCHOCHILIDAE Koken, 1925
Genus SCAEVOGYRA Whitfield, 1878

Type species. Scaevogyra swezeyi Whitfield (1878, p. 61; 1882, p. 198, pl. 3, figs. 7–8), late Cambrian, Mendota, Wisconsin, U.S.A.; designated Miller (1889).

Scaevogyra sp. indet.

Plate 39, figs. 23–24

Material. Two specimens, TM 5416, 5417, both steinkerns retaining only small patches of shell near the columellar area.

Description. The specimens are subglobose in outline, possessing few whorls, which expand at a rapid rate (Pl. 39, fig. 23). The nucleus and earliest whorls are unknown, and only two complete whorls remain. The pleural angle on one specimen is nearly 40°; on the second it is nearly 30° but the specimen may have been distorted (Pl. 39, fig. 24). Coiling is hyperstrophic or sinistral, rather than dextral. On the steinkerns the sutures are distinct but not greatly sunken. The whorl profile is generally arcuate, being quite well rounded near the suture, much less obviously curved throughout most of the length of the side, and again well arched across the periphery which is low on the whorl. The basal area is not well known but seems to be in smooth continuous curvature with the periphery so that a depression is formed. However, because the specimens are steinkerns there is no certainty that any umbilicus was present on the shell. So many critical features cannot be determined that a formal name is unwarranted.

Discussion. Scaevogyra is a characteristic late Cambrian genus in North America and north-eastern Asia. Although some of the described species are lower-spired than this new form, a few specimens attributed to the type species *S. swezeyi* Whitfield and others attributed to *S. elevata* Whitfield (1882, p. 199, pl. 3, fig. 11) have the same spire height as the Antarctic material. In spite of the limitations imposed by the quality of the Antarctic specimens, they can be confidently assigned to *Scaevogyra* and thus indicate a late Cambrian, possibly even Trempealeauan, age for the faunule.

Matherella Walcott, 1912, another hyperstrophic late Cambrian genus, is only slightly higher-spired than the Antarctic species; it has a sharp periphery, however, and a distinctly inclined basal surface. *Matherellina* Kobayashi, 1937*a*, an early Ordovician hyperstrophic genus, is lower-spired, but has more flattened whorls on which ribs are prominent.

Mollusca INCERTAE SEDIS
Family PELAGIELLIDAE Knight, 1956
Genus PELAGIELLA Matthew, 1895

Type species. Cyrtolithes atlantoides Matthew (1894, p. 64, pl. 16, fig. 8*a*-*b*), early Cambrian, Hanford Brook, New Brunswick; designated Matthew (1895).

'*Pelagiella*' sp. indet.

Plate 39, figs. 10, 13-20

Material. Five specimens of which the following are figured: TM 5406, 5407, 5408, 5409.

Description. Compressed, asymmetrical, rapidly expanding shells with fine growth lines; nucleus unknown. The shell expands at a rapid rate and completes little more than one whorl, which apparently remains in contact along its inner margin through its growth. The upper suture is depressed with the whorl profile rising strongly upward from it for only a short distance, then following a gentle arch across most of the width, curving downward somewhat more strongly in the outer part of the surface and then dropping abruptly, but smoothly, to form a narrow well-rounded periphery. The profile below the periphery curves strongly inward and more gently downward, shell width below periphery being about twice that above it. The lowest part of the base is near midwhorl, beyond which the surface is arched gently upward and continues inward with little curvature for most of the distance, but at a faint angulation it bends abruptly upward to form the wall of a shallow, narrow umbilicus. Growth lines are unknown on the upper surface and across the periphery, possibly of sweeping opisthocline type below the periphery, but orthocline for at least the inner one-third of the base. Ornament is unknown except for fine, closely spaced growth lines on the inner part of the base. The shell is thin but its structure unknown.

Discussion. Generic assignment of the Antarctic form is uncertain, for the pelagiellids are in need of revision. The type of *Pelagiella*, *C. atlantoides* Matthew, is an early Cambrian species with a strongly inflated lower profile, whereas the Antarctic form is quite lenticular (Pl. 39, fig. 16). Because the specimens cannot be freed from the matrix (Pl. 39, figs. 17, 20) it is difficult to convey their relative compression.

One of the interesting peculiarities of the pelagiellids is the rapid rate of expansion of the coil. The Antarctic species seems to have the whorl in contact (Pl. 39, fig. 18), but others do not complete one full volution. If one assumes that all the Antarctic material is conspecific and then projects the smallest specimen (Pl. 39, fig. 18) on to the largest (Pl. 39, fig. 14) scarcely more than one full volution is completed. This rapid rate of expansion is quite atypical of gastropods and there is no compelling reason to assign *Pelagiella* and its allies to that class. It is therefore left here as *incertae sedis*.

Most of the few Antarctic specimens are steinkerns; only two (Pl. 39, figs. 13–14, 20) retain patches of the shell. The apparent difference between the Antarctic steinkerns (Pl. 39, figs. 15–16), which show a pattern superficially resembling growth lines in some areas but chevron-shaped in other areas, and the patches of shell (Pl. 39, fig. 20) of this species, in which true growth lines are preserved, demonstrates the need to deal with well-preserved material in studying the group. Horny (1964) described two genera of middle Cambrian pelagiellids differentiated to a large extent on their growth lines and ornament.

A survey of the literature suggests that the pelagiellids might have some stratigraphic potential when they are thoroughly monographed; meanwhile, because so many of the species and genera are poorly known, they cannot be used for dating rocks with any degree of confidence.

Phylum ARTHROPODA (by J. H. Shergold)
Class TRILOBITA Walch, 1771
Order MIOMERA Jaekel, 1909
Suborder AGNOSTINA Salter, 1864
Family DIPLAGNOSTIDAE Whitehouse, 1936 emend. Öpik, 1967
Subfamily PSEUDAGNOSTINAE Whitehouse, 1936
Genus PSEUDAGNOSTUS Jaekel, 1909 *sensu lato*

Type species. Agnostus cyclopyge Tullberg (1880, p. 27, pl. 2, fig. 15*a–c*), designated Jaekel (1909, p. 400), from the late *Olenus* and *Parabolina spinulosa* with *Orusia lenticularis* Zones, Andrarum, Skaane, Sweden (see Westergaard 1922, pp. 116–17).

Other species. Other species of *Pseudagnostus* are too numerous to list here: eighty-eight specific taxa can be incorporated in *Pseudagnostus sensu lato.*

Age and distribution. Cosmopolitan, occurring in Alaska, Canada, U.S.A., South America, Europe, U.S.S.R., China, Manchuria, Korea, Vietnam, Australia, and now recorded from Antarctica, during the time span of earliest late Cambrian to early Ordovician.

Pseudagnostus sp. undet.

Plate 41, figs. 9–11

Material. Two cephala and fragments of three pygidia; specimens are preserved with shell, are exfoliated, or preserved as moulds. The two complete cephala have lengths of 3·20 and 3·60 mm; and two assessable pygidia have lengths exclusive of the articulating half-ring, of 3·20 and 3·40 mm. Specimens AR 601–603 are illustrated.

Description. The cephalon is subovate, en grande tenue (Öpik 1961, p. 55; 1967, p. 56), with deliquiate (Shergold 1975, p. 41) marginal furrows. The cephalic acrolobe is unconstricted laterally, and is divided sagittally by a median preglabellar furrow. The glabella, occupying about 75% of the cephalic length (sag.), possesses a sagittally pointed anterior lobe fully 33% of the glabellar length (sag.). The anterior lobe is separated from the remainder of the glabella by a transverse anterior furrow, arched backwards and deepened abaxially around the front of the anterolateral lobes. The axial glabellar node lies behind the anterior furrow and behind the anterolateral lobes. Basal lobes are small and triangular. The external cephalic surface bears a finely araneavelate prosopon.

The pygidium, like the cephalon, is subovate, en grande tenue, with deliquiate marginal furrows. The acrolobe is gently constricted. Axial furrows defining the anterior two segments of the rhachis converge rearwards to the level of the second transverse furrow. Accessory furrows are well developed; thus the species is plethoid (Shergold 1972, p. 15) and deuterolobate. Although the deuterolobe is relatively narrow (tr.) on the illustrated specimens, the pleural areas are restricted. Posterolateral spines are situated in front of a transverse line drawn across the rear of the deuterolobe. The pygidial prosopon, where preserved, appears to be similar to that of the cephalon.

Discussion. The species cannot be accurately determined from the available material, but it exhibits similarity with the type species, *P. cyclopyge* (Tullberg), and its immediate allies, e.g. *P. communis* (Hall and Whitfield) *sensu* Lu *et al.* (1965, pp. 41–42, pl. 4, figs. 6–8) from China; *P. idalis* Öpik (1967, p. 153, pl. 63, figs. 1, 3; pl. 62, figs. 8–9) and *P. ampullatus* Öpik (1967, p. 150, pl. 61, figs. 7–11) from Australia; *P. leptoplastorum* Westergaard (1944, p. 39, pl. 1, fig. 1) from Sweden; and *P. pseudocyclopyge* Ivshin (1956, pp. 17–19, pl. 1, figs. 1–8, 10, 16–17; 1962, p. 18, pl. 1, figs. 19–22) from Kazakhstan. The pygidium of the North American species *P. gyps* Clark (1923, p. 124, pl. 1, fig. 9; 1924, p. 16, pl. 3, fig. 2; Rasetti 1944, p. 234, pl. 36, figs. 20–22) resembles that of the Antarctic specimens.

The combination of cephalon and pygidium represented in the Victoria Land collection is most similar to that described in Lu *et al.* (1965) as *P. communis* (Hall and Whitfield). The only difference appears to be that the Chinese specimen lacks a median preglabellar furrow. Pygidial and cephalic shapes, acrolobes, glabellar proportions, degree of incision of furrows and visibility of lobes, position of axial nodes, and the nature of the marginal furrows are similar. Our material is not referred to the Chinese species, however, as (1) the Chinese species is not conspecific with the

North American *P. communis*, which in general is more effaced and has narrower and shallower marginal furrows, and (2) the provenance of the Chinese form is not known to us, all reference details being published in Chinese.

Both Antarctic and Chinese species differ from *P. cyclopyge* (Tullberg) in cephalic shape; their axial glabellar nodes are situated further rearwards and their anterior glabellar furrows are decidedly transverse. *P. idalis* Öpik and *P. ampullatus* Öpik have similar cephala, but the pygidia of *idalis* have posterolateral spines situated further rearwards, and pygidia of *ampullatus* possess a more bulbous deuterolobe completely encircled by accessory furrows. Some comparison may be made with the pygidia referred by Ivshin (1962) to *P. pseudocyclopyge*, but the cephalon of that species appears to possess V-form anterior glabellar furrows.

The observed prosopon of *Pseudagnostus* sp. probably sets it apart from most other described species. Often, however, these have been previously described from indifferent or inadequate material, or are parietal surfaces which do not show the external prosopon. *P. araneavelatus* Shaw (1951, p. 113, pl. 24, figs. 12–16), from Vermont, has a comparable prosopon, albeit somewhat heavier. This species differs quite substantially, however, in both glabellar and pygidial characteristics from that treated here, and also occurs at a considerably later date (early Ordovician). I hesitate to erect yet another species of an already abused genus; the collection of further material, however, might aid interpretation substantially.

Order PTYCHOPARIIDA Swinnerton, 1915
Superfamily PTYCHOPARIACEA Matthew, 1887
Family EULOMATIDAE Kobayashi, 1955
(*pro* EULOMIDAE Kobayashi, 1955, *sensu* Öpik, 1963)
Genus STIGMATOA Öpik, 1963

Type species. By original designation, *Stigmatoa diloma* Öpik (1963, pp. 89–90, pl. 4, fig. 2), from the *Erixanium sentum* Zone, Georgina and Pomegranate Limestones, western Queensland, Australia.

Other species. S. silex Öpik (1963, pp. 90–91, pl. 4, fig. 4), *E. sentum* Zone, O'Hara Shale, Pomegranate Limestone, western Queensland, Australia. *S. sidonia* Öpik (1963, pp. 91–92, pl. 4, fig. 1), *Irvingella tropica* with *Agnostotes inconstans* Zone, Pomegranate Limestone, western Queensland, Australia. *S. tysoni* Öpik (1963, pp. 92–93, pl. 4, fig. 3), *E. sentum* Zone, Georgina Limestone, western Queensland, Australia.

Age and distribution. All previously known species occur in Australia, mainly in carbonate sequences of western Queensland, where their age is early late Cambrian, late Idamean, Zones of *E. sentum* and *I. tropica* with *A. inconstans.*

Stigmatoa sp. undet.

Plate 41, figs. 1–2

Material. A single cranidial fragment, AR 604, which has a glabellar length of 3·70 mm.

Discussion. Stigmatoa sp. is characterized by a stout occipital spine (Pl. 41, fig. 2), sigmoidal preoccipital glabellar furrows, large palpebral lobes situated close to the glabella, and a finely granulose prosopon.

Although neither preglabellar area nor posterolateral limbs are preserved on the only available specimen, the combination of characteristics is sufficient to differentiate *Stigmatoa* sp. from other species of the genus. *S. diloma* has a similarly stout occipital spine, but wider (tr.) palpebral areas, and hence longer ocular ridges. *S. silex* has similarly sited palpebral lobes and similarly stout occipital spine, but appears to have a punctate test. *S. sidonia* has only a short occipital spine and a minutely punctate test. *S. tysoni*, perhaps the closest species to *Stigmatoa* sp. in terms of gross morphology, has a similar relationship of palpebral lobes to glabella, but possesses a shorter occipital spine and apparently a 'cambric prosopon' (Öpik 1963, p. 92), presumably having a woven rather than granular appearance.

Family ELVINIIDAE Kobayashi, 1935 *sensu* Palmer, 1960

Subfamily ELVINIINAE Kobayashi, 1935 *sensu* Palmer, 1960

Genus OLENTELLA Ivshin, 1956

Type species. By original designation, *Olentella olentensis* Ivshin (1956, pp. 66–67, pl. V, figs. 1–11; pl. VI, figs. ?6, ?10; *in* Nikitin 1956, pl. XI, fig. 7), from the late Tuorian (Ivshin and Pokrovskaya 1968, p. 101), *Aphelaspis–Kujandaspis* Zone, Tortkuduk Suite, central Kazakhstan, U.S.S.R.

Other species. O. shidertensis Ivshin (1956, pp. 68–69, pl. VI, figs. 1–11; pl. VII, figs. 1–8), locality and horizon as for the type species. *O. illustris* Lazarenko (1966, pp. 64–65, pl. VIII, figs. 4–8), Kyutyungd depression, River Olenek, North Siberian Platform, Zone of *Irvingella/Cedarellus felix*.

Age and distribution. U.S.S.R., Kazakhstan, late Tuorian, *Aphelaspis–Kujandaspis* Zone; North Siberian Platform, early Shidertan, *Irvingella/Cedarellus felix* Zone; Antarctica, Northern Victoria Land, probably late Idamean/early Franconian.

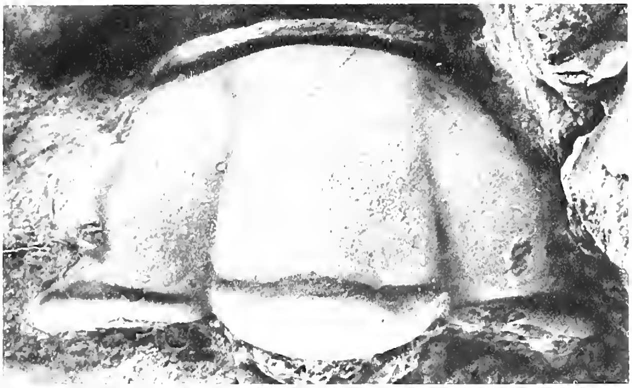
Discussion. As far as cranidial characteristics are concerned, *Olentella* Ivshin, 1956, together with *Kujandaspis* Ivshin, 1956, *Pedinocephalus* Ivshin, 1956, *Pedinaspis* Ivshin, 1962, and possibly *Apheloides* Ivshin, 1962 appear to form a morphologically related group. Their closest affinities seem to lie with Elviniinae of the *Dunderbergia–Elburgia–Elvinia* generic group, and Dokimocephalinae (*Iddingsia*) of North America, with which it is proposed that they be classified.

Cranidia of *Olentella* and *Dunderbergia* have much in common; they have similar shapes and segmentation and preglabellar areas of similar appearance. The preoccipital furrows are sagittally discontinuous in both genera. *Olentella* is distinguished by possessing a relatively narrower (tr.) preglabellar area, relatively shorter (sag.) preglabellar field but, a thicker (sag.) anterior cranidial border. The palpebral lobes of *Dunderbergia* are further from the glabella. The closely spaced palpebral lobes of *Olentella*, and proportions and relationships of the components of the preglabellar area, relate the Kazakhstan genus to *Iddingsia*, but the latter has a more inflated, less-tapered glabella, and stronger glabellar furrows.

EXPLANATION OF PLATE 40

Figs. 1–6. *Prochuangia* sp. aff. *P. granulosa* Lu, 1956. 1, AR 617, cranidium retaining test, showing faint granulosity, dorsal view, ×8. 2, AR 617, as above, lateral view, ×8. 3, AR 618, partially exfoliated cranidium with granulose prosopon, dorsal view, ×8. 4, AR 620, pygidium retaining external test, granulose, dorsal view, ×18. 5, AR 621, latex cast from mould of exfoliated pygidium showing traces of caecal network, dorsal view, ×6. 6, AR 619, librigena retaining test, oblique dorsal view, ×8.

Figs. 7–9. *Proceratopyge* (*Proceratopyge*) cf. *P. lata* Whitehouse, 1939. 7, AR 622, early holaspid cranidium with test, dorsal view, ×12. 8, AR 622, as above, lateral view, ×12. 9, AR 623, pygidial fragment, oblique dorsal view, ×12.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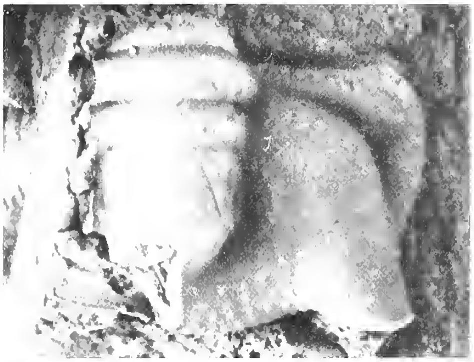
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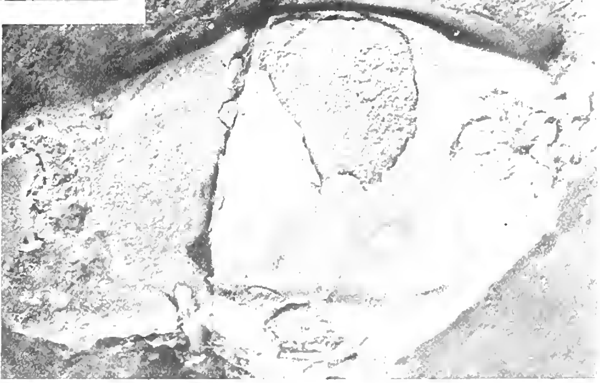
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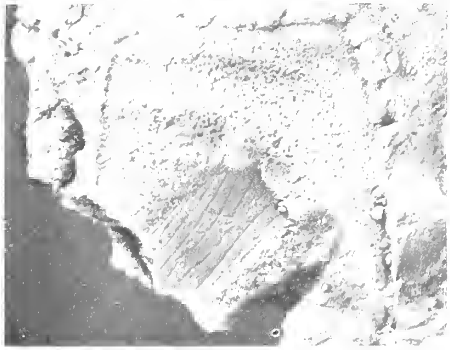
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Olentella cf. *olentensis* Ivshin, 1956

Plate 42, figs. 1–2, 3?, 7?, 9–10

cf. 1956 *Olentella olentensis* gen. et sp. nov., Ivshin 1956, pp. 66–67, pl. V, figs. 1–11; pl. VI, figs. ?6, ?10.

Material. Four cranidial fragments, a possible librigena, a thoracic fragment, and six pygidial fragments. Specimens AR 605–609 are figured. Measured cranidia vary in length between an estimated 3·40 and 5·60 mm; the lengths of the pygidia, excluding the articulating half-ring, vary between 2·20 and 7·40 mm.

Description. The cranidium is sagittally very convex (Pl. 42, fig. 2) in profile. Its glabella is conical, bounded by anteriorly converging axial furrows. Glabellar furrowing is ill-defined, three pairs of furrows being faintly discernible, all sloping adaxially and rearwards. The preoccipital furrows are apparently sigmoidal; their extremities very nearly merge sagittally.

The occipital ring is broken on all the available specimens, but appears to be slightly wider (tr.) than the preoccipital glabellar lobes, and differentiated from the glabella by a clearly defined occipital furrow.

Preocular facial sutures diverge strongly forwards, enclosing a wide (sag.) anterior cranidial border and shorter (sag.), gently convex (sag.) preglabellar field. The anterior cranidial contour (plan view) is strongly arched forwards, as is the anterior marginal furrow. Postocular sections of the facial suture enclose short (tr.) triangular posterolateral limbs bearing distally widened (exsag.) marginal furrows.

The palpebral lobes are arcuate, situated close to the glabella, and long, extending forwards from the anterior part of the preoccipital lobes to the level of the very faint anterior lateral furrows. Ocular ridges are short, slope rearwards, and are faintly duplicated. Where they intersect the axial furrows the glabella and preocular areas are joined, presumably by an underlying caecal diverticulum. The palpebral areas are narrow (tr.).

The prosopon of exfoliated cranidia is punctate, but that of testaceous specimens is composed of irregularly and sparsely scattered granules set in a very fine dense matrix of smaller granules.

The librigena (Pl. 42, fig. 3), which is tentatively placed in the species, is aphelaspidinid in aspect, possessing prominent lateral and posterior borders defined by

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EXPLANATION OF PLATE 41

Figs. 1–2. *Stigmatoa* sp. undet. 1, AR 604, cranidial fragment retaining test, finely granulose prosopon, dorsal view, × 8. 2, AR 604, as above, oblique lateral profile to show occipital spine, × 8.

Fig. 3. *Pedinocephalus* cf. *bublichenkoi* Ivshin, 1956. AR 611, testaceous cranidial fragment, dorsal view, × 6.

Fig. 4. Aphelaspid sp. 1. AR 612, cranidial fragment, dorsal view, × 8.

Fig. 5. Trilobita genus et species incertae sedis, sp. 4. AR 626, partially exfoliated librigena, dorsal view, × 6.

Fig. 6. Olenid sp. undet. AR 616, latex cast from external mould of incomplete cranidium, dorsal view, approx. × 12.

Fig. 7. Aphelaspid sp. 2. AR 613, mainly exfoliated pygidium, dorsal view, × 8.

Fig. 8. *Irvingella*? sp. undet. AR 610, damaged pygidial fragment, dorsal view, × 8.

Figs. 9–11. *Pseudagnostus* sp. undet. 9, AR 601, testaceous cephalon with finely granulose prosopon, dorsal view, × 12. 10, AR 603, latex cast from external mould of exfoliated pygidium, dorsal view, × 12. 11, AR 602, mainly exfoliated pygidium, dorsal view, × 12.

PLATE 41

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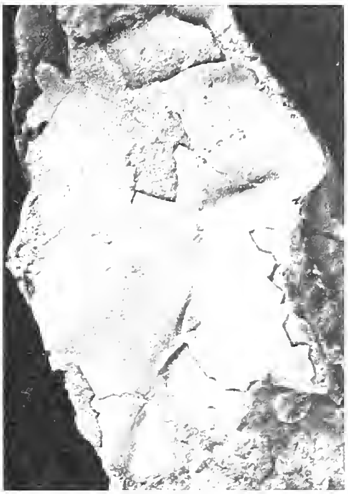

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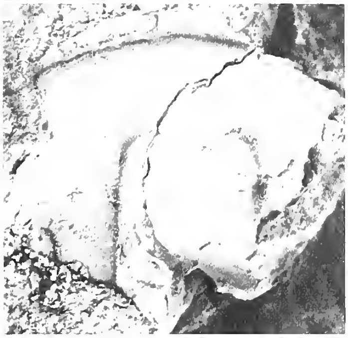

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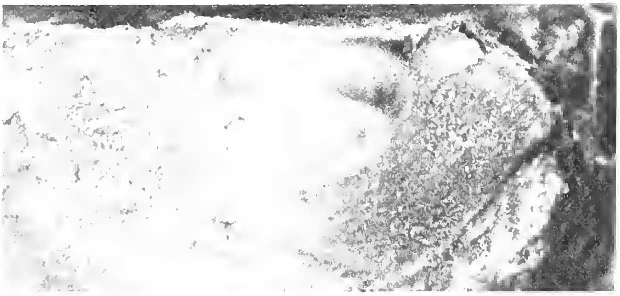

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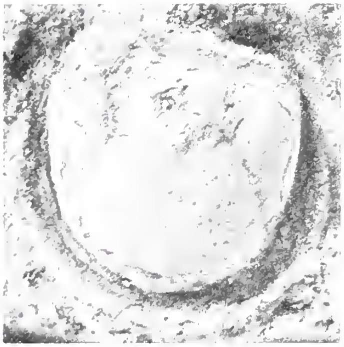

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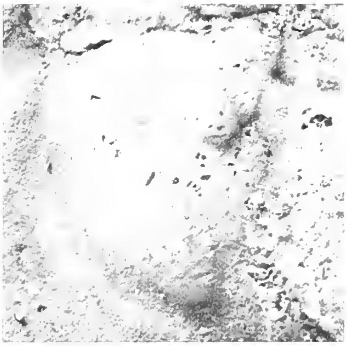

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shallow marginal furrows which combine at the genal spine base and continue a short distance along the centre of the spine. The genal spine, although broken off, appears to have been long and stout. The genal field has low convexity (tr., exsag.) and bears a radiating caecal system which is suppressed at the lateral marginal furrow. The lateral margins bear terrace lines. Other visible portions of the librigena carry a fine dense granulation.

The thoracic segment (Pl. 42, fig. 7), tentatively included in the species, has a similar prosopon to that of the cranidium. It is weakly fulcrate, but anterolaterally bears a broad articulating facet. Its pleural furrow is wide (exsag.), very clearly defined, striking obliquely across the pleuron. The axial portion of the segment bears a sagittal node. Although it is bluntly pointed, the segment appears to lack a free distal spine.

The six associated pygidia are semicircular in shape. All possess wide (tr., exsag.) flange-like borders, widened out laterally. The borders are well delineated from the furrowed pleural zone by shallow and prominent marginal furrows. There is evidence for three pleural segments bearing shallow pleural furrows which terminate at the marginal furrows. Interpleural furrows are present, but faint. The axis contains three, possibly four, segments and a fused terminal piece. The species lacks a post-axial ridge. The pygidial prosopon is similar to that of the cranidium: the axial rings bear small fine granules, and larger scattered ones occur along the pleural 'ribs'.

Discussion. Although referred to *Olentella* cf. *olentensis*, the illustrated cranidia share properties of both that species and *O. shidertensis* Ivshin, 1956; they have the acutely rounded glabella of *O. olentensis* combined with the convexities of *O. shidertensis.* The Antarctic material possesses characteristics of the preglabellar area similar not only to *Olentella*, but also to material which Ivshin (1962, pl. III, figs. 1–12) referred to *Aphelaspis nobilis.* Pygidia referred here to *Olentella* are most comparable to that which Ivshin also assigned to *A. nobilis* (loc. cit., fig. 13). The librigena illustrated here resembles that of *A. subditus* Palmer (1965, pl. 8, fig. 24). The parts here assembled to represent *Olentella* cf. *olentensis* may, therefore, be erroneously associated. Taxonomic assessment is made difficult by the fact that such trilobites appear to bridge the concepts of the families Elviniidae and Pterocephaliidae as presently understood.

Genus IRVINGELLA Ulrich and Resser, 1924

Type species. By original designation, *Irvingella major* Ulrich and Resser (*in* Walcott 1924*b*, p. 58, pl. 10, fig. 3), type locality and formation not stated. Full discussion and synonymy associated with this species are given by Palmer (1965, p. 48).

Other species. Palmer (1965, p. 45) has noted that '39 specific names have been applied to trilobites having the characteristics of *Irvingella*'. Those listed here are the few species in which the pygidium is known with some certainty: *I.* (*Irvingellina*)? sp. undet., Kobayashi (1938, p. 176, pl. XV, fig. 3*a*), *Elvinia* Limestone, Mount Hunter, B.C., Canada. *Irvingella media* Resser, 1942 (*sensu* Wilson 1949, p. 39, pl. 11, figs. 16–17, 19–20), *Elvinia* Zone, Wilberns Formation, central Texas, U.S.A. *I. obliquoensis* Rusconi, 1953 (*sensu* Rusconi 1954, p. 31, pl. 2, figs. 8–9; text-figs. 17–18), Quebradita Oblicua, Argentina. *I. tropica* Öpik (1963, pp. 96–97, pl. 4, figs. 5–8), Zone of *I. tropica* with *Agnostotes inconstans*, Pomegranate Limestone, western Queensland, Australia. *I. flohri* Resser, 1942 (*sensu* Palmer 1965, pp. 47–48, pl. 6, figs. 16, 19–20, 24), *Elvinia* Zone, Nevada and Utah, U.S.A. *I. major* Ulrich and Resser, 1924 (*sensu* Palmer 1965, p. 48, pl. 6, figs. 9–15), *Elvinia* Zone, Nevada, U.S.A. *I. nuneatonensis* (Sharman, 1886) (*sensu* Rushton 1967, pp. 339–348, pl. 52, figs. 1–12), *Olenus* Zone (younger than *O. dentatus*), Outwood Shales, Warwickshire, U.K. *I. perfecta*

Tchernysheva (1968, pp. 207–210, pl. 22, figs. 1–8), Chopkin Suite, Norilsk region, North-west Siberian Platform.

Age and distribution. Irvingella is a cosmopolitan genus occurring in or about the *Elvinia* Zone and its time equivalents in Europe, Siberia, China, Australia, South America, U.S.A., and Canada.

Irvingella? sp. undet.

Plate 41, fig. 8

Material. A single incomplete exfoliated pygidium, AR 610, with sagittal length of 2 mm.

Description. The pygidial outline is trapezoidal, with a slightly indented posterior margin. Borders are not preserved laterally. The pleurae are appreciably convex (tr.); only the first pleural segment bears a pleural furrow; interpleural furrows are completely effaced. The axis is strongly raised above the pleurae and was originally composed of two segments and a rather prominent bulbous terminal piece; the articulating half-ring and the anterior portion of the first axial segment are, however, broken away. A faint post-axial ridge is present.

Discussion. Although the pygidial fragment is inadequate for detailed comparison, the Antarctic *Irvingella*? appears to be most similar in segmentation to the North American species *I. major* (as interpreted by Palmer 1965, pl. 6, figs. 9 and 11) and the Australian *I. tropica* Öpik (1963, pl. 4, fig. 8). *I. nuneatonensis* (Sharman) has, according to Rushton (1967, p. 342), three axial segments, as has *I. perfecta* Tchernysheva (1968). *I. tropica* and *I. flohri* Resser have considerably thicker (sag., exsag.) posterior borders than that evident from *Irvingella*? sp.

The over-all appearance of *Irvingella*? sp. is somewhat similar to that of species of *Dunderbergia* described by Palmer (1960). Although pygidia of *D. variagranula* Palmer (1954, p. 761, pl. 88, fig. 7; 1960, p. 68, pl. 4, figs. 22, 25–26, 29), *D. polybothra* Palmer (1960, pp. 67–68, pl. 5, figs. 1–4, 6–7, 9, 14), and *D. bigranulosa* Palmer (1960, pp. 66–67, pl. 5, figs. 10–13, 15–23) have similar shapes to that of *Irvingella*? sp., they differ in having longer (sag.) axes with at least three distinct segments and less bulbous terminations.

Family PTEROCEPHALIIDAE Kobayashi, 1935
Subfamily PTEROCEPHALIINAE Kobayashi, 1935
Genus PEDINOCEPHALUS Ivshin, 1956

Type species. By original designation, *Pedinocephalus bublichenkoi* Ivshin (1956, pp. 58–60, pl. II, figs. 1–8), late Tuorian, *Aphelaspis*–*Kujandaspis* Zone, Tortkuduk Suite, central Kazakhstan, U.S.S.R.

Other species. P. kasachstanensis Ivshin (1956, pp. 60–62, pl. II, figs. 9–10, ?11, 12), horizon and locality as for type species. *P. bykovae* Ivshin (1956, pp. 62–64, pl. I, figs. 24–26, 28–29), locality as for type species. *Taenicephalus*? *peregrinus* Henningsmoen (1957, pp. 167–169, pl. 1, figs. 1–6), Subzone of *Olenus gibbosus* with *O. transversus*, Västergötland, Sweden. *P. simplex* Ivshin (1962, pp. 96–98, pl. IV, fig. 2), horizon as for type species.

Age and distribution. U.S.S.R., central Kazakhstan, late Tuorian, *Aphelaspis*–*Kujandaspis* Zone; Sweden, Västergötland, *Olenus* Series, *O. gibbosus*–*O. transversus* Subzone; Antarctica, Northern Victoria Land, late Idamean/early Franconian.

Pedinocephalus cf. *bublichenkoi* Ivshin, 1956

Plate 41, fig. 3

cf. 1956 *Pedinocephalus bublichenkoi* sp. nov., Ivshin 1956, pp. 58–60, pl. II, figs. 1–8.

Material. A single incomplete cranidial fragment preserved with shell, AR 611. The left posterolateral limb and the whole of the right-hand side of the specimen, including the occipital ring, are broken away. The specimen is insufficiently complete for measurement; an estimated length is 11 mm.

Description. The glabella tapers markedly towards its anterior end, which is gently and obtusely rounded. Glabellar furrowing is indistinct on the available fragment, preoccipital and median lateral furrows being poorly preserved. The anterior lateral furrows, which lie just behind the intersection of the ocular ridges and the axial furrows, are short and faint, and directed anteriorly and adaxially.

Palpebral lobes are not preserved, but nevertheless appear to have been short (exsag.), probably sited a little anterior of the mid-point of the glabella. Ocular ridges are long, abaxially and posteriorly inclined. They appear to be continuous across the axial furrows, connecting with the anterolateral corners of the glabella.

The preglabellar area is long (sag.), composed of a gently convex (sag.) preglabellar field and equally convex (sag.) anterior cranidial border, about half as long (sag.) as the preglabellar field. The preglabellar furrow is pitted on each side of the sagittal line and faint traces of a parafrontal band are present between the pits. The preglabellar field bears a caecal system which radiates from the vicinity of these pits.

The cranidium has a punctate prosopon.

Discussion. Pedinocephalus cf. *bublichenkoi* is best compared with the holotype of the species (Ivshin 1956, pl. II, fig. 1). The two specimens have similarly strong glabellar taper and degree of anterior rounding, and similarly pitted preglabellar furrow. Preservation of the Antarctic fragment prevents further comparison. By the same characteristics, *P.* cf. *bublichenkoi* can be compared with *P. kasachstanensis* and probably *P. bykovae*. *P.* cf. *kasachstanensis* (see Ivshin 1956, pl. II, fig. 11) has a narrower (tr.), more acutely rounded glabella. *P. simplex* has a glabella with less anterior taper and presumed larger palpebral lobes; and *P. peregrinus* (Henningsmoen) has a considerably shorter (sag.) preglabellar field with less sagittal convexity.

Subfamily APHELASPIDINAE Palmer, 1960

This taxon is used as emended by Palmer in 1962 (p. F32). Three Antarctic taxa are temporarily assigned to it, and are left under open nomenclature.

Aphelaspid species 1

Plate 41, fig. 4

Material. A single cranidial fragment, AR 612, lacking the greater part of the right palpebral area, palpebral lobe, and posterolateral limb. The left posterolateral limb cannot be exposed because the specimen lies adjacent to the *Prochuangia* cranidium figured on Plate 40, fig. 1.

Description. The illustrated cranidium is characterized by diverging preocular facial sutures, short (sag.) anterior cranidial border, and well-defined anterior marginal furrow; in lateral profile the preglabellar field is gently sigmoidal. The glabella is rectangular, parallel-sided, squared off anteriorly, and faintly furrowed. The occipital ring is not preserved. Linear transverse ocular ridges run abaxially from the corners of the frontal lobe. The preserved palpebral lobe has slightly over half the glabellar length (exsag.), and is anteriorly situated. Anterior and posterior palpebral widths (tr.) are equivalent. A fine caecal network radiates across the preglabellar field, otherwise the test is smooth.

Discussion. Aphelaspid sp. 1 is difficult to classify, but is referred to Aphelaspidinae on account of its partial similarity to *Aphelaspis buttsi* (Kobayashi). It can be equally well compared with certain species of *Eugonocare* Whitehouse and *Olenaspella* Wilson.

The available specimen has a preglabellar area of similar appearance to that of holotype of *A. buttsi* (see *Proaulocopleura buttsi*, Kobayashi 1936, p. 93, pl. 15, fig. 6; Resser 1938, p. 95, pl. 16, fig. 8) from Alabama, as refigured by Palmer (1962, p. 35, pl. 4, fig. 31). The palpebral lobes of *A. buttsi* are somewhat shorter (exsag.), but they are connected to the axial furrows by ocular ridges of similar length (tr.) and orientation. *A. buttsi* has a similarly truncate glabella which is less parallel-sided than that of the Antarctic species. Comparison with the many species of *Aphelaspis* is not undertaken as these, in general, have anteriorly tapered and rounded glabellae, and usually their preglabellar areas are structurally and proportionately different.

The nature of the preglabellar area links Aphelaspid sp. 1 with both *Eugonocare* and *Olenaspella*, which have morphologically identical cranidia—being differentiated solely on the absence of pygidial spines in the former (Palmer 1965, p. 64). As in the case of the North American species of *Aphelaspis*, the glabellae of *Eugonocare* and *Olenaspella* are anteriorly tapered and rounded, and glabellar furrowing is generally well defined. The ocular ridges of these genera are less transverse than those of *A. buttsi* and the aphelaspidinid at hand, usually having a gentle inclination to the palpebral lobes which lie somewhat more posteriorly on the genae.

The glabellar and ocular characteristics of Aphelaspid sp. 1 are similar to those of *Olenus asiaticus* Kobayashi, 1944 (see Kobayashi 1962, pp. 54–55, pl. IX, fig. 16*a–b*) but the preocular facial sutures diverge more strongly.

Aphelaspid species 2

Plate 41, fig. 7

Material. A single, mostly complete, mainly exfoliated pygidium, AR 613, whose length, including the articulating half-ring, is 3·80 mm.

Description. The pygidium determined as Aphelaspid sp. 2 has a semicircular shape, with length (sag.), including the articulating half-ring, about 42% of the estimated width (tr.). The axis, which occupies about 85% of the length (sag., including the half-ring), is conical, and composed of three well-delineated segments, a poorly defined fourth, and a terminal piece which may contain one additional fused segment. There is no post-axial ridge. Three pleural segments separated by very faint interpleural furrows are present. They bear wide and shallow pleural furrows which extend close to the pygidial margins. A very narrow border is perhaps present laterally, but merges into the post-axial convexity of the shield posteriorly. The pygidial margins are entire, non-spinose. The articulating half-ring is a simple bar, and fulcration is weak. Faint traces of a caecal network are present post-axially.

Discussion. Shape and segmentation indicate classification within Aphelaspidinae; *A. buttsi* (Kobayashi) as illustrated by Palmer (1962, pl. 4, figs. 26, 31) again offers closest comparison. Aphelaspid sp. 2 may in fact represent the pygidium of the cranidium described as Aphelaspid sp. 1. With *A. buttsi* there is comparable degree of segmentation, similar style of pleural furrowing, and narrow borders. Aphelaspid sp. 2, however, has a more fully rounded shape, less triangular than that of *A. buttsi*. *A. brachyaspis* Palmer (1962, p. 33, pl. 4, figs. 1–19), from the *Aphelaspis* Zone of Nevada, has a similar shape, albeit with outline somewhat indented post-axially, but has fewer segments in both axial and pleural zones.

Aphelaspid species 3

Plate 42, fig. 6

Material. Mould and counterpart of a single incomplete cranidium, AR 614, the specimen lacking palpebral lobes and posterolateral limbs with estimated cranidial length of 6 mm.

Description. Aphelaspid sp. 3 is characterized by widely divergent preocular facial sutures which enclose a preglabellar area comprising a convex (sag.) preglabellar field, narrow (sag.) but deeply and sharply incised anterior cranidial marginal furrow, and relatively narrow (sag.) cranidial border turned slightly addorsally in lateral profile. Ocular ridges are transverse or very slightly sloping posteriorly. The glabella tapers markedly towards the anterior, and has three faint pairs of backwardly directed glabellar furrows; the preoccipital pair is sigmoidal. Only anterolaterally is the occipital ring as wide (tr.) as the preoccipital glabellar lobes. Although the specimen is fairly deeply weathered, Aphelaspid sp. 3 appears to have a granulose prosopon.

Discussion. This species is again difficult to classify because of incompleteness and lack of supporting material. Although probably an aphelaspidinid, its preocular facial sutures are too divergent and its anterior cranidial marginal furrow too sharply incised for inclusion within *Aphelaspis* Resser.

EXPLANATION OF PLATE 42

Figs. 1–2. *Olentella* cf. *olentensis* Ivshin, 1956. 1, AR 605, testaceous cranidium, dorsal view, ×12. 2, AR 605, as above, lateral profile, ×12.

Fig. 3. ?*Olentella* cf. *olentensis* Ivshin, 1956. AR 609, librigena showing caecal network, dorsal view, ×12.

Fig. 4. Trilobita genus et species incertae sedis, sp. 1. AR 623, cranidial fragment, ×8.

Fig. 5. Trilobita genus et species incertae sedis, sp. 2. AR 624, partially exfoliated cranidial fragment, dorsal view, ×4.

Fig. 6. Aphelaspid sp. 3. AR 614, exfoliated mould of incomplete cranidium, dorsal view, ×8.

Fig. 7. ?*Olentella* cf. *olentensis* Ivshin, 1956. AR 606, fragment of thoracic segment which may belong to this species, dorsal view, ×8.

Fig. 8. Trilobita genus et species incertae sedis, sp. 3. AR 625, partially exfoliated librigena, dorsal view, ×8.

Figs. 9–10. *Olentella* cf. *olentensis* Ivshin, 1956. 9, AR 607, exfoliated pygidium, dorsal view, ×12. 10, AR 608, latex cast from external mould of exfoliated pygidial fragment, ×6.

Fig. 11. *Talbotinella*? sp. undet. AR 615, mainly testaceous cranidial fragment, dorsal view, ×8.

Fig. 12. Trilobita genus et species incertae sedis, sp. 5. AR 627, indeterminate early meraspid cephalon, dorsal view, ×28.


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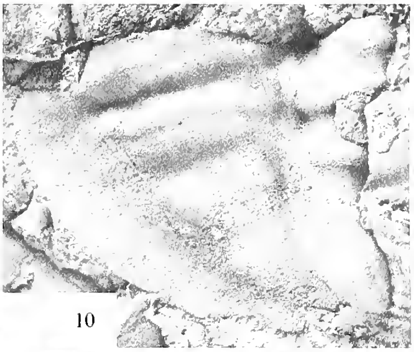
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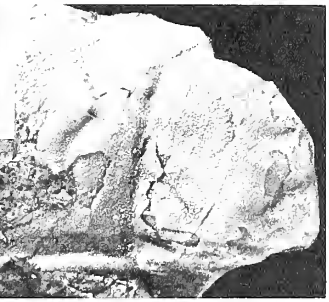
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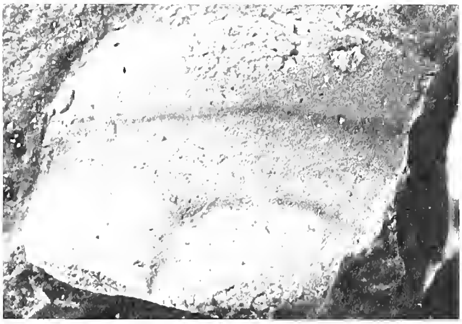
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5

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Aphelaspid sp. 3 most closely resembles two species which have been previously assigned to *Aphelaspis* but which may not belong with this genus. The Antarctic species is considered to have closest affinity with a Chinese species, *A. granulata* Kuo (1963, p. 59, pl. 14, figs. 7–11; *in* Lu *et al.* 1965, p. 177, pl. 30, figs. 1–4), which has similar glabellar shape and furrowing, and apparently a similar preglabellar area. *A. nobilis* Ivshin (1956, pp. 33–36, pl. III, figs. 1–13, 27; pl. IV, figs. 16–17), from central Kazakhstan, also has a similar preglabellar area, but is distinguished by an anteriorly more truncate glabella, and more steeply inclined ocular ridges. *A. granulata* and *A. nobilis* appear to differ from North American species of *Aphelaspis* by the same characteristics which distinguish Aphelaspid sp. 3.

Superfamily OLENACEA Burmeister, 1843
Family TALBOTINELLIDAE Öpik, 1963
Genus TALBOTINELLA Poulsen, 1960 *sensu* Öpik, 1963

Type species. By original designation, *Talbotinella communis* Poulsen (1960, pp. 24–25, pl. 2, figs. 2–8; pl. 3, fig. 2), from the *Bolaspidella* Zone, Cerillo El Solitario, Canota region, Mendoza, Argentina.

Other species. T. leanzai Poulsen (1960, pp. 25–26, pl. 2, figs. 9–12) locality as for type species. *T. rusconii* Poulsen (1960, p. 27, pl. 2, figs. 13–15), locality as above. *T. notulata* Öpik (1963, pp. 73–75, pl. 6, fig. 9), *Glyptagnostus stolidotus* Zone, Georgina Limestone, western Queensland, Australia.

Age and distribution. South America, Argentina, late middle Cambrian, *Bolaspidella* Zone; Australia, late Cambrian, *G. stolidotus* Zone; Antarctica, Northern Victoria Land, late Cambrian, late Idamean/early Franconian.

Talbotinella? sp. undet.

Plate 42, fig. 11

Material. A single imperfectly preserved and partially exfoliated cranidium, AR 615. The specimen lacks most of its preglabellar area and occipital ring, and the whole of the right pleural portion of the cranidium.

Description. The portion preserved is characterized by a conical glabella, rounded anteriorly, bearing three pairs of furrows; it has short sloping ocular ridges, small palpebral lobes situated mostly in advance of the mid-point of the glabella, broad triangular posterolateral limbs, and anteriorly diverging preocular facial sutures. The over-all prosopon is finely and densely granulose; the granules coalesce to form a dense rugosity.

Discussion. Although the general morphology is somewhat similar to that of *T. notulata* Öpik, there are several points of difference. The glabella of the Antarctic species is less conical than that of *T. notulata*, its palpebral lobes are longer (exsag.), its preoccipital glabellar furrows are non-bifurcated, and its anterior lateral furrows, although very faint, are in fact furrows and not pits. No comparison of preglabellar areas can be offered. The test of the Australian species is smooth.

The material illustrated appears to be classified in Talbotinellidae as envisaged by Öpik, but is inadequate to critically evaluate the determined genus, reference to which is therefore queried.

Several other species have similar morphology to the fragment from Victoria Land. In particular, attention may be drawn to the cranidium that Palmer (1954, p. 745, pl. 84, fig. 11) assigned to *Aphelaspis constricta*, a species from the *Aphelaspis* Zone of Texas; and one of the paratype cranidia of *Crepicephalus orientalis* described by Endo (*in* Endo and Resser 1937, p. 344, pl. 66, fig. 12) from the Paishan Formation of Fengtien Province, Manchuria.

Family OLENIDAE Burmeister, 1843
Subfamilia et genus INCERTAE SEDIS
Olenid sp. undet.

Plate 41, fig. 6

Material. A single incomplete, partially exfoliated cranidium, AR 616, preserved as an external mould, with estimated cranidial length (sag.) of 4 mm.

Description. This species is characterized by divergent preocular facial sutures, convex (sag.) preglabellar field, and well-defined anterior cranidial border and marginal furrow. The glabella is parallel-sided, anteriorly rounded, and its furrowing is effaced. The occipital furrow does not reach the axial furrows laterally, and the occipital ring possesses an occipital node. Posterolateral limbs are narrow (exsag.), long (tr.), and triangular. The preserved palpebral lobe is arcuate, equidistant from the axial furrows anteriorly and posteriorly, anteriorly sited, and about one-half the glabellar length (exsag.). Ocular ridges may be curved.

Discussion. If the ocular ridges are curved the species is differentiated from Aphelaspidinae (Pterocephaliidae) and related to Olenidae. Characteristics of the glabella and preglabellar area are also not inconsistent with classification among Olenidae. Insufficient material, however, prevents a qualified determination.

Comparison can be made with few other described species. *Hancrania brevilimbata* Kobayashi (1962, p. 55, pl. IX, figs. 2–6) from the Machari fauna of South Korea, is most similar, but its glabella has a slight anterior taper and considerably stronger furrowing, and its ocular ridges are perhaps sloping rather than curved. Several species of *Olenus* have curved ocular ridges and similarly shaped glabellae, but their glabellar furrowing is invariably stronger, e.g. *O. ogilviei* Öpik (1963, pp. 59–62, pl. 1, figs. 1–9; pl. 2, figs. 2–4). Effacement of the glabellar furrows is, however, no barrier to classification within Olenidae. Well-established genera such as *Peltura* and *Peltocare*, as well as the recently proposed *Leurostega* Robison and Pantoja-Alor, 1968, *Psilocara* Fortey, 1974, and *Svalbardites* Fortey, 1974, all have effaced glabellae. Partial effacement characterizes several others, e.g. *Leptoplastus*.

Superfamily LEIOSTEGIACEA Bradley, 1925
Family LEIOSTEGIIDAE Bradley, 1925
Subfamily PAGODIINAE Kobayashi, 1935
Genus PROCHUANGIA Kobayashi, 1935

Type species. By original designation, *Prochuangia mansuyi* Kobayashi (1935, pp. 186–187, pl. VIII, fig. 8; pl. X, figs. 1–7), from Saisho-ri, South Korea.

Other species. Conocephalites quadriceps Dames (1883, p. 9, pl. 1, figs. 13–18; Lorenz 1906, p. 94, text-fig., referred to *Schantungia* Lorenz; Kobayashi 1937*b*, pp. 75–76, pl. 17, fig. 2*a–c*, referred to *Prochuangia* Kobayashi; Lu *et al.* 1965, p. 416, pl. 79, figs. 2–4), from Saimaki, Liaotung, Manchuria. *P. angusta*

Kobayashi (1935, pp. 188–189, pl. IX, fig. 12), from Saisho-ri, South Korea. *P. posterospina* Kobayashi (1935, pp. 187–188, pl. X, fig. 8), from Saisho-ri, South Korea. *P. imamurai* Endo (1944, pp. 69–70, pl. 10, fig. 12; refigured *in* Lu *et al.* 1965, p. 415, pl. 79, fig. 1), from the Paishan Formation, near Tungchinglien, Liaoyanghsien, Fengtien Province, Manchuria. *P. granulosa* Lu (1956, pp. 376–377, pl. 1, fig. 5; refigured with additional material *in* Lu *et al.* 1965, p. 414, pl. 78, figs. 22–23), from Lungtienchung, Yüping district, eastern Kweichow, China. *P.? berryi* Lochman (1940, pp. 39–40, pl. 4, figs. 17–20), from the *Cedaria* Zone, Bonneterre Dolomite, Missouri, is not referable to *Prochuangia*.

Age and distribution. Before 1967 *Prochuangia* was known only from Asia: Vietnam, China, Manchuria, and South Korea. Since that time, however, Colchen (1967) has recorded its association with *Chuangia* at the eastern end of the Sierra de la Demanda in Logrono Province, northern Spain, and *Prochuangia* is now recorded from Antarctica.

Throughout its range in Asia, *Prochuangia* has a Paishanian (late Dresbachian/Idamean) age, and its occurrence has been thought by Kobayashi (1935, 1960, 1966*a*, 1966*b*, 1967, 1971) to represent a distinct biostratigraphical zone resting with pronounced faunal discontinuity on the *Drepanura* Zone below and directly subjacent to the *Chuangia* faunas. In South Korea, however, a species of *Prochuangia* is found in association with the *Chuangia* faunas (Kobayashi 1966*a*, p. 34, listed), and some doubt must now be expressed on the limited range of the genus. The Antarctic occurrence seems to indicate that the genus existed at least until early Franconian (*Elvinia*) time, i.e. latest *Chuangia* Zone.

Discussion. Concerning the type species, Kobayashi (1935, p. 186) synonymizes specimens from the Tonkin–Yunnan border region of Vietnam and southern China, which were referred by Mansuy (1915, pp. 20–22, pl. II, fig. 14*a–g*) to *C. nais* Walcott. Mansuy (op. cit., explanation to pl. II) indicates, however, that his material was obtained from two distinct horizons; in particular, one pygidium is from his zone of *Ptychaspis angulata* (latest Cambrian) and is very probably not conspecific with the remainder of the figured specimens. Concepts of *Prochuangia* derived from the type species should therefore be based on the Korean material described by Kobayashi.

According to Kobayashi (1935, p. 185) *Prochuangia* is differentiated from *Chuangia* Walcott, 1911 in possessing a pair of pygidial spines, and less 'acutely edged' anterior cranidial border. The absence of a posterior marginal furrow in the pygidium distinguishes it from *Kaolishania*, which also possesses spines. Kobayashi (1935) has noted that the external shell of the glabella is basically unfurrowed, but that the parietal surface possesses three pairs of glabellar furrows, a situation also observed in *Chuangia*.

The most reliable characteristics for the determination of *Prochuangia* appear to be those of the pygidium, as cranidia of the species listed above are not readily distinguished from those of *Chuangia* or *Pagodia*, especially species of the *C. nitida* group (Walcott 1911, pp. 85–86, pl. 15, fig. 6), and of *P.* (*Idamea*) Whitehouse, 1939, *sensu* Öpik, 1967 (see below).

Prochuangia sp., aff. *P. granulosa* Lu, 1956

Plate 40, figs. 1–6

aff. 1956 *Prochuangia granulosa* Lu (sp. nov.), Lu 1956, pp. 376–377, pl. 1, fig. 5.
aff. 1965 *Prochuangia granulosa* Lu, *in* Lu *et al.* 1965, p. 414, pl. 78, figs. 22–23.

Material. This species is known from fragments of thirteen cranidia, eight pygidia, and three librigenae, which make this the most abundantly represented taxon in the collection studied. The illustrated specimens are numbered AR 617-621. Measurable cranidial lengths (sag.) vary between 5·50 and 6·30 mm; pygidial lengths (sag.), excluding the articulating half-ring, measure between 2·00 and 4·20 mm.

Description. The cranidium and librigena illustrated on Plate 40 are well matched and are probably correctly associated with the pygidium, which certainly represents *Prochuangia.* No other combination is possible among the available specimens.

The anterior cranidial margin is gently curved (tr.), passing into a narrow (sag.) upturned anterior cranidial border which bears terrace lines on its adventral and anterior-facing surface. The border is separated from the frontal lobe of the glabella by a deep, narrow (sag.) preglabellar furrow. No preglabellar field intervenes between glabella and border.

The glabella, abutting against the cranidial border, is obtusely rounded anteriorly, and laterally constricted immediately in front of the point at which the ocular ridges intersect the axial furrows, giving the frontal lobe an anterolaterally expanded appearance. Two pairs of glabellar furrows are faintly indicated on the external test: both are arcuate, curving rearwards and adaxially; the preoccipital furrows possibly bifurcate adaxially (Pl. 40, fig. 3).

The occipital furrow is deeply incised, distinctly widened sagittally to form a platform. The occipital ring is slightly wider (tr.) than the glabella, sagittally extended rearwards (Pl. 40, fig. 2), and bears a faint occipital node.

The palpebral lobes are gently arcuate, mainly lying posterior to the mid-point of the glabella, and the palpebral furrows strongly defined. Faint ocular ridges connect the anterior ends of the palpebral lobes to the axial furrows, constricting the glabella at the point of intersection. The preocular facial sutures run exsagittally forwards, intersecting the cranidial margin at an obtuse angle. The postocular facial sutures run obliquely to the posterior margin, enclosing short (tr.), triangular posterolateral limbs. Posterior marginal furrows are sinuous, clearly defined, and wide, and are characterized by a sigmoidal course distally. They close before the extremity of the posterolateral limbs, where a narrow ridge is formed, and apparently do not continue on to the librigena. The cranidial prosopon is finely granulose.

The associated librigena, very similar to that of *Pagodia* (*Idamea*) *baccata* Öpik, 1967, is characterized by a thickened lateral border which bears, across its marginal convexity, branching terrace lines continuing to the doublure of the genal spine posterolaterally, and on to the anterior cranidial border anterolaterally. The lateral marginal furrow terminates a considerable distance from the genal angle. There is apparently no posterior marginal furrow, and accordingly the genal field has a strong convexity (exsag.). An eye socle is preserved on the illustrated specimens, surmounting a very shallow subocular groove. The granulose prosopon is similar to that of the cranidium.

If its spines are neglected, the pygidium is semicircular. The anterior margin, between the axial furrows and the geniculation, is often a straight sharp edge, which rises anterolaterally to form very prominent fulcral points before passing into obtusely rounded anterolateral corners. The pygidial outline is broken by a pair of long, stout, posterolateral spines which are drawn from the opisthopleuron of the first and propleuron of the second pleural segments. Only two pleural segments are indicated; the first bears a deeply incised pleural furrow which defines the anterior margin of the posterolateral spine base, and extends close to the lateral margin of the shield, curving parallel to this margin over the distal portion of its course. The pleural furrow of the second segment is no more than a shallow depression. Marginal furrows are not evident. The axis, containing four, possibly five, segments and a terminal piece, is connected to the posterior margin by a short postaxial ridge. The articulating half-ring is a simple crescent. The dorsal surface of the test bears a fine low-density granulation. Weak traces of the caecal system of the parietal surface are indicated on specimen AR 621, Plate 40, fig. 5.

Discussion. All species of *Prochuangia* have very similar pygidia: all have similar shape and similar relationship of pleurae to spines. Only two pleural segments are known in all species which are interpretable. *Prochuangia* pygidia are differentiated by the orientation of their spines and degree of segmentation of their axes.

Orientation of the posterolateral spines, straight backwards to give the pygidium an elongate form, distinguishes *P. posterospina* Kobayashi from all other species assigned to the genus.

The pygidium of *Prochuangia* sp. aff. *P. granulosa* is distinguished from the type species, *P. mansuyi* Kobayashi, in having probably one less segment in the axis—unless Kobayashi (1935, p. 186) included the terminal piece in his count of axial rings. *P. granulosa* Lu has at least one additional axial segment, a total of six (Lu 1956, p. 376). In other respects, however, especially the form of the spines and the granulose prosopon, *Prochuangia* sp. and *P. granulosa* are closely comparable. Neither Dames (1883, pp. 9–11) nor Kobayashi (1937*b*, p. 426) give any indication of the axial segmentation for *P. quadriceps* (Dames 1883), but Kobayashi's illustrations of at least one of the type pygidia (1937*b*, pl. 17, fig. 2*b*) look closely comparable to the Antarctic *Prochuangia* sp.

Other genera whose pygidial morphology is similar are *Chuangioides* Chu (based on *C. punctatus* Chu, 1959, p. 123, pl. VII, figs. 1–2), which has similar shape, segmentation, and furrowing, but lacks spines; *Pagodia* (*Idamea*) Whitehouse (based on *I. venusta* Whitehouse, 1939, pp. 232–233, pl. XXIV, figs. 4–6, emended Öpik 1967, p. 258 et seq.), which has similar shape and segmentation, but different furrowing, and also lacks spines; *Chuangia* Walcott (based on *C. batia* Walcott, 1905, figured 1911, p. 85, pl. 15, fig. 3, 3*a*), which lacks spines and has a considerably broader, flatter pygidial shield, but has similar segmentation although partially effaced. *Iranochuangia* Kobayashi (1960, p. 263, based on *C. nais* var. *persicum* King, 1937, p. 15, pl. 4, fig. 4*a*–*d*) has a pygidium similar to that of *P.* (*Idamea*) and *Chuangioides*, lacking spines. *P.* (*Lotosoides*) Shergold, 1975 has a spinose pygidium closely comparable with that of *Prochuangia* sp., but occurs considerably later. *Lotosoides* is closely related to other late Cambrian pagodiids which are non-spinose.

The cranidium of *Prochuangia* sp. differs from that of *P. mansuyi* in having a narrower (sag.) anterior cranidial border, anterosagittally rather than exsagittally curved preocular facial sutures, and glabella anterolaterally more obviously constricted at the confluence of the ocular ridges and the axial furrows. *P. quadriceps* (Dames) as refigured by Kobayashi (1937*b*, p. 426, pl. 17, fig. 2*a*) has considerably more obvious glabellar furrowing, but the relationship of its cranidial border to the glabella appears similar. *P. angusta* Kobayashi is quite different in glabellar shape, the course of its preocular facial sutures, the shape of its anterior cranidial margin, the relationship of its anterior cranidial border to the glabella, and the position of its palpebral lobes. It more closely resembles some species previously placed in *Chuangia* than other species of *Prochuangia*. The cranidium attributed to *P. granulosa* Lu (*in* Lu *et al.* 1965) is probably the most closely comparable with *Prochuangia* sp., although it has a less obviously constricted glabella and perhaps narrower (tr.) palpebral areas.

With respect to the various groups of *Chuangia* species which can be recognized, *Prochuangia* sp. is closest, by virtue of the nature of the relationship of the anterior cranidial border to the glabella and courses of the preocular facial sutures, to the *nitida-tawenkouensis-kawadai* group. It is primarily differentiated from these species on account of the anterolateral constriction of its glabella. This latter characteristic, however, is one of the main diagnostic features of *Iranochuangia*; but species of this genus apparently have a depressed and flattened anterior cranidial border. *Prochuangia* sp. is related cranidially to species of *Pagodia* (*Idamea*) by the same characteristics that unite it with the *Chuangia* species of the *nitida-tawenkouensis-kawadai* group, and is mainly differentiated by glabellar shape. Whereas the glabella of *Prochuangia* sp. is merely anterolaterally expanded, that of Idamean species is often extended into anterolateral ridges which connect with the preocular areas and block the axial furrows immediately in front of their convergence with the ocular ridges. Species of both *Idamea* and *Prochuangia* have similar prosopon, and similarly structured librigenae, that of *Prochuangia* sp. being nearly identical in morphology with that illustrated by Öpik (1967, p. 262, pl. 18, fig. 1) for *Pagodia* (*Idamea*) *baccata*. In both species terrace lines are strong on the lateral librigenal margin, and continue on to the adventral surface of the narrow upturned anterior cranidial border.

Order ASAPHINA Salter, 1864
Superfamily CERATOPYGACEA Linnarsson, 1869
Family CERATOPYGIDAE Linnarsson, 1869
Subfamily PROCERATOPYGINAE Wallerius, 1895
Genus PROCERATOPYGE Wallerius, 1895
Subgenus PROCERATOPYGE Wallerius, 1895

Type species. By original designation, *Proceratopyge conifrons* Wallerius (1895, pp. 56–57, fig. 6; Westergaard 1948, pp. 5–6, pl. 1, figs. 7–16), middle Cambrian, *Leiopyge laevigata* Zone, Gudhem, Falbygden area, Västergötland, Sweden.

Other species. Numerous other species have been described. Following Öpik (1963, p. 98), those with five or fewer axial segments in the pygidium are classified as *Proceratopyge* (*Proceratopyge*); those with more than five are referred to *P.* (*Lopnorites*) Troedsson, 1937. Listed regardless of synonymy other species of *P.* (*Proceratopyge*) include: *P. asiatica* Ivshin (1956, pp. 24–26, pl. VIII, figs. 17–23; 1962, p. 287, pl. XIX, fig. 14), Kuyanda horizon, Tortkuduk Suite, Kazakhstan, U.S.S.R. *P. captiosa* Lazarenko (1966, pp. 54–55, pl. IV, figs. 7–10), *Irvingella–Cedarellus felix* Zone, Kyutyungd depression, Karaulakh Mountains, River Lena below Chekurovka, Northern Siberian Platform, U.S.S.R. *P. chuhsiensis* Lu (1956, pp. 280–282, pl. 1, figs. 1–6; Lu *et al.* 1965, p. 547, pl. 114, figs. 3–6), south-western Chuhsien, North Anwhei, China. *P.* cf. *chuhsiensis* Lu *sensu* Öpik (1963, pp. 99–100, pl. 5, fig. AA), *I. tropica–Agnostotes inconstans* Zone, western Queensland, Australia. *P. lata* Whitehouse (1939, pp. 248–249, pl. XXV, figs. 12, ?13; Öpik 1963, pp. 98–99, pl. 4, figs. 9–10; pl. 5, figs. CC, EF, GF), *Glyptagnostus reticulatus* through *I. tropica* with *A. inconstans* Zones, western Queensland, Australia. *P.* (*P.*) *liaotungensis* Kobayashi and Ichikawa (1955, p. 69, pl. 11, figs. 1–9; Lu *et al.* 1965, p. 550, pl. 115, figs. 6–11), *Chuangia* Zone, Chinchiachengtzu, Manchuria. *P. magnicauda* Westergaard (1947, p. 32, pl. 2, fig. 11 (no description); 1948, pp. 6–7, pl. 1, figs. 17–18), *Leiopyge laevigata* Zone, Andrarum, Sweden. *P. nathorsti* Westergaard (1922, p. 120, pl. 2, figs. 3–5; 1947, p. 10, pl. 2, figs. 2–7), *A. pisiformis* Zone, Andrarum, Möckleby, Öland, Sweden. *P. nectans*

Whitehouse (1939, pp. 249–250, pl. XXV, fig. 8*a–b*), *G. reticulatus* Zone, western Queensland, Australia. *P. portentosa* Lazarenko (1966, pp. 52–54, pl. IV, figs. 1–6), horizon and locality as for *captiosa*. *P. similis* Westergaard (1947, pp. 10–11, pl. 2, fig. 1), *A. pisiformis* Zone?, Andrarum?, Sweden. *P. tenuita* Lazarenko (1966, pp. 51–52, pl. III, figs. 10–16), locality and horizon as for *captiosa*. *P. triangulata* Ivshin (1962, pp. 288–289, pl. XIX, fig. 15), Seletin horizon, Kuyanda Stage, Tortkuduk Suite, Kazakhstan, U.S.S.R. *P. tullbergi* Westergaard (1922, p. 121, pl. 2, figs. 6–7; 1947, pp. 11–12, pl. 2, figs. 8–10), *Protopeltura aciculata* Subzone, Andrarum, Sweden. Species formerly referred to *Proceratopyge*, but not listed here under *P.* (*Proceratopyge*), are presently considered to belong to *P.* (*Lopnorites*), to *P.* (*Kogenium*) Kobayashi, 1935, or to genera other than *Proceratopyge*.

Age and distribution. Cosmopolitan. Late middle Cambrian to late Cambrian, *Leiopyge laevigata* to *Protepeltura aciculata* Zones in Europe (England, Sweden, Norway); late Cambrian, Tuorian, *A. pisiformis* with *Homagnostus fecundus* Zone, to early Shidertan, *Irvingella–Cedarellus felix* Zone, Kazakhstan, Siberian Platform, U.S.S.R.; late Cambrian, Paishanian, *Chuangia* Zone, Manchuria, China; late Cambrian, Idamean, *G. reticulatus* to *I. tropica–Agnostotes inconstans* Zones, Australia; late Cambrian, late Idamean–early Franconian, Northern Victoria Land, Antarctica.

Proceratopyge (*Proceratopyge*) cf. *lata* Whitehouse, 1939

Plate 40, figs. 7–9

cf. 1939 *Proceratopyge lata* sp. nov., Whitehouse, 1939, pp. 248–249, pl. XXV, figs. 12, ?13.
cf. 1963 *Proceratopyge lata* Whitehouse, 1939; Öpik 1963, pp. 98–99, pl. 4, figs. 9–10; pl. 5, figs. CC, EF, GF.

Material. A single cranidium, AR 622, with sagittal length of 3·50 mm, and a single pygidial fragment lacking left pleuron and axis, AR 623.

Description. The cranidium assigned to *Proceratopyge* cf. *lata* Whitehouse has low convexity (tr. sag.), and gently arcuate anterior cranidial outline. The glabella is conical, anteriorly rounded, widest (tr.) in the vicinity of the preoccipital furrows. Glabellar furrowing is indistinct: anterior lateral furrows are transverse, slightly curvilinear; median lateral furrows are short, transverse, slightly sloping adaxially and rearwards; preoccipital furrows are complex, bifurcated, and apparently connected to the occipital furrow. A glabellar node is sited medially between the bifurcations of the preoccipital furrows.

The occipital ring is compound, possessing anterolateral lobules connected abaxially with the glabella so that the occipital furrow does not connect with the axial furrows. These anterolateral lobulae are distinguished from the remainder of the occipital ring by faint furrows which merge sagittally into the occipital furrow.

Palpebral lobes are arcuate in plan view, equidistant anteriorly and posteriorly from the axial furrows, extending from opposite the confluence of the anterior lateral glabellar furrows and the axial furrows to the preoccipital furrows. A palpebral furrow is indistinct, the palpebral lobes themselves being narrow (tr.) and rim-like. Anteriorly they pass into short indistinct ocular ridges which are transverse and merge into the preocular areas adjacent to the axial furrows and opposite the anterior lateral glabellar furrows.

The preocular facial sutures diverge appreciably to enclose a preglabellar area slightly less wide (tr.) than the palpebral cranidial width. Gently convex (exsag.) preocular areas pass sagittally into a depressed plectral area, and are defined anteriorly by plectral lines. A shallow marginal furrow is present, and a narrow (sag.) cranidial border is upturned. The preglabellar field bears a caecal network which extends across the marginal furrow on to the cranidial border. A pair of diverticula, crossing the preglabellar furrow, connect the preocular areas with the anterolateral portions of the glabella. The postocular facial sutures diverge very strongly to the posterior cranidial border and enclose narrow (exsag.) but long (tr.), strap-like posterolateral limbs. These bear shallow marginal furrows widening (exsag.) distally.

Apart from the prosopon of the preglabellar area, and the presence of transverse terrace lines along the anterior extremity of the anterior cranidial border, the cranidium lacks surface details.

Only a fragment of a pygidium is available for description. The shield is assumed to have been subtriangular, with an axis containing most probably only three or four axial rings, and pleural zones containing only two well-defined segments. The pleural furrows that are preserved are wide (exsag.) and shallow. Inter-pleural furrows are effaced. A delicate lateral spine is preserved, formed from the opisthopleuron of the first and propleuron of the second pleural segments. The second pleural furrow, extending close to the margin of the pygidium, defines the rear of the spine base. The spine itself bears longitudinal terrace lines. A broad doublure is evident, bearing nine roughly concentric terrace lines.

Discussion. P. cf. *lata* Whitehouse belongs to a group of species characterized by rather widely diverging preocular facial sutures, well-developed plectral lines, long (exsag.) palpebral lobes with strap-like posterolateral limbs, and a paucifurrowed pygidium. Excluded from comparison are all those species possessing a narrow (tr.) preglabellar area, or more than five axial rings in the pygidium. *P.* cf. *lata* can therefore be compared only with *P. lata* Whitehouse, *P. liaotungensis* Kobayashi and Ichikawa, and *P. tullbergi* Westergaard.

P. cf. *lata* may be compared with what is known of the holotype cranidial fragment of *P. lata sensu* Whitehouse (1939, pp. 248–249, pl. XXV, fig. 12). Both species have similarly faint glabellar furrowing, similarly wide (tr.) preglabellar area, and similarly shaped and extensive posterolateral limbs. Palpebral characteristics cannot be adequately compared as the type specimen of *P. lata* lacks palpebral lobes. The faint ocular ridges of *P. lata* appear to be more strongly inclined than those of the Antarctic species and intervening occipital lobulae and furrows are less well developed; the Antarctic species is therefore identified as *P.* cf. *lata.* Pygidial characteristics cannot be compared because of the uncertainty of assignment of the pygidium of *P. lata* (see Whitehouse 1939, p. 249), and the inadequacy of the preservation of the Antarctic specimen.

Although its palpebral lobes may be somewhat shorter (exsag.) and its ocular ridges less transverse, the cranidium of *P. lata* Whitehouse *sensu* Öpik (1963, pp. 98–99, pl. 4, figs. 9–10; pl. 5, figs. CC, EF, GF) is essentially similar to that of *P.* cf. *lata.* Similar characteristics, and especially the more strongly sloping ocular ridges, distinguish *P. liaotungensis* Kobayashi and Ichikawa (1955, p. 69, pl. 11, figs. 1–9) from *P.* cf. *lata.* The Manchurian species appears also to have a slightly wider (tr.) preglabellar area, almost as wide (tr.) as the palpebral cranidial width. From what is known of the pygidium of *P.* cf. *lata*, it is closely comparable with that of *P. liaotungensis.* The second pleural furrow is, however, less deeply incised on the Antarctic material.

P. tullbergi Westergaard (1922, p. 121, pl. 2, figs. 6–7; 1947, pp. 11–12, pl. 2, figs. 8–10), though similar to *P.* cf. *lata* in many respects, has apparently a longer (sag.) preglabellar area, and wider (exsag.) posterolateral limbs. Its pygidium would appear comparable in shape and degree of segmentation with those of both *P.* cf. *lata* and *P. liaotungensis*.

TRILOBITA FAMILIAE, GENERA ET SPECIES INCERTAE SEDIS

Specimen 1

Plate 42, fig. 4

Material. A single cranidial fragment preserving only a portion of the glabella and the preglabellar area, AR 623.

Description. The preglabellar area is fractionally wider (tr.) than long (sag.) and is enclosed apparently by preocular facial sutures running virtually straight forwards from the anterior end of the palpebral lobes (not preserved). It is composed of a flat (sag.) or slightly concave (sag.) preglabellar field and gently convex (sag.) anterior border of equal length (sag.). The anterior marginal furrow is bowed slightly forwards at the sagittal line. Ocular ridges appear to have been straight, inclined slightly abaxially and posteriorly, and the palpebral areas to have been about half the anterior glabellar width (tr.). The fragment of glabella preserved shows it to have been rounded and narrowed anteriorly. The preglabellar furrow is pitted on either side of the sagittal line. The prosopon is very finely granular with occasional larger granules randomly scattered on the preglabellar field and preocular areas.

Discussion. The morphology of the fragment is similar to that of species which Ivshin (1962) has named from central Kazakhstan; notably his specimen of *Pedinocephalus simplex* (1962, pp. 96–98, pl. VI, fig. 2) and his species *Apheloides striatiferus* (1962, pp. 105–108, pl. VII, figs. 1–3). The former has similarly wide (sag.) preglabellar field and cranidial border, and marginal furrow sagittally anteriorly curved; its preglabellar area, however, appears to be wider (tr.). *A. striatiferus* appears to have a convex (tr.) preglabellar field and more steeply inclined ocular ridges, and the course of its marginal furrow may also differ.

Specimen 2

Plate 42, fig. 5

Material. A single partially exfoliated cranidial fragment preserving the complete preglabellar area and the anterior portion of the glabella, AR 624.

Description. Anteriorly divergent preocular facial sutures enclose a preglabellar area three times as wide (tr.) as long (sag.), composed of a flat or concave (sag.) preglabellar field and convex (sag.) cranidial border. The latter is thicker (sag.) than the sagittal dimension of the preglabellar field, is sagittally slightly depressed, and rises abruptly from the prominent transverse marginal furrow. The portion preserved indicates an anteriorly tapered glabella. Traces of the anterior lateral glabellar furrows preserved show them to be short (tr.), faint and straight, while the median lateral furrows are similar but inclined slightly rearwards. Ocular ridges are straight, gently inclined abaxially and posteriorly, and are short. A faintly granulose prosopon is observed.

Discussion. Specimen 2 may be representative of Pterocephaliidae (Aphelaspidinae) through resemblance to *Litocephalus*, e.g. *L. verruculopeza* Palmer (1960, p. 83, pl. 8, figs. 12–13, 15–16, 19–20; 1965, p. 63, pl. 11, figs. 7–9), from the *Dunderbergia* Zone of Nevada. The preglabellar area also resembles that of the specimen which Palmer (1965, pl. 2, fig. 11) ascribed to *Iddingsia robusta* Walcott (Dokimocephalinae, Elviniidae) from the *Elvinia* Zone of Nevada; and that which Lazarenko (*in* Lazarenko and Nikiforova 1968, pp. 50–51, pl. IX, fig. 12) has referred to *Faciura infida* Lazarenko, from the *Faciura–Garbiella* Zone, Kulyumbe River, north-west Siberian Platform.

Specimen 3

Plate 42, fig. 8

Material. Three librigenae, one of which is illustrated here, AR 625.

Description. This specimen is characterized by a rather convex (exsag., tr.) genal field sloping to wide (tr.), shallow lateral marginal furrows, and short somewhat deeper posterior ones. The marginal furrows intersect at the genal angle but do not continue into the spine base. The genal spine (broken on the illustrated specimen) appears to have been long and stout. The anterolateral prong is short and pointed. From the configuration of the posterior margin the associating cranidium must have possessed long triangular posterolateral limbs. A finely granulose prosopon is evident on which are superimposed low density randomly distributed larger granules. The lateral and anterolateral borders bear terrace lines, as presumably did the adventral surface of the genal spine.

Discussion. Librigenae represented by Specimen 3 are difficult to classify. Their prosopon is similar to that seen on Specimen 1, and on *Olentella* cf. *olentensis* Ivshin described above, and they are probably attributable to a pterocephaliid trilobite.

Specimen 4

Plate 41, fig. 5

Material. Two librigenae, the illustrated specimen being complete, AR 626.

Description. Both specimens are characterized by the presence of advanced genal spines, long posterior margins, and deeply incised marginal furrows which meet at the genal angle but do not continue into the spine bases. The illustrated specimen indicates that the cranidium to which it was attached possessed long (exsag.) palpebral lobes, and short broadly triangular posterolateral limbs. Both lateral and posterior borders are narrow. The genal field bears a rather sparse and faint caecal system, some caeca crossing the marginal furrows and passing into the borders. An underlying parietal prosopon appears to be finely granulose.

Discussion. The available material defies definite classification. The only cranidium among the collected specimens with palpebral lobes sufficiently long to accommodate this type of librigena is that assigned here to *Stigmatoa*. Librigenae are previously undescribed for this genus, preventing direct comparison.

Specimen 5

Plate 42, fig. 12

Material. A single cephalon, AR 627, with cephalic length of 0·75 mm.

Discussion. The specimen represents an indeterminate meraspid cephalon which presumably could belong to any of the pterocephaliid, or elviniid trilobites described here.

This meraspid appears to represent a cephalon with fused genae. The glabella is anteriorly undifferentiated from the front portion of the cranidium and may have five segments. A strongly differentiated occipital ring is evident. Short faint transverse ocular ridges arise from a position opposite the middle of the frontal lobe and are orientated in olenid fashion. Palpebral lobes are either very short (exsag.) or merge imperceptibly into the general convexity of the specimen.

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MULTILAMELLAR GROWTH IN TWO JURASSIC CYCLOSTOMATOUS BRYOZOA

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ABSTRACT. The bryozoans *Reptomultisparsa incrustans* d'Orbigny and *Mesenteripora undulata* (Michelin) constructed multilamellar zoaria composed of a succession of overgrowing zooecial layers. The taxonomic status of the two species is reviewed briefly, and a mode of formation of the multilamellar zoarium common to both species is described. This involves overgrowth of old zooecia by young zooecia budded at C-shaped growth margins, the two ends of which remain stationary and function as points about which growth pivots. Complex patterns of growth result from the interactions between adjacent growth margins. The implications of this mode of growth to the colony during life are discussed.

As part of a current revision of the Jurassic cyclostomatous Bryozoa, the multilamellar species *Reptomultisparsa incrustans* d'Orbigny and *Mesenteripora undulata* (Michelin) have been re-examined. *M. undulata* occurs in the Bathonian and Callovian, where it encrusts a variety of substrates. *R. incrustans* attaches itself exclusively to the shells of Bathonian and ?Bajocian trochoform gastropods (Pl. 43, figs. 1, 2) and is known only from France. It is of special palaeoecological interest because most of the gastropod shells which it encrusted were occupied, subsequent to the death of the gastropod, by hermit crabs (Buge and Fischer 1970; Palmer and Hancock 1973). In addition, *R. incrustans* has a zoarial surface covered by monticules whose function was probably to provide a colonial water-current system for feeding purposes (Taylor, in press). The mode of growth of the multilamellar zoarium has not previously been described and the present study has shown how this is achieved in an identical manner in both species.

Material. R. incrustans. Bathonian of Ranville, Normandy: BMNH D2113, BMNH 60221, BMNH 60242.

M. undulata. Bathonian (Bradford Clay) of Bradford-on-Avon, Wiltshire: BMNH D2126, BMNH 35249, BMNH 35250. Bathonian (White Limestone) of Northleach, Gloucestershire: PDT 535, PDT 536. Bathonian of the Richmond boring, Surrey: BMNH D1911. Bathonian of Ranville, Normandy: BMNH D2088, BMNH 60346. 'Lower Oolite': BMNH B4850.

BMNH—British Museum (Natural History).

PDT—P. D. Taylor Collection, University of Durham.

TAXONOMIC REMARKS

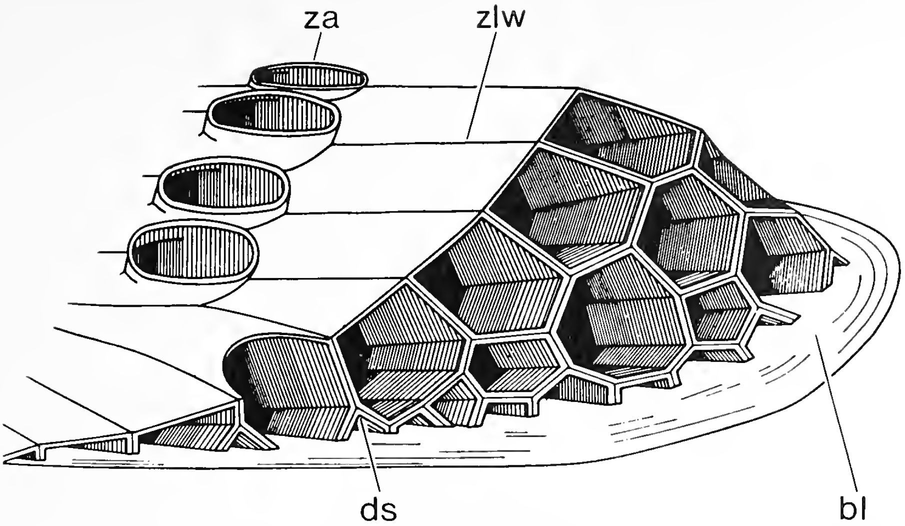
In 1852 d'Orbigny founded the genus *Reptomultisparsa* for multilamellar species allied to *Berenicea*. In it he included five species, two from the Jurassic and three from the Cretaceous. Two species of Bryozoa from the Jurassic were referred to the genus *Reptomultisparsa* by Gregory (1896). He considered the two Jurassic species described by d'Orbigny, *R. microstoma* and *R. diluviana*, to be synonymous and he gave

[Palaeontology, Vol. 19, Part 2, 1976, pp. 293–306, pls. 43–44.]

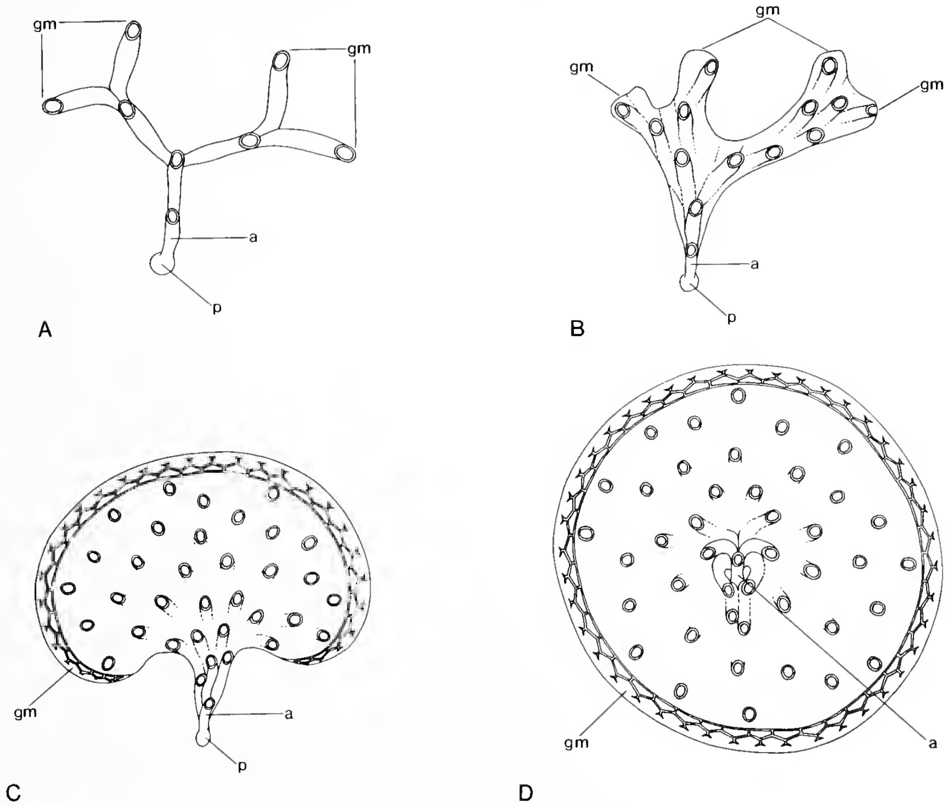
R. microstoma priority, designating it the genotype of *Reptomultisparsa*. In addition, Gregory also introduced a form, initially described by Michelin in 1846 under the name *Diastopora undulata*, into the genus *Reptomultisparsa* as *R. undulata* (Michelin). However, Gregory (1896, p. 113) himself cast doubts on the validity of the genus *Reptomultisparsa*, stating that 'the whole of the Tubuliporidae (genera included in the suborder Tubuliporina by Bassler 1953) ought to be formed into one genus. So long as it is recognised that the genera in this group are of no absolute value, but are only used as a matter of relative convenience, it is wisest to accept them, and *Reptomultisparsa* has as good a claim to recognition as the rest'. Taxonomic division of the Tubuliporina based on growth form is now known to be of limited value and it has generally been replaced by a method largely utilizing the form of the ovicells (Canu 1918). In 1969 the results of a restudy of Jurassic Bryozoa by Walter were published. His classification of the cyclostomes, relying heavily on the character of the ovicells, left *R. microstoma* in the redefined genus *Reptomultisparsa* (see Walter 1969, p. 75) but removed *R. undulata* from *Reptomultisparsa* into *Mesenteripora* (Walter 1969, p. 107). Walter (1969) considered that the form described by Gregory as *R. microstoma* is not the same as that described by d'Orbigny (1852) under the same name, but does agree with a form described by d'Orbigny in 1850 as *D. incrustans* and later in 1852 as *R. diluviana*. Thus Gregory's view that d'Orbigny's two Jurassic species of *Reptomultisparsa* are synonymous is incorrect. Both *D. incrustans* d'Orbigny and *R. diluviana* d'Orbigny were referred to *R. incrustans* d'Orbigny by Walter. *Atractosoecia*, with *A. edwardsi* as its genotype, was introduced by Canu and Bassler in 1922. Walter (1969) placed *R. incrustans* and *A. edwardsi* in synonymy. The view of Buge and Fischer (1970) that the synonymy cannot be accepted without a decision of the International Commission on Zoological Nomenclature seems incorrect, for this is a subjective and not an absolute synonymy. Brood (1972) considered that there is no significant difference in ovicell structure between *Reptomultisparsa*, *Mesenteripora*, and *Diastopora*. Therefore, on the grounds of priority, both *Reptomultisparsa* and *Mesenteripora* should be included in *Diastopora*. The validity of this view depends on a more extensive study of cyclostomatous Bryozoa and, for the present, the names *R. incrustans* and *M. undulata* are retained.

MODE OF GROWTH AND COLONY FORM IN ADNATE TUBULIPORINIDEAN BRYOZOA

In adnate tubuliporinidean Bryozoa, new zooecia are budded off by septal division on a basal lamina. A vertical septum separating two zooecia bifurcates at its junction with the basal lamina, the split widens and extends upwards as growth continues, and a new zooecium is thus partitioned off (text-fig. 1). This process occurs at the growth margin of the colony, which was shown by Borg (1926) to be enclosed beneath a common (hypostegal) coelom during life and which he termed the common bud. The longitudinal axis of each zooecium is oblique to the basal lamina for most of its length, but distally it bends upward to meet the zoarial surface at a high angle. The form taken by the adnate zoarium is controlled largely by its relative rate of lateral expansion, which in turn depends upon the frequency of zooecial budding. If there is no lateral expansion, then a uniserial branching zoarium of the stomatoporiiform type is developed (text-fig. 2A). A limited rate of lateral expansion produces



TEXT-FIG. 1. The growth margin of an adnate tubuliporinidean Bryozoa (after Illies 1968). bl, basal lamina; ds, dividing septum; za, zooecial aperture; zlw, zooecial lateral wall.



TEXT-FIG. 2. Growth forms of adnate tubuliporinidean Bryozoa. A, stomatoporiform. B, proboscinii-form. C, fan-shaped bereniciiform. D, discoidal bereniciiform. a, ancestrula; gm, growth margin; p, protoecium.

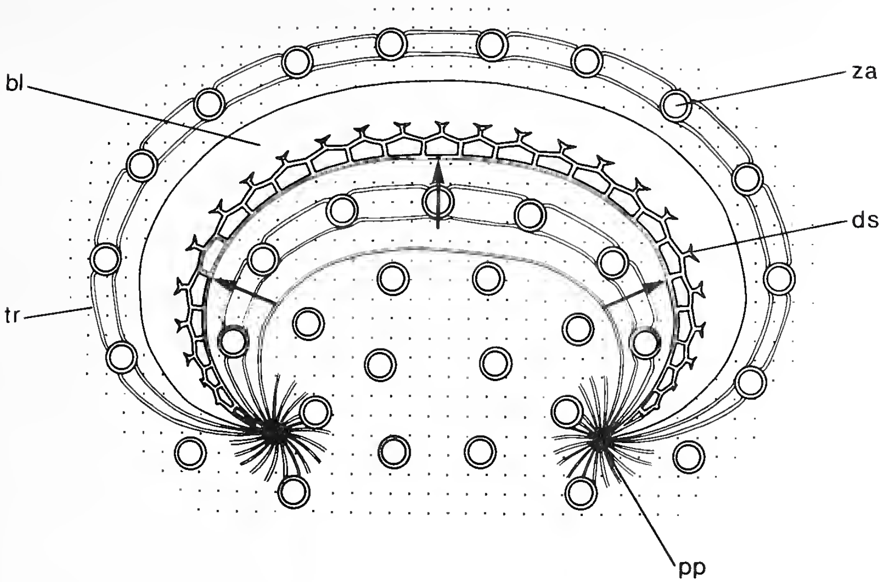
a zoarium of the multiserial probosciniiform type (text-fig. 2B), whereas a rapid rate of lateral expansion gives a multiserial bereniciiform type of zoarium. It may vary from fan-shaped (text-fig. 2C) to discoidal (text-fig. 2D). In the fan-like zoarium the growth margin is C-shaped, in the discoidal zoarium it forms a complete ring.

MODE OF MULTILAMELLAR GROWTH IN *REPTOMULTISPARSA INCRUSTANS* AND *MESENTERIPORA UNDULATA*

Basic principles. All of the zoarial forms mentioned above consist of a single zooecial layer and are said to be unilamellar. In contrast, a multilamellar zoarium is formed by a sequence of bereniciiform zooecial layers (each floored by a basal lamina) occurring one on top of the other (Pl. 43, fig. 3), the oldest (i.e. astogenetically earliest) layer being at the base of the series, attached to the substratum. Multilamellar zoaria may arise in a variety of ways. Growth around a closed shape, from a single growth margin, can produce a multilamellar zoarium in which older zooecia would be covered by the subsequent extension of the growth margin which initially produced them. Alternatively, a multilamellar zoarium could be produced by a new zooecial layer being initiated proximally to the growth margin by the extrusion of secretory epithelium through a zooecial aperture on to the surface of the established zoarium. However, both of these modes of formation of multilamellar zoaria are excluded in *R. incrustans* and *M. undulata*, in which each zoarium possesses a number of discrete growth margins budding off zooecia in many different directions. Observations have shown that growth is continuous between zooecial layers, for it is not obvious where one layer ends and the next begins.

Patterns of growth of the multilamellar zoarium can be distinguished using zooecial lateral wall traces in *R. incrustans* (Pl. 43, fig. 8) and transverse calcareous ridges in *M. undulata*. In *R. incrustans* the traces of lateral bounding walls of zooecia can occasionally be discerned on the zoarial surface. They parallel the direction of growth of the zoarium and are therefore normal to the growth margin which secreted them. Thus the orientation of zoarial growth can be determined. The direction of zoarial growth is found from its orientation and from the fact that zooecial apertures are distally placed. Past positions of growth margins of *M. undulata* are indicated by closely spaced low calcareous ridges on the zoarial surface. These ridges are formed parallel to the growth margins and are transverse to the zooecia. Effectively, therefore, they are growth lines, their spacing reflecting the relative rate of growth.

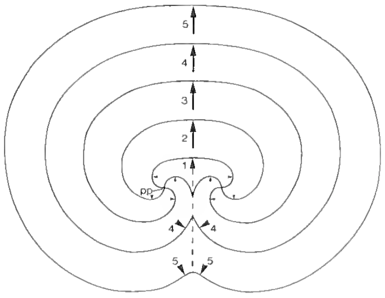
The transverse ridges are seen to converge at the ends of existing growth margins (Pl. 43, fig. 7). Therefore, growth must have been nil at these points, for they have remained stationary on the zoarial surface. Maximum separation between transverse ridges, and hence maximum growth rate, is located between the fixed ends of the growth margins. As a result, the two end points of a growth margin behaved as axes about which growth pivoted, and they may be termed pivot points. This mode of growth results in established zooecia being overgrown by newer ones orientated in exactly the same direction, as is seen in *R. incrustans* in which the lateral walls of young zooecia immediately proximal to a growth margin are parallel to those of the older zooecia they are overgrowing (Pl. 43, fig. 8). Near a pivot point, the zooecia



TEXT-FIG. 3. Simplified diagram of a C-shaped growth margin. Arrows indicate direction of growth. Zoarial surface stippled; bl, distal part of the basal lamina; ds, dividing septum in the region of zooecial budding; pp, pivot point; tr, transverse ridge; za, zooecial aperture.

are strongly and concentrically curved about that point. The typical features of the resultant C-shaped growth margin are shown in text-fig. 3.

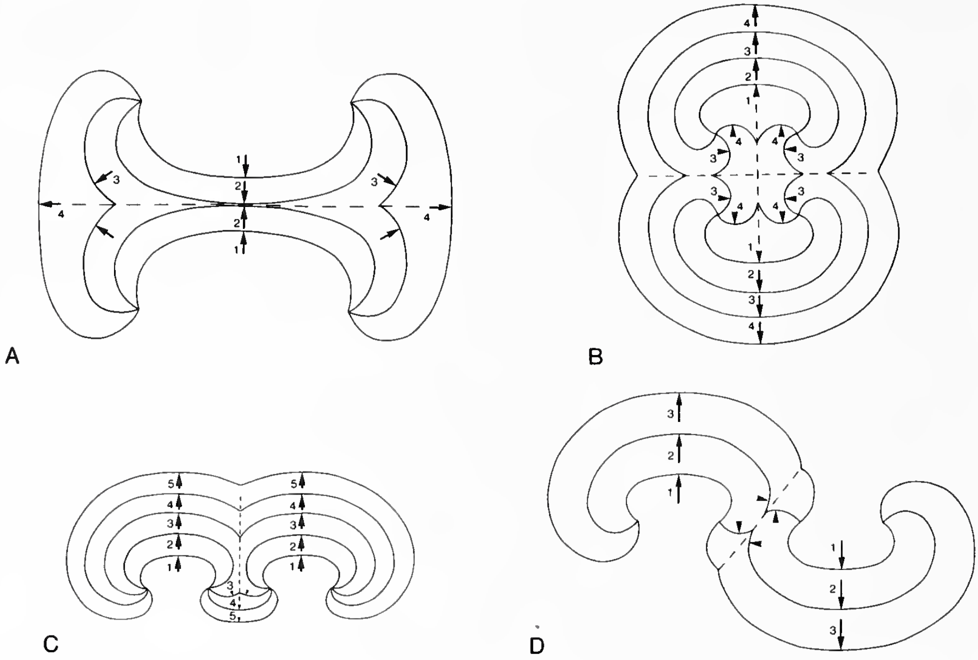
Growth at an isolated growth margin. Although interactions between adjacent growth margins are extremely frequent in these multilamellar Bryozoa, it is useful to consider the stages of growth of an isolated growth margin (text-fig. 4). The growth margin develops two lateral lobes which grow towards one another. Eventually the lobes meet and coalesce. Zooecia continue to be budded from each lobe, causing the line of anastomosis to lengthen in both directions. The anastomosis can be recognized by a band of irregularly, and closely, spaced apertures (Pl. 44, fig. 1). Anastomosis ceases when the zooecia being budded off by each lobe become parallel. A pair of growth margins at right angles to the line of anastomosis results. One of the growth margins is ring-like, lacks pivot points, and spreads outwards by budding off radially disposed zooecia. The other has the two original pivot points at its ends and soon



TEXT-FIG. 4. Growth at an isolated C-shaped growth margin arbitrarily divided into stages 1-5. Line of anastomosis dashed; pp, pivot point. Arrows indicate growth directions.

assumes a C-shaped form. It buds zooecia over those already formed to initiate a new cycle of growth. In this way each cycle of growth generates a ring growth margin and leaves behind a C-shaped growth margin (Pl. 43, fig. 6).

Interactions between adjacent growth margins. Before the lateral lobes of a growth margin have met, they invariably contact an adjacent growth margin. Some of the possible interactions between pairs of growth margins are illustrated diagrammatically in text-fig. 5. In cases A, C, and D, two C-shaped growth margins are left, whilst

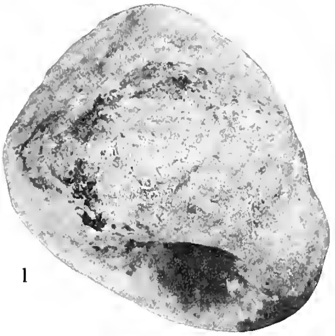


TEXT-FIG. 5. Interactions between pairs of C-shaped growth margins. A, growing towards one another. B, growing away from one another. C, adjacent and growing in the same direction. D, adjacent and growing in opposite directions. Lines of anastomosis dashed.

EXPLANATION OF PLATE 43

Figs. 1, 2, 8. *Reptomultisparsa incrustans* d'Orbigny. Bathonian, Ranville. 1, BMNH 60242, thick encrustation on a gastropod shell, × 2. 2, BMNH 60221, acetate peel taken from a transverse section of a zoarium composed of about twenty zooecial layers encrusting a gastropod shell with sediment infilling, × 1·7. 8, BMNH 60242, worn portion of a zoarium showing the zooecial lateral walls. The zooecia in the overgrowing layer are parallel to those which are being overgrown, × 14.

Figs. 3–7. *Mesenteripora undulata* (Michelin). Bathonian. 3, BMNH 35250, worn zoarium showing zooecial layers, Bradford-on-Avon, × 1·7. 4, BMNH D2088, young zoarium encrusting an annelid tube, Ranville, × 1·9. 5, BMNH B4850, zoarium intergrown with bereniciiform bryozoan on ?annelid tube, ?locality, × 1·1. 6, BMNH B4850, characteristic C-shaped growth margin (the area figured by Gregory 1896, pl. VI, fig. 2), ?locality, × 14. 7, BMNH D2088, transverse ridges converging on a pivot point at the end of a growth margin, Ranville, × 25.



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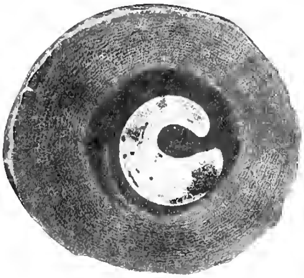

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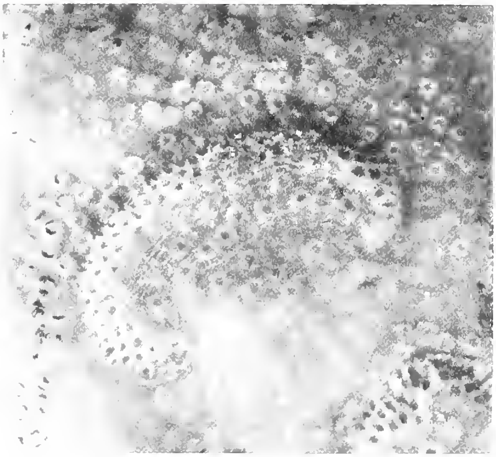

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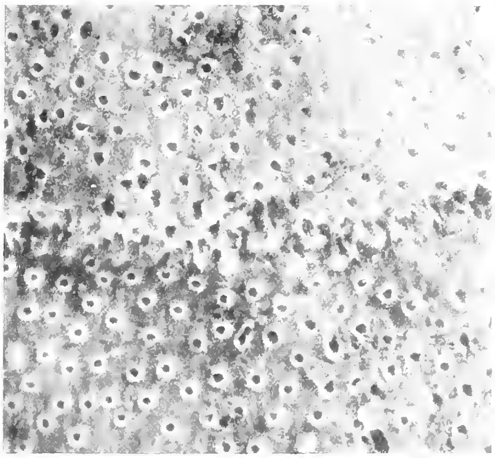
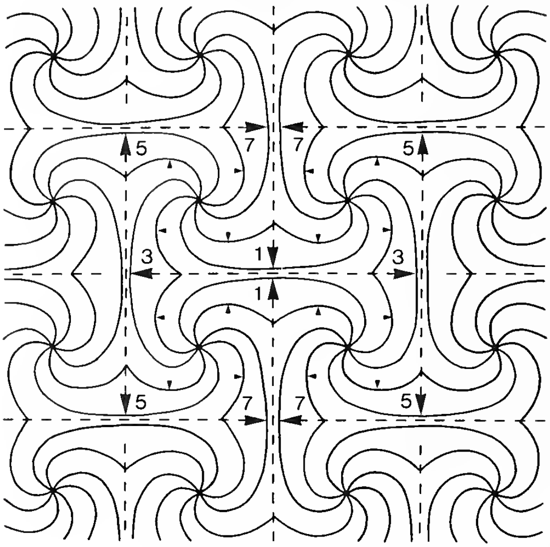


8

TAYLOR, growth in cyclostomatous Bryozoa case B in addition generates a ring-like growth margin. The pivot points are retained in all cases, but resultant growth margins span pairs of pivot points different from those spanned by the original growth margins.

The four cases described for interaction between pairs of growth margins can be considered as end members from a series of possible interactions. Adjustment of the angle between the principal growth directions of adjacent margins allows further possible constructions. In addition, by altering the relative spacing between the pivot points, modification of the resultant growth pattern occurs. Further complexities arise when more than two growth margins are operative. If they are irregularly and/or closely spaced, then the interactions between them may produce very involved patterns of growth. Indeed, in practice, the spacing of pivot points determining the disposition of the growth margins is usually extremely irregular. However, to illustrate interaction between multiple growth margins, a theoretical arrangement is considered in which the pivot points are equally spaced in a rectilinear manner. The consequent pattern of zoarial growth is illustrated in text-fig. 6. Two growth margins meet, anastomose, and produce a pair of growth margins growing at right angles to the original margins and in opposite directions to each other. They both subsequently anastomose with margins growing towards them and produce new margins normal to them. When four sets of growth margins, each normal to the preceding one, have been generated the cycle has returned to its starting point. An even covering of zooecia results.

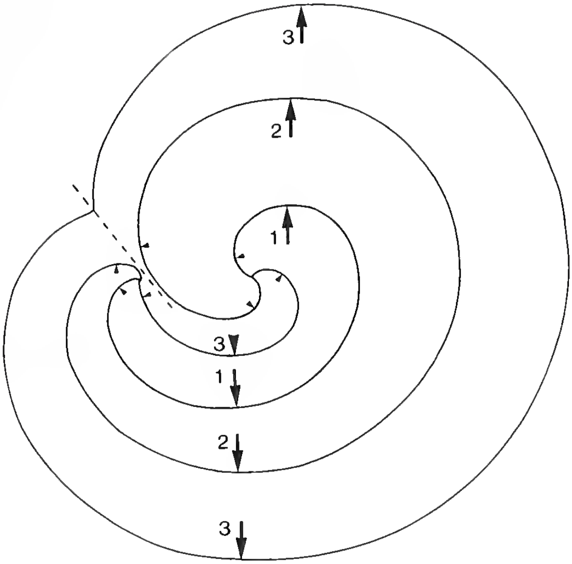


TEXT-FIG. 6. Growth pattern resulting from a rectilinear arrangement of pivot points. Cycle arbitrarily divided into eight stages, alternate stages numbered. Lines of anastomosis dashed.

The typical zoarium has a much more irregular disposition of its pivot points, frequently with an inner area of small irregularly arranged C-shaped growth margins.

By their coalescence these produce a surrounding area of larger, outward-spreading growth margins.

Modifications to the basic pattern of growth. Occasionally, the growth rates along the length of a C-shaped growth margin are asymmetrical, one side of the margin having a more rapid rate of growth than the other. When this occurs, the growth margin acquires a spiral appearance, often with a slight hummock at the apex of the spiral, where the growth rate is greatest. Growth margins of this type frequently develop in isolation, for the rapid growth rate at one side allows it to anastomose with the more slowly growing side (text-fig. 7), producing a ring-like growth margin which prevents the C-shaped growth margin from contacting other growth margins. One thick zoarium of *R. incrustans* (BMNH 60221) has apparently been formed wholly by an asymmetrical C-shaped growth margin, which has generated a succession of ring-like growth margins progressing from the apex towards the aperture of the encrusted gastropod shell.

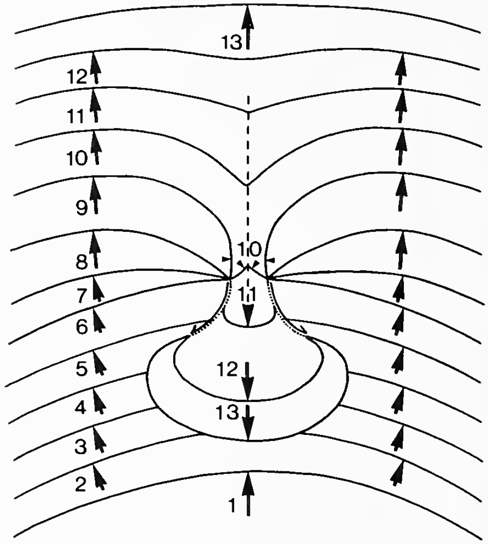


TEXT-FIG. 7. Growth at an asymmetrical growth margin. Line of anastomosis dashed.

Sometimes three or more growth margins converge at a point on the zoarium. They usually anastomose and growth ceases (Pl. 44, fig. 3). However, zoaria of *M. undulata* occasionally develop an erect habit, which almost certainly results from such a junction between three or more growth margins. The transition between encrusting and erect states has not been observed, but it seems probable that the basal laminae of converging growth margins on the adnate portion of the zoarium join to form a vertical axial lamina from which zooecia are budded to produce a cylindrical stem. If the axial lamina has been formed by the convergence of three growth margins, then in transverse section it will be Y-shaped, if by four growth margins, then it will be X-shaped, etc. (see Walter 1969, pl. 11, fig. 4). New zooecial layers produced on the adnate portion of the zoarium may subsequently grow up the erect stem.

Pivot points are not always stationary on the surface of the zoarium. Sometimes a small rate of growth at a pivot point causes it to move slightly. The path of its migration is marked by a zoarial lateral wall which forms a discontinuity between the overgrowing and overgrown zooecial layers. Pivot-point migration is an important process during the formation of a stable pattern of pivot points in immature zoaria.

Young zoaria and the establishment of new pivot points. Although no very young zoaria have been examined, it seems likely that they are of the fan-shaped bereniciiform type (text-fig. 2C). The sides of the zoarium would be formed by zoarial lateral walls, the junctions of which with the growth margin can be looked upon as migrating pivot points. Eventually growth ceases at these points, and they become the first true pair of pivot points on the zoarium. Growth can now proceed in a manner similar to that described for the theoretical case of an isolated growth margin. Although this manner of growth will produce a series of ring-like growth margins, it is incapable of generating new pivot points and hence additional C-shaped growth margins. A mechanism for the formation of new pivot points must be sought, since mature zoaria usually possess a large number of C-shaped growth margins. A multilamellar zoarium could be adequately produced by a solitary C-shaped growth margin spanning a pair of pivot points, but the acquisition of additional pivot points would, however, allow a faster rate of overgrowth. The formation of new pivot points is displayed by an immature specimen of *M. undulata* (BMNH D2088) from the Bathonian of Ranville (Pl. 43, fig. 4). Growth ceases along a short length of the growth margin, thus establishing pivot points at the two ends of that length (text-fig. 8). What was

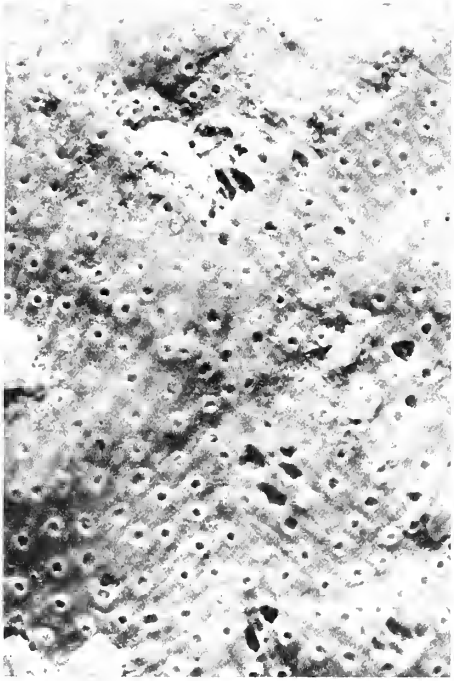


TEXT-FIG. 8. Formation of a new C-shaped growth margin. Line of anastomosis dashed. Zoarial lateral walls formed by pivot-point migration are dotted and marked with half arrows.

EXPLANATION OF PLATE 44

Figs. 1, 2. *Reptomultisparsa incrustans* d'Orbigny. Bathonian, Ranville. 1, BMNH 60242, a line of anastomosis formed at the junction between growth margins budding off zooecia from the bottom left and bottom right, × 14. 2, BMNH D2113, growth margin budding off zooecia parallel to those they are overgrowing, × 14.

Figs. 3, 4. *Mesenteripora undulata* (Michelin). Bathonian, Ranville. 3, BMNH D2088, growth margin terminated by a pivot point, left central. The elevated area at bottom left has been formed where three growth margins have converged, × 14. 4, BMNH D2088, an unusual case in which a new growth margin, centre right, has been formed and has immediately divided. Both margins so formed would have eventually coalesced with the larger margin growing towards them, × 14.



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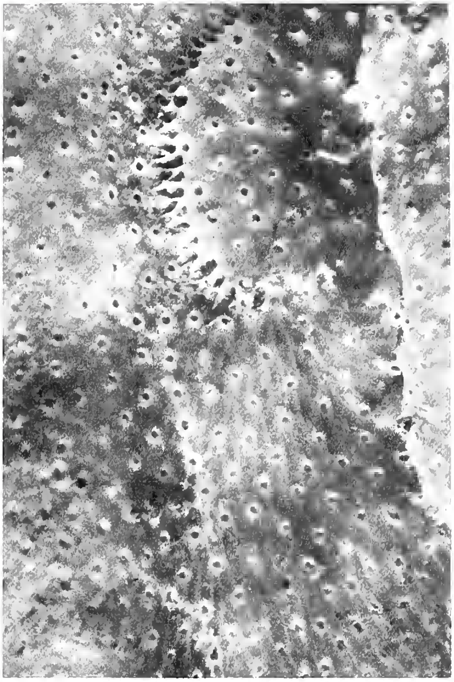

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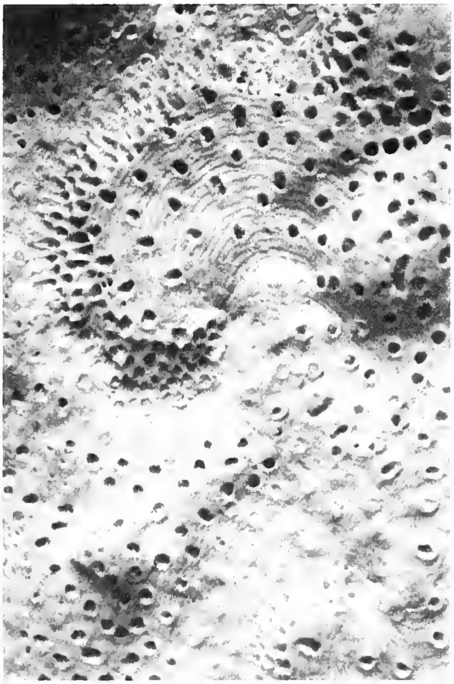

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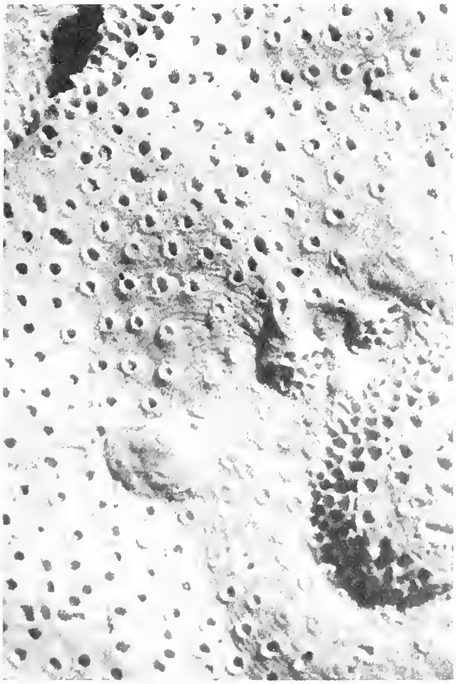

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TAYLOR, growth in cyclostomatous Bryozoa originally a single growth margin has now become two growth margins, separated by the length at which growth has ceased. Each extends between one of the original pair of pivot points and one of the new pair. The two growth margins begin to extend lobes towards each other, in the manner of those shown in text-fig. 5C. The lobes anastomose, producing a large growth margin growing distally and a smaller one growing proximally. The pivot points of the small growth margin move apart whilst migrating proximally, their path being marked by zoarial lateral walls. When the pivot points are a sufficient distance apart (usually about 5 mm), growth ceases at them, and a conventional C-shaped growth margin results.

DISCUSSION

R. incrustans and *M. undulata*, belonging to the suborder Tupuliporina (Acamptostega of Borg 1926), are grouped with the single-walled stenolaematous Bryozoa of Borg (1926). In single-walled stenolaemates, a hypostegal coelom exists only over the growth margin, a region termed the common bud by Borg (1926). Where a common coelom exists, a relatively high degree of colonial co-ordination of growth is expected (Boardman and Cheetham 1973). Proximal to the growth margin, calcification takes place at the level of the individual; it is usually limited to the extension of zooecial tubes in the form of peristomes, and to the secretion of diaphragms. Zoarial growth in these single-walled forms is largely co-ordinated and determined by events occurring at the growth margin. Hence, the multilamellar growth of the species under consideration is predominantly controlled at the common buds or growth margins. Individual growth margins are not connected by a common coelom and therefore function fairly autonomously. However, co-ordination of calcification within them must be relatively precise to produce the observed variation of growth rates along their length. It is thought unlikely that growth at an encroaching growth margin is in any way guided or influenced by the disposition of the transverse ridges or zooecia in the layer being overgrown. Thus, the parallel nature of transverse ridges and zooecia in successive layers is simply a result of the intrinsic properties of the growth margins.

Where separate growth margins meet, continuity of soft tissues is achieved, and parts of these apparently separate later with onward extension of the growing edges. For example, in text-fig. 5A, a part of the common coelom covering each of the original two growth margins contributes to the common coeloms of the two resultant growth margins. The coalescence and unification of growth margins from different parts of a single colony after they have grown apart has been termed autosyndrome by Knight-Jones and Moyse (1961). It has been observed in a variety of Bryozoa (Stebbing 1973) and clearly occurs in these multilamellar species. Homosyndrome is the process of coalescence and unification of growth margins from separate colonies of the same species. Although less common than autosyndrome, homosyndrome is known to occur occasionally in Bryozoa. This raises the possibility that some specimens of *R. incrustans* and *M. undulata* may have a multiple origin.

The feeding water-current system of each polypide in a bryozoan colony draws water in at the top of the tentacle crown and passes it out at the sides between the tentacles (Borg 1926, fig. 10). Hence, exhalant water is directed towards adjacent polypides, a situation not desirable for the efficient feeding of the colony as a whole.

In many adnate tubuliporinideans, polypides are only found in the zooecia in a band a few millimetres wide just proximal to the growth margin (Silén and Harmelin 1974). This situation allows for the maintenance of an efficient colonial water-current system by permitting the exhalent water currents of the polypides to escape distally and proximally at the sides of this band. A similar arrangement probably occurred in colonies of *M. undulata* during life, for zooecia more than a few millimetres behind the growth margins are usually closed by terminal diaphragms and therefore cannot have protruded a polypide. Those zooecia adjacent to the growth margin are commonly open. Thus, the overgrowing zooecia of *M. undulata* always covered zooecia lacking polypides.

Banta *et al.* (1974) have suggested an alternative method by which an efficient colonial water-current system may have been maintained. This involves protuberances on the zoarial surface, known as monticules, which acted as areas for the collection and upward discharge of zooidal exhalant currents. Monticules have been described from *R. incrustans* (Taylor 1975). In this species it is suggested that functional polypides were present throughout the whole of the zoarium but were in a somewhat smaller concentration on the monticules, i.e. polypides were present well proximal to the growth margins. Sections through zoaria of *R. incrustans* show that many of the overgrown zooecial apertures were open and therefore could have protruded a polypide at the time of overgrowth. Hence, in colonies of *R. incrustans*, when the individuals reached a certain age (equivalent to the length of time it took for one cycle of overgrowth to be completed) they were probably smothered by an overgrowing zooecial layer. The covering of gerontic zooids seems less of a disadvantage when looked at in the light of polypide degeneration and brown body formation (Ryland 1970).

Multilamellar growth by the mechanism described allows all zooids an equal length of time before they are covered, and produces a zoarium of even thickness. Its prime advantage is that it enables a single colony to make the best possible use of a substratum by repeated encrustation, allowing a considerable increase in the life-span of a colony. In particular, where the number and extent of substrata are limited, a multilamellar zoarium has a special advantage. Hence, *R. incrustans* probably attached itself to the only substratum available at the time, namely shells inhabited by hermit crabs. It became highly adapted to its mode of life, by the acquisition of monticules and a multilamellar growth form. Attachment to the shell occupied by a hermit crab may have prevented the colony being covered by sediment accumulating at a relatively rapid rate. In contrast, adnate multilamellar zoaria of *M. undulata* could probably only have developed where there was a low rate of sedimentation.

The same mechanism for multilamellar growth has evidently arisen independently in two species which are taxonomically fairly well separated. Perhaps the potential for multilamellar growth by this method is present in other normally unilamellar adnate tubuliporinidean Bryozoa. It is hoped that a clearer understanding of the way in which adnate tubuliporinidean zoaria are constructed will be gained by application to other species of the principles of pivot point and anastomosis.

Acknowledgements. This work was carried out during the tenure of a N.E.R.C. research studentship, which I gratefully acknowledge. I wish to thank Dr. G. Larwood for supervision, and Miss P. L. Cook of the British Museum (Natural History) for criticizing the draft manuscript.

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A NEW PTEROPSID FRUCTIFICATION FROM THE MIDDLE PENNSYLVANIAN OF KANSAS

by GAR W. ROTHWELL

ABSTRACT. Discovery of a well-preserved, fertile frond segment in Middle Pennsylvanian petrifaction material from Kansas provides the basis for description of an annulate pteropsid fructification. Numerous sporangia are attached to the abaxial surface of laminar pinnules in either a solitary fashion or in groups of from two to six. Individual sporangia range up to 240 × 320 μm and are divided into a narrow stalk and a spheroid distal region. Sporangial walls are one cell layer thick. Cells over much of the sporangium exhibit thick walls and represent a massive annulus. Thin-walled sporangial cells occur as a narrow, vertically oriented zone. Spores are radial, 16–20 μm and exhibit a prominent trilete mark. Little or no wall ornamentation is present. Fructifications of this type suggest the presence of leptosporangiate, possibly filicalean, ferns during Pennsylvanian time.

INTERPRETATIONS of fern phylogeny rely heavily upon evidence from Palaeozoic fossil forms. This includes numerous pteropsid fructifications from the Carboniferous of Europe and equivalent strata of North America. Many of these are assignable to the Marattiales or Coenopteridales, while others are of less-certain affinities. Still others may represent progenitors of extant filicaleans. Although relationships to this latter group remain uncertain, the description of several Palaeozoic taxa with abaxially borne, annulate sporangia (e.g. *Oligocarpa*, *Senftenbergia*) increases the probability that leptosporangiate ferns were present during Palaeozoic time. The purpose of this study is to describe an additional late Palaeozoic fructification with these features.

The distinctive suite of characteristics described below demonstrates that this fructification is unlike any previously reported form. It is therefore interpreted as a new genus of Pennsylvanian pteropsid. The generic name *Norwoodia* is proposed in recognition of significant contributions to Palaeozoic palaeobotany by Professor Thomas Norwood Taylor. The specific epithet *angustum* (L. *angustus* = narrow) refers to the sporangial stalk.

The fructification occurs in carbonate petrifaction material collected at the mine dump of the Pittsburg and Midway Coal Company No. 19 Mine, which is located south-west of the town of West Mineral in south-eastern Kansas. The source of these coal balls is the commercially mined, Middle Pennsylvanian Fleming Coal. Material was prepared for microscopic examination by the cellulose acetate peel technique (Joy *et al.* 1956). Morphological features were reconstructed from closely spaced serial sections. Spores were macerated from the matrix with 5% HCl and mounted for light microscopy in Harleco Synthetic Resin. Specimens examined with the scanning electron microscope were allowed to dry from drops of distilled water on specimen stubs and coated with gold.

[Palaeontology, Vol. 19, Part 2, 1976, pp. 307–315, pls. 45–46.]

SYSTEMATIC DESCRIPTION

Division PTERIDOPHYTA

Genus NORWOODIA gen. nov.

Type species. Norwoodia angustum sp. nov.

Diagnosis. Form genus of pteropsid fructifications consisting of stalked sporangia superficially borne on laminar pinnules; sporangia solitary-soral, maturation simple; sporangial walls one cell layer thick at maturity, consisting of a massive annulus and a narrow, longitudinally oriented, zone of thin-walled cells; spores radial, trilete.

Norwoodia angustum sp. nov.

Plate 45, figs. 1–6; Plate 46, figs. 1–10

Diagnosis. Features of species those of genus; pinnules alternately arranged on terete penultimate frond segment, constricted at base with lobed margins and open dichotomous veination. Sporangia 270–320 μm long, 200–240 μm in maximum diameter, with narrow stalk and spheroid distal region. Spores approximately 250 per sporangium, 16–20 μm in diameter, trilete extending to near equatorial plane with raised commissure and prominent lips; exine thin, homogeneous, psilate.

Holotype. Peels and slides of specimen in University of Alberta coal ball 318D (1) top; nos. 2281–2310 in the Paleobotanical Collection, University of Alberta, Edmonton, Alberta, Canada.

Locality. (West Mineral.) Mine dump of the Pittsburg and Midway Coal Company No. 19 Mine located W. $\frac{1}{4}$, Sec. 5, T. 33 S., R. 22 E., Columbus Quadrangle, Cherokee County, Kansas, U.S.A.

Stratigraphic position. Fleming Coal, Cabaniss Subgroup, Cherokee Group, Desmoinesian Series, Middle Pennsylvanian (Kansas).

Description. Norwoodia angustum is represented by a single well-preserved frond segment. A terete, penultimate axis bears two ranks of alternately arranged pinnules (text-fig. 1*a*; Pl. 45, fig. 4) that are bent and contorted in such a way as to resemble a loosely arranged cupule-like structure in some sections (Pl. 45, fig. 1). The axis measures 0·3 mm in diameter and contains a single rod of tracheids with scalariform wall thickenings (Pl. 45, fig. 6). A zone of axially elongate, thin-walled cortical parenchyma cells surrounds the bundle (Pl. 45, fig. 4). Cells at the outer margin of the axis are more isodiametric with irregular margins and dark internal contents (Pl. 45, fig. 4). Pinnules are narrowly attached (Pl. 45, fig. 4, arrows at left), but expand

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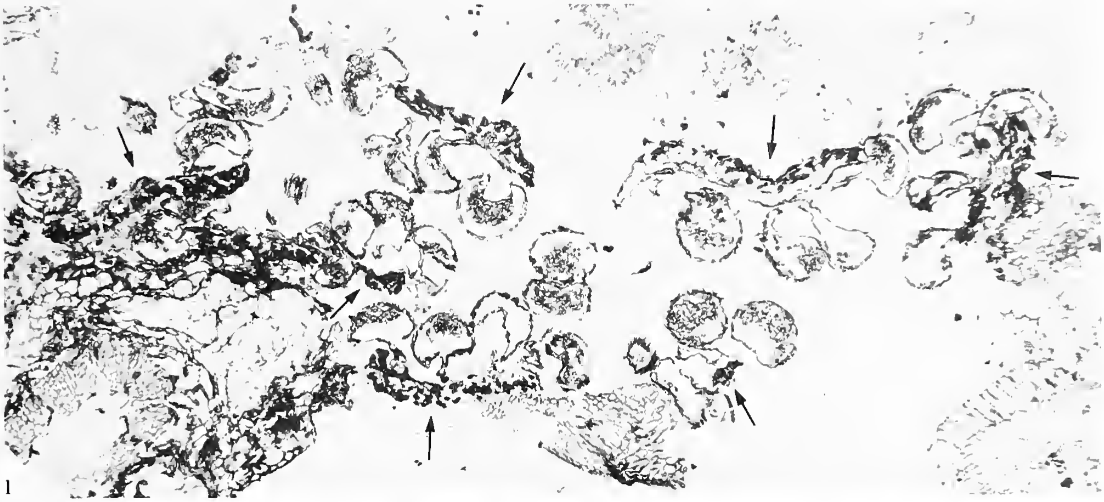
EXPLANATION OF PLATE 45

Figs. 1–6. *Norwoodia angustum* gen. et sp. nov. 1, transverse section of several fertile pinnules (at arrows) arranged such that they resemble a loosely disposed cupule. C.B. 318D top no. 13, ×26. 2, pinnule fragment with sporangia attached in a soral cluster. C.B. 318D top no. 6, ×68. 3, pinnule with sporangia attached along the entire abaxial surface. C.B. 318D top no. 7, ×68. 4, longitudinal section of penultimate pinna showing positions of pinnule attachment (at arrows). Arrows at left indicate pinnules that are sectioned at the point of attachment. C.B. 318D top no. 1, ×50. 5, transverse section near pinnule-lobe tip showing sporangial attachment and anatomical features. C.B. 318D top no. 14, ×210. 6, longitudinal section of vascular bundle showing tracheids with scalariform wall-thickening patterns. C.B. 318D top no. 4, ×340. (p = pinnule, pa = palisade, s = sporangial stalk, v = vascular bundle.)



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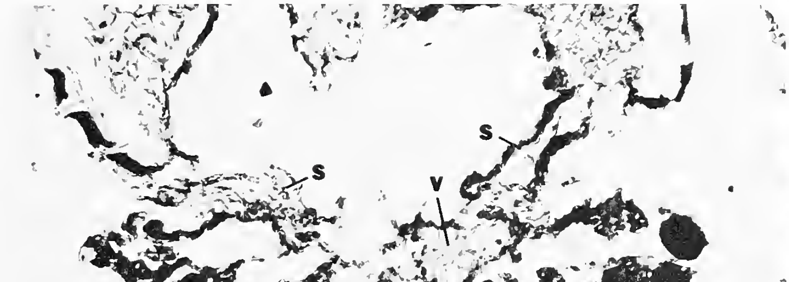

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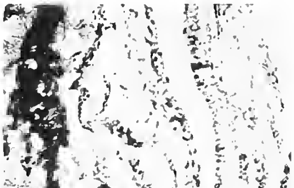

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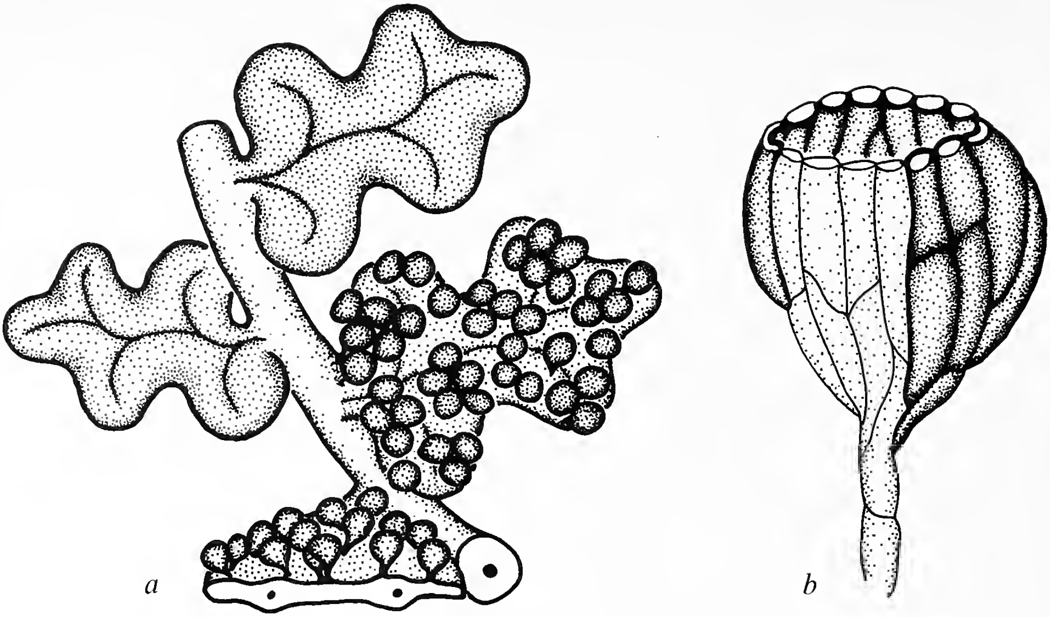
ROTHWELL, *Norwoodia angustum* gen. et sp. nov.



TEXT-FIG. 1. *Norwoodia angustum* gen. et sp. nov. 1*a*, reconstruction of small frond segment showing general features of pinnules, pinnule arrangement, and sporangial attachment from an abaxial view. Sporangia included on basal pinnules only. 1*b*, cut-away reconstruction of a single sporangium.

rapidly and are laminar in more distal regions (Pl. 45, fig. 3). Examination of serial sections indicates that the pinnules have lobed margins. A single vascular bundle enters the base of each pinnule (Pl. 45, fig. 4, at arrows) and dichotomizes to supply a strand to each lobe (Pl. 45, fig. 5). Individual strands consist of six to nine tracheids with scalariform wall thickenings (Pl. 45, fig. 6). A single layer of palisade parenchyma with internal contents like those at the outer margin of the penultimate pinna (Pl. 45, figs. 3, 5) delimits the abaxial margin of most pinnules. Cells toward the abaxial surface are thin-walled and periclinally elongated (Pl. 45, fig. 3). Toward the tips of the lobes this latter zone is reduced or absent (Pl. 45, fig. 5). Larger, more thick-walled cells occur between the vascular bundle and the palisade in some sections. A few cells are occasionally present at the adaxial margin of the palisade and may represent remnants of a poorly preserved epidermis (Pl. 46, fig. 1, at arrow).

Numerous small, closely spaced sporangia are attached to the abaxial surface of each pinnule (Pl. 45, figs. 1–3). They are not restricted to the marginal areas or to the proximity of vascular bundles, but appear to be distributed over the entire pinnule surface (text-fig. 1*a*; Pl. 45, figs. 1, 3). Some sporangia occur in a solitary fashion (Pl. 45, fig. 3), while others form sori of from two to six (Pl. 45, fig. 2). Individual sporangia are 270–320 μm long and 200–240 μm in maximum diameter. They are differentiated into a narrow stalk (Pl. 45, fig. 5) and spheroid distal region (Pl. 45, fig. 3; Pl. 46, fig. 1). Sporangial stalks are up to 100 μm long and in some sporangia appear to consist of a single cell at the point of attachment (Pl. 45, fig. 5; Pl. 46, fig. 1). There is no evidence of a specialized receptacle region.

Sporangial walls are one cell layer thick, with no evidence of what may have been a tapetum (Pl. 46, figs. 1–3). In section view most of the sporangial cells exhibit thickened walls (Pl. 46, figs. 1, 3). This is especially true of the inner and lateral cell walls (Pl. 46, fig. 1, at right). Dark internal contents are present in many of these cells (Pl. 45, fig. 5; Pl. 46, figs. 2, 3). In surface view, cells of this type are longitudinally elongated (Pl. 46, fig. 4) except at the sporangial tip where they are more isodiametric (Pl. 46, fig. 5). These cells are interpreted as representing a massive annulus. In longitudinal sections of some sporangia the annulus extends from the base of the sporangium to a point slightly beyond the apex (Pl. 46, fig. 2). In others it extends completely over the distal end of the sporangium (Pl. 46, fig. 1). In transverse sections cells of the annulus make up about three-quarters of the wall surface (Pl. 46, fig. 3). By comparison of sporangia seen in these views it is concluded that the annulus extends over the entire sporangium except in a narrow, longitudinally oriented zone on one side (text-fig. 1*b*). This latter zone is made up of poorly preserved, thin-walled cells that presumably function as a stomium. All sporangia appear to be preserved at comparable stages of development, suggesting that maturation is of the simultaneous or simple type.

None of the sporangia have dehisced, but spores occupy only about one-half of each sporangial cavity. They are usually closely packed together toward one side of the sporangium (Pl. 45, fig. 1; Pl. 46, fig. 1) and appear to have been subjected to a hypertonic salt concentration prior to fossilization. Thirty to fifty spores can be seen in a single sporangial section (Pl. 46, figs. 1, 3) suggesting a spore production of about 250 per sporangium. Individual spores are radial and trilete, and are highly folded and collapsed (Pl. 46, figs. 6–8). Consequently, accurate observations of spore size and shape could not be made. Measurements of macerated spores range from 16 to 20 μm. Many spores are folded along the trilete, suggesting that their original shape was triangular (Pl. 46, figs. 6–8); possibly with concave interradial sides. Rays of the trilete are prominent and extend nearly to the equatorial plane. The commissure is conspicuously raised and typically closed (Pl. 46, fig. 8). The lips are also raised, and up to 2 μm wide on each side of the commissure (Pl. 46, figs. 7–8). Spore walls are thin (0·3–0·5 μm) and psilate (Pl. 46, fig. 9). Examination of broken walls in section view indicate that they are solid and homogeneous (Pl. 46, fig. 10). Spores of this type are possibly referable to dispersed spore genus *Granulatisporites* (Ibrahim) Schopf, *et al.* (1944), which is of frequent occurrence throughout Middle Pennsylvanian sediments of North America (Peppers 1970; Schopf *et al.* 1944). Spores of the *Granulatisporites* type are known from previously described Carboniferous fern fructifications (i.e. *Boweria*, *Renaultia*, Knox 1938) and possibly represent a natural group of pteropsid origin (Schopf *et al.* 1944). Other *sporae-dispersae* genera to which *Norwoodia* spores may possibly be assigned are *Leotriletes* (Naumova) Potonié and Kremp (1954), *Punctatisporites* (Ibrahim) Potonié and Kremp (1954), or *Triquitrites* (Wilson and Coe) Schopf *et al.* (1944). Species of these genera typically range from slightly larger to much larger than the spores of *Norwoodia*, and usually also have more ornamented exines (e.g. Peppers 1964, 1970). At the present time it is not known whether this is entirely due to taxonomic dissimilarity or whether ontogenetic variation may also be a factor. Specimens assignable to *Calamospora* Schopf *et al.* (1944) are also somewhat similar to *Norwoodia* spores. They are sometimes as small and typically have smooth, folded exines, but are characterized by a much less extensive trilete and are typically associated with sphenopsid fructifications.

DISCUSSION

In many respects *Norwoodia* resembles several previously described Palaeozoic pteropsids. Among these *Oligocarpa* Goeppert (1841), *Senftenbergia* Corda (1845), *Renaultia* Stur (1883), *Boweria* Kidston (1911), *Tedelia* Eggert and Taylor (1966), and *Sermaya* Eggert and Delevoryas (1967) also have independent annulate sporangia that are borne on the abaxial surface of lobed, possibly sphenopterid, pinnules. However, none of these exhibit an annulus similar to that of *Norwoodia.* In *Senftenbergia* and *Tedelia* the annulus is terminal, while that of *Oligocarpa* is horizontal-oblique. In *Boweria* and *Sermaya* cells of the annulus are described as extending over the apex of the sporangium and down each side for a short distance. That of *Renaultia* is apparently rudimentary. Thick-walled cells extend over almost the entire *Norwoodia* sporangium and comprise the most massive annulus thus far discovered in either fossil or extant material. If the phylogenetic reduction in annulus size proposed among representatives of the Schizeaceae (Radforth 1938, 1939) can be considered as characteristic of fern evolution in other families, then the extensive annulus of *Norwoodia* must be considered extremely primitive.

The sporangial stalk of *Norwoodia* is also of interest. In Palaeozoic taxa superficially borne sporangia are typically sessile or have only poorly differentiated stalks. The sporangia of *Norwoodia* are distinctly stalked and possibly attached by a single cell; features associated with relatively advanced filicalean families. *Oligocarpa* is an additional Palaeozoic genus with stalked sporangia (Abbott 1954). Unfortunately specimens of this genus are typically preserved as compressions so that a more precise comparison to the sporangial stalks of *Norwoodia* cannot be made.

The small, undehisced sporangia and folded pinnules of *Norwoodia* are reminiscent of quite immature pteropsid fructifications. Thin-walled, unornamented spores are also suggestive of an early maturation stage. One must therefore question whether a more mature specimen would exhibit similar features, or perhaps be recognized as an additional specimen of a previously described taxon. As indicated above, the

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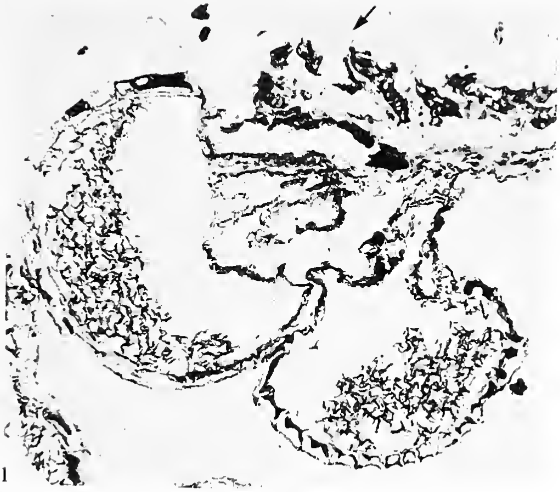
EXPLANATION OF PLATE 46

Figs. 1–10. *Norwoodia angustum* gen. et sp. nov. 1, longitudinal section of two attached sporangia. Note the disposition of the thick-walled annulus cells and possible pinnule epidermis (at arrow). C.B. 318D top no. 8, ×165. 2, longitudinal section of sporangia showing disposition of annulus, from sporangial base to slightly beyond the apex. C.B. 318D top no. 3, ×165. 3, transverse section of sporangium showing disposition of the annulus. 4, surface view of sporangium showing longitudinal orientation of annulus cells. C.B. 318D top no. 10, ×210. 5, transverse section near sporangial tip showing isodiametric annulus cells in surface view. C.B. 318D top no. 11, ×210. 6, aggregation of spores from maceration preparation. C.B. 318D top no. A, ×1500. 7, isolated spore from maceration preparation showing folded, psilate exine and prominent trilete. C.B. 318D top no. C, ×1880. 8, scanning electron microscope (S.E.M.) photograph of spore similar to that in 7. Note the distinctly raised commissure and absence of surface ornamentation, ×2000. 9, S.E.M. close-up of spore wall, ×6500. 10, S.E.M. of broken section of spore wall with solid apparently homogeneous structure, ×15000.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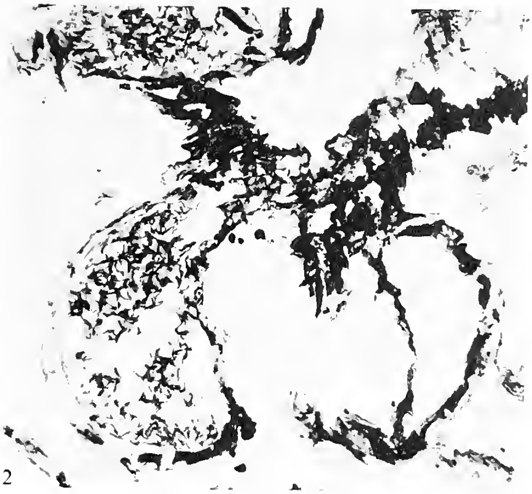
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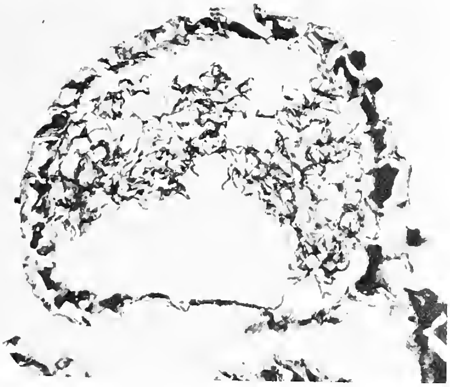
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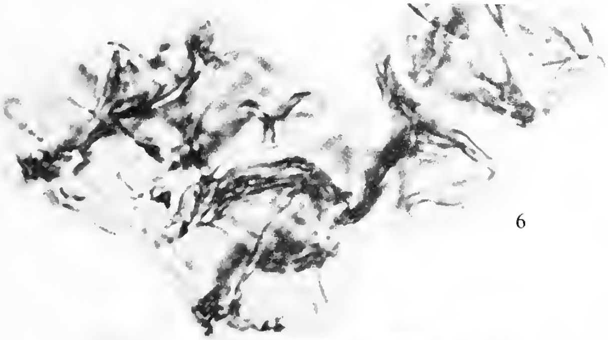
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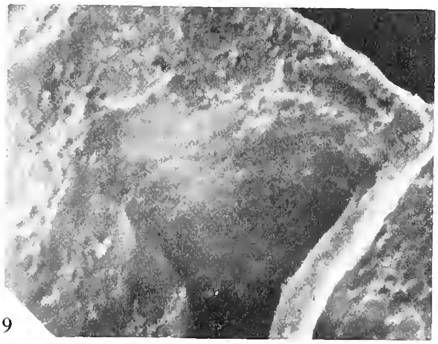
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ROTHWELL, *Norwoodia angustum* gen. et sp. nov.

massive annulus of *Norwoodia* is much more extensive than that of any other known pteropsid fructification. In light of the thick-walled nature of the annulus cells it is unlikely that any substantial changes in sporangial size or shape would occur with further development. The complete absence of a tapetum in all sporangia also suggests that they are more mature than the above features would indicate. Moreover, in crosiers of fertile pteropsids the pinnules are folded with the sporangia (abaxial surfaces) facing outward, while the sporangia of *Norwoodia* are oriented toward the centre of the aggregation (text-fig. 1). Maturity of the spores is more difficult to determine. It is quite possible that mature spores of this species are small and unornamented. On the other hand, in at least two genera of Palaeozoic pteropsids, *Senftenbergia* (Radforth 1938) and *Tedelia* (Eggert and Taylor 1966) spores from what otherwise appear to be relatively mature sporangia are known to exhibit a wide range of size and exine ornamentation. These differences are interpreted as representing ontogenetic variations; the smallest unornamented spores being the least mature (Eggert and Taylor 1966). While there is at present no evidence of such variation among *Norwoodia* spores, one cannot overlook the possibility that further development may significantly alter both spore size and exine ornamentation.

The features discussed above clearly distinguish *Norwoodia* as an independent genus of Palaeozoic ferns. However, its relationships to other pteropsids are more difficult to interpret. Among extant ferns sporangia with a well-developed annulus are found only among the Filicales, and are traditionally regarded as indicating leptosporangiate development. Similar features in Palaeozoic ferns are unfortunately less diagnostic. For instance, sporangia of this type are known to have been produced by *Botryopteris* (e.g. Phillips 1961), *Sermaya* (Eggert and Delevoryas 1967), *Ankyropteris* (Jennings and Eggert 1972), and possibly *Zygopteris* (e.g. Bertrand 1911; Mamay 1957), but the vegetative anatomy of these clearly allies them with Coenopteridales. On the other hand, Palaeozoic fructifications are sometimes interpreted as possible filicaleans when more proximal structures are unknown (e.g. *Oligocarpa*) or even when vegetative structures conform to those of the Coenopteridales (e.g. *Tedelia*, Eggert and Taylor 1966). While the early sporangial development of these fossil forms remains unknown it is impossible to determine if they are truly leptosporangiate or if they are derived from more than one sporangial initial. The occurrence of this latter development in presumably primitive, extant filicaleans (e.g. *Stromatopteris*, *Osmunda*, Bierhorst 1971) suggests a similar development in the Palaeozoic taxa that have small, annulate sporangia.

At the present time the affinities of *Norwoodia* remain uncertain. The small sporangial size, distinct annulus, single-cell layered wall, and prominent stalk demonstrate the similarity of the superficially borne *Norwoodia* sporangia to those of more recent filicaleans. However, many of these features are also shared by late Palaeozoic coenopterids. If future studies document the origin of the filicaleans from among the Coenopteridales, *Norwoodia* may represent a transitional form or even an early representative of the former. When one considers that there are several, simple, Pennsylvanian ferns for which fertile parts have not yet been assigned (i.e. *Apotropteris minuta* Morgan and Delevoryas, 1954; *Catenopteris simplex* Phillips and Andrews, 1965; *Rabdoxylon americanum* Dennis, 1968) it is likely that unquestionable filicaleans may be discovered in the late Palaeozoic of North America.

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A NEW TURTLE SKULL FROM THE PURBECKIAN OF ENGLAND AND A NOTE ON THE EARLY DICHOTOMIES OF CRYPTODIRE TURTLES

by JEANNE EVANS *and* T. S. KEMP

ABSTRACT. A new cryptodire turtle skull, *Dorsetochelys delairi*, is described from the Purbeckian of Dorset. It possesses features of both the Glyptopidae and the Baenidae, but cannot be accommodated satisfactorily in either of these two families. Early dichotomies of the cryptodires are discussed. It is concluded that the family Glyptopidae is the sister group of all other forms, and that only subsequently did the Baenidae diverge from the typical cryptodires, which include the modern forms.

THE specimen described in this paper is a complete skull lacking all traces of lower jaws and postcranial skeleton, which belongs to the Dorset County Museum in Dorchester. It came to our attention as a result of a reference to it by Delair (1958), who stated that Smith Woodward referred it to the genus *Pleurosternum* in 1909 on the basis of the ornamentation of the skull, which resembles the shell ornament of that genus.

There are seven turtle genera known from the Purbeckian of Dorset (Lydekker 1889; Delair 1958). All lack skulls, and several of these cannot be distinguished from one another on dermal ornament alone. On the other hand, there are now two skulls, *Mesochelys* (Evans and Kemp 1975) and the present specimen which, although quite different from one another, cannot be distinguished on the cranial ornament alone. At the present time, therefore, it is impossible to identify this new skull as belonging to a genus based on the shell. Though it may eventually prove to belong to an existing genus currently based on postcranial remains, we cannot at the present time be certain of this, and we have therefore decided to name and diagnose it now, as a new genus and species, for immediate scientific convenience.

Before preparation the skull was only exposed dorsally. The matrix is a hard, buff limestone, and complete preparation by the acetic acid method has exposed the palatal surface. It is severely but symmetrically crushed dorso-ventrally, and the anterior part of the palate is slightly damaged. Less reliance can be placed on dorso-ventral dimensions of the reconstruction than on others.

SYSTEMATIC PALAEONTOLOGY

The specimen corresponds in skull structure to the primitive cryptodire superfamily Baenoidea as defined by Gaffney (1972), in possessing nasal bones; prefrontals not meeting in the midline; foramen posterior canalis carotici interni opening midway along the basisphenoid-pterygoid suture. However, it shows a mosaic of features of

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the two families, Glyptopidae and Baenidae, that Gaffney placed in the Baenoidea. Glyptopid characters are the dorsal exposure of the prefrontal; limited posterior emargination of the skull roof; ossified epipterygoid. Baenid characters are the failure of the basisphenoid to extend for the full length of the pterygoids; wider triturating surface to which the palatine contributes significantly; greater postero-medial extent of the pterygoid, flooring the cavum acustico-jugularis and making a relatively long suture with the basioccipital. As discussed later, this new form cannot be incorporated satisfactorily in either of these two families in a strictly monophyletic sense.

Dorsetochelys gen. nov.

Type species. D. delairi sp. nov.

Diagnosis. Primitive cryptodire with the skull slightly longer than wide; very little posterior emargination; parietal meeting squamosal in a long suture; nasals large; prefrontal with moderate dorsal exposure; basisphenoid long but not extending for the full length of the pterygoids; ossified epipterygoid; palatine makes substantial contribution to the triturating surface; dorsal triangular exposure of the supra-occipital between the parietals.

Dorsetochelys delairi sp. nov.

Text-figs. 1–2

Diagnosis. As for genus.

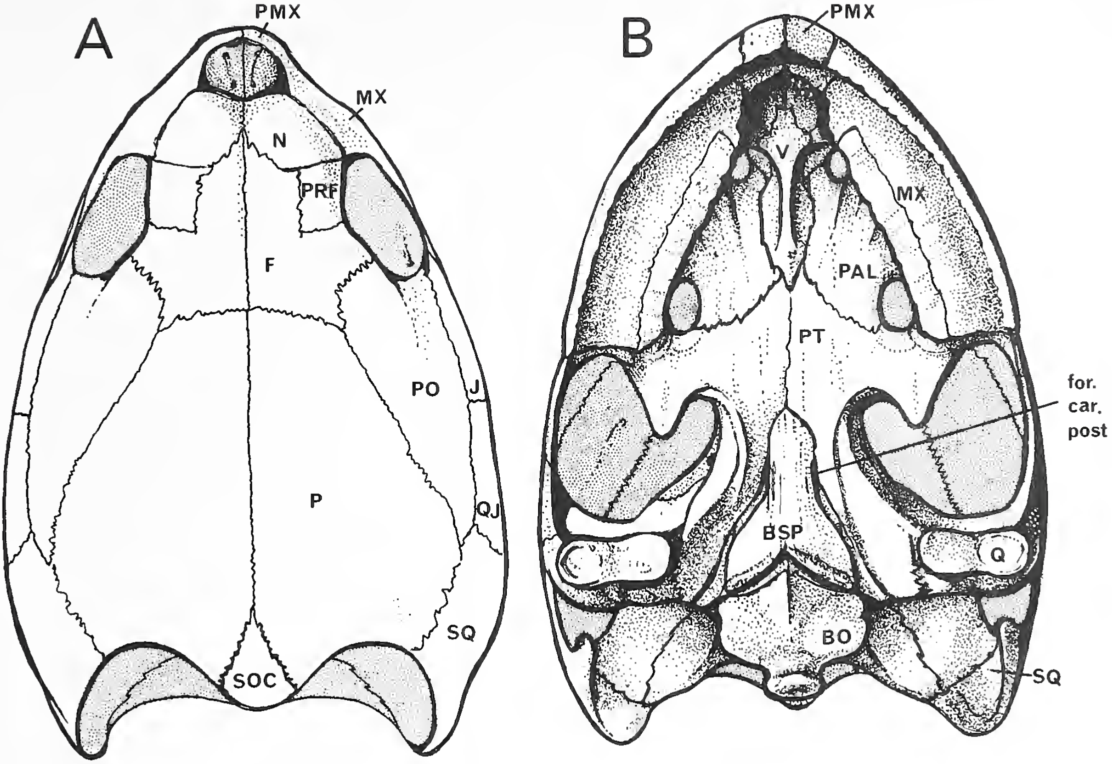
Holotype. Dorset County Museum, Dorchester. Spec. no. G23. Skull lacking lower jaws.

Locality. Swanage, Dorset.

Horizon. Purbeckian, Lower Cretaceous.

Description. The precise original shape of the skull is not certain because of the extensive dorso-ventral distortion, but it seems to have been almost oval in dorsal view with the length exceeding the maximum breadth. The lateral profile was rather low. There is a relatively very small degree of emargination of the posterior border of the skull roof, and the foramen stapedio-temporale is not visible from above. There is an equally slight degree of emargination of the ventro-lateral skull margin.

The sutural pattern on the dorsal surface of the skull is clear from text-fig. 1A. The relatively large size of the nasals is notable; they meet the frontals in an oblique suture reminiscent of the condition in *Mesochelys* (Evans and Kemp 1975). The dorsal exposure of the prefrontal is similar to that of typical reptiles, being neither expanded to the midline as in most cryptodires, nor reduced as in typical baenids. A typically cryptodire antero-ventral process of the prefrontal descends, in contact with the maxilla, to meet the dorsal surface of the palate and form the anterior wall of the orbit. The suture between the maxilla and the nasal is straight and horizontal, and closely resembles the condition in the primitive baenid *Trinitichelys* (Gaffney 1972). The very extensive sutural contact between the squamosal and the parietal is correlated with the low degree of emargination of the posterior part of the skull. A peculiar feature of the posterior part of the skull roof is a broad triangular exposure



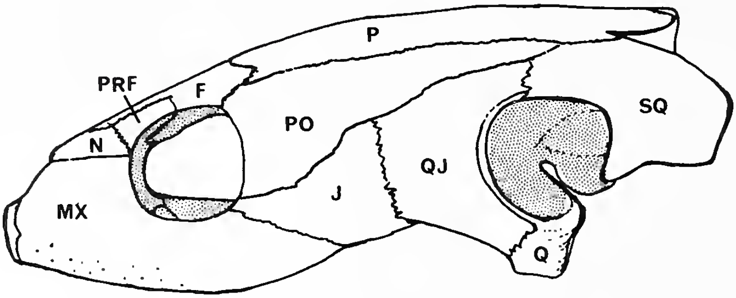
TEXT-FIG. 1. *Dorsetochelys delairi*. A, skull in dorsal view, × 1. B, skull in ventral view, × 1.

Abbreviations: BO, basioccipital; BSP, basisphenoid; F, frontal; for. car. post, foramen posterior canalis carotici interni; J, jugal; MX, maxilla; N, nasal; P, parietal; PAL, palatine; PMX, premaxilla; PO, postorbital; PRF, prefrontal; PT, pterygoid; Q, quadrate; QJ, quadratojugal; SOC, supraoccipital; SQ, squamosal; V, vomer.

of the supraoccipital between the hind ends of the paired parietals. The surface texture of this part of the supraoccipital is preserved, indicating that its exposure is not the result of damage to the bones in the area. There is no posterior extension of a supraoccipital crest and, although apparently undamaged, this condition may have resulted from the crushing of the skull.

In ventral view, text-fig. 1B, the palate is broad and flat, with very little vaulting between the triturating surfaces. The triturating surface itself is fairly broad and it widens slightly posteriorly. The extent to which the palatine contributes is unusual, and there is a deep, sharp labial ridge along the external margin, but no tomial ridge is developed. The paired pterygoids meet in the midline and contact the vomer anteriorly, separating the palatines from one another. The basisphenoid is much shorter than the pterygoids but is still relatively long, and there is no sign of a specific basipterygoid articulation as there is in *Mesochelys*. The posterior foramen for the internal carotid artery lies rather forward of the midway point of the basisphenoid, and the canal disappears anteriorly into the bone. A distinct groove runs backwards from the foramen along the lateral edge of the basisphenoid, and then postero-laterally across the pterygoid to the hind edge; this must have carried the internal carotid artery. Enclosure of this groove ventrally would correspond to the typical cryptodire condition, in which the carotid canal opens more posteriorly. Behind the basisphenoid there is a relatively extensive contact between the pterygoid and the basioccipital; this is because the pterygoid extends further medially than in *Mesochelys* and *Glyptops*.

A large epipterygoid is present, its base lying against the lateral edge of the pterygoid flange of the palate.



TEXT-FIG. 2. *Dorsetochelys delairi*. Skull in lateral view, × 1.

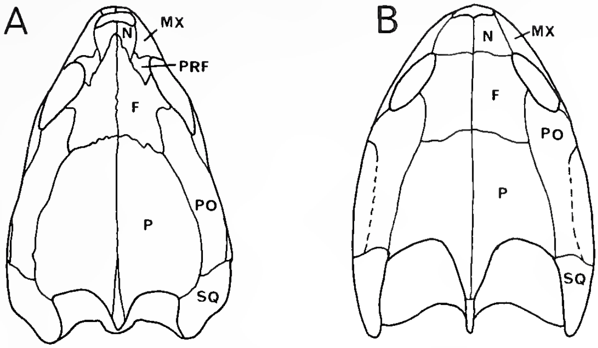
The extensive dorso-ventral crushing has badly distorted the occiput, but it appears to be of standard chelonian form. Two foramina nervi hypoglossi emerge through the ventro-medial part of the exoccipital bone, the posterior one being considerably larger than the anterior one.

Both the quadrates are crushed, but it is clear that the stapedial notch is open posteriorly and that there was a normally developed antrum postoticum.

DISCUSSION

The cranial anatomy of all the better-known Upper Jurassic and Lower Cretaceous turtles indicates that they are members of the Suborder Cryptodira, despite the absence of the characteristic postcranial modifications of the modern members of the group, and they should no longer be retained in Lydekker's suborder 'Amphichelydia' (see Gaffney 1972; Evans and Kemp 1975). These remarks apply equally to *Dorsetochelys*. Interpretation of the interrelationships of these early forms is difficult, because all of them have achieved an essentially modern cranial morphology which tends to mask the differences which do exist between them. Nevertheless, there appear to be three characters of particular significance:

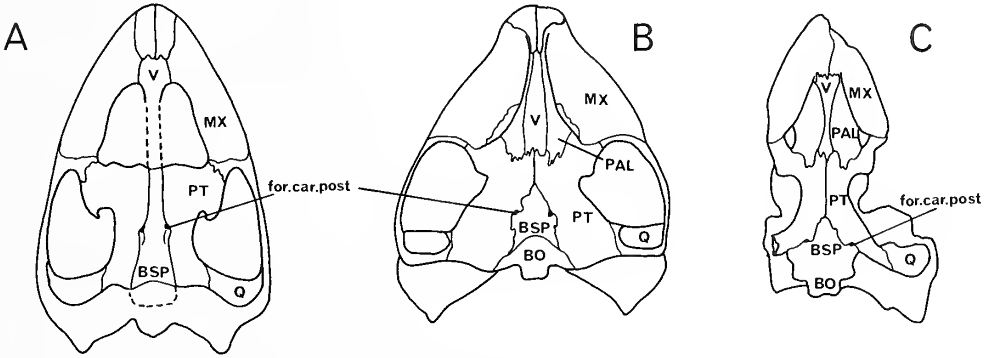
1. Condition of the prefrontal bones (text-fig. 3). The ancestral condition is surely that of a moderate dorsal exposure as found in the glyptopids *Glyptops* (Gaffney 1972) and *Mesochelys* (Evans and Kemp 1975) and in *Rhinochelys* from the Cambridge Greensand (Collins 1970), because of its close resemblance to the standard reptilian form. Two derived conditions are reduction of the dorsal exposure as in the baenids (Gaffney 1972), and expansion of the dorsal lappet to meet its fellow in the midline as in most other cryptodires. In this respect *Dorsetochelys* has retained the ancestral type of prefrontal.



TEXT-FIG. 3. Dorsal views of the skulls of A, *Mesochelys* (glyptopid); B, *Trinitichelys* (baenid). (A, after Evans and Kemp 1975; B, after Gaffney 1972.)

2. Position of the foramen posterior canalis carotici interni (text-fig. 4). In the glyptopids, baenids and also *Dorsetochelys*, this lies anteriorly, half-way along the suture between the basisphenoid and pterygoid bones. In all other known cryptodires it lies posteriorly, near the hind border of the skull. Gaffney has argued that both these conditions are derived from an as yet unknown ancestral position of the foramen. However, there appear to be good grounds for considering the anterior position to be ancestral to the posterior position, because the former approximates to the position of the foramen in typical reptiles. Furthermore, in *Mesochelys* the foramen is intimately associated with a very primitive arrangement of the basipterygoid articulation whereby the remnant of the reptilian basipterygoid process of the basisphenoid is still discernible (Evans and Kemp 1975). Furthermore, *Dorsetochelys* indicates how the posterior position of the foramen might readily be derived from the anterior position by a roofing over of the groove leading backwards from the foramen to the hind border of the skull.

3. The relative midline length of the basisphenoid (text-fig. 4). In the glyptopids, the basisphenoid extends anteriorly to reach the vomer and thus separates the



TEXT-FIG. 4. Ventral views of the skulls of A, *Mesochelys* (glyptopid); B, *Eubaena* (baenid); C, the 'Portland' skull ('typical cryptodire'). (A, after Evans and Kemp 1975; B, after Gaffney 1972; C, after Parsons and Williams 1961.)

pterygoids completely from one another (a similar but probably secondary condition occurs in the trionychid cryptodires). In contrast, the basisphenoid of other forms is shorter than the pterygoids, so that the latter pair of bones meet in the midline anterior to the basisphenoid. It is difficult to know which of these two conditions should be regarded as ancestral for cryptodires, but the generally primitive nature of the basisphenoid in the glyptopids in other respects suggests that it may be primitive in this respect also, in agreement with the view of Gaffney (1972).

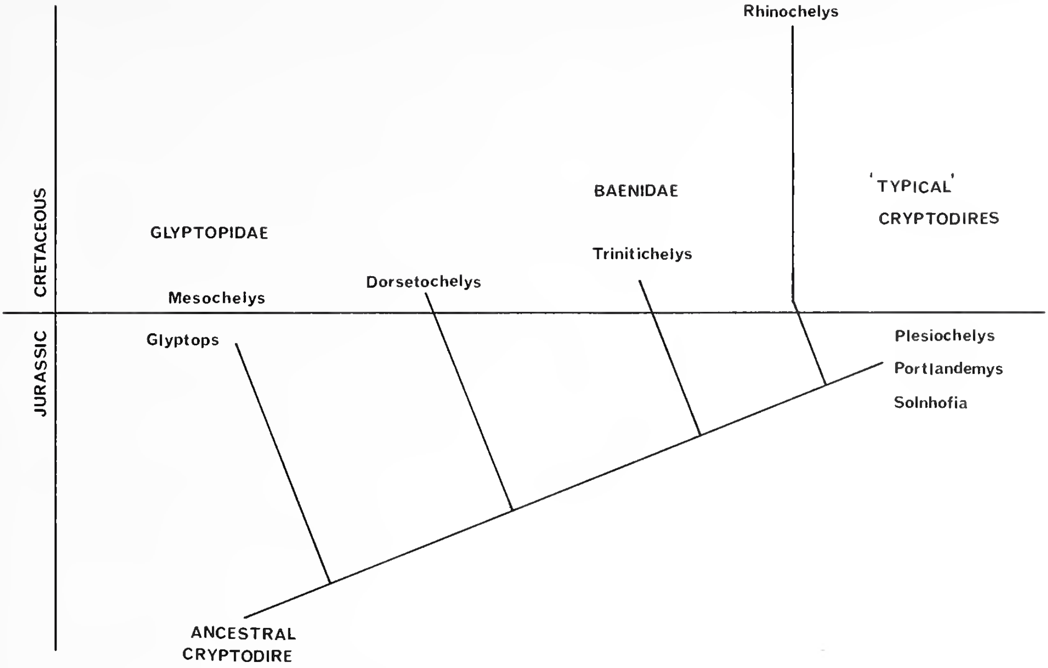
Certain other features found only in the glyptopids are probably also ancestral for the cryptodires as a whole—for example, the failure of the pterygoids completely to floor the cavum acustico-jugulare, with a correspondingly very limited contact between the pterygoid and the basioccipital, and the presence of an ossified epipterygoid. On the other hand, certain other features of members of this family, such as the elongation of the skull and the narrow triturating surfaces, are more likely to be specializations related immediately to the particular habit of the group.

The only characters which link the glyptopids with the baenids (and also with *Dorsetochelys*) are the anterior position of the carotid foramen and the absence of the expanded type of prefrontal bone. However, both are no more than ancestral cryptodire features, and therefore Gaffney's (1972, 1975*b*) proposed superfamily Baenoidea which consists of these two families alone is of doubtful phylogenetic validity, since they share no derived characters in common. We propose therefore that the superfamily Baenoidea should be abandoned and its constituent families Glyptopidae and Baenidae be considered separately.

Using the above key characters, and assuming that the indicated derived character states were in fact uniquely derived, the following phylogeny of early cryptodires is suggested (text-fig. 5).

The first dichotomy was between the glyptopids (*Glyptops* and *Mesochelys*) on the one hand, which retain the primitive character states except for a number of minor modifications including skull elongation, and all the remaining cryptodires on the other, which lost the remnant of the reptilian basipterygoid articulation, shortened the basisphenoid, and expanded the pterygoid postero-medially. Another major dichotomy separated the baenids, which reduced the prefrontal bones but retained the anterior position of the carotid foramen, from the rest of the known cryptodires in which the posterior position of the carotid foramen evolved. Within these remaining cryptodires, which include the Upper Jurassic *Portlandemys* (Gaffney 1975*a*), *Solnhofia* (Gaffney 1975*b*), and *Plesiochelys* (Bräm 1965; Gaffney 1975*a*) as well as the modern forms, the Upper Cretaceous *Rhinochelys* (Collins 1970) is unusual in retaining the primitive moderate-sized prefrontals. It is separated therefore from what might be termed the 'typical' cryptodires in which the prefrontals have expanded to meet in the midline.

Within the context of the phylogeny, the position of *Dorsetochelys* is ambiguous. It is clearly a member of the non-glyptopids but, since it lacks the derived characters of both the baenids and the 'typical' cryptodires respectively, it is not possible to know whether it separated before or after the divergence of these two groups. Its own particular specializations are relatively trivial, and include the expansion of the supraoccipital between the parietals and other details of the suture pattern of the dermal



TEXT-FIG. 5. Phylogeny of early cryptodire turtles known by their skulls.

bones. In general terms it must lie quite close to the ancestry of both the baenids and the 'typical' cryptodires. However, there is a distinct trend towards emargination of the posterior border of the skull roof within both these groups, and the absence of any such tendency in *Dorsetochelys* may be interpreted as evidence that this genus diverged before the establishment of either the baenid or the 'typical' cryptodire type of skull. By this admittedly slightly tenuous reasoning, *Dorsetochelys* is seen as a sister-group of all the other non-glyptopid cryptodires.

No formal classification of these early cryptodires is attempted on the basis of this tentative phylogeny. To judge from the number of genera known only from shell anatomy, there must be a considerable range of skulls not yet known which may ultimately radically change ideas about the evolution of the cryptodire skull.

Acknowledgements. We wish to thank the Dorset County Museum for loan of the specimen described in this paper, and Dr. Gene Gaffney for providing us with copies of his unpublished work. One of us (J. E.) has to thank the late Professor T. Weis-Fogh and Dr. K. A. Joysey for permission to work in the Cambridge University Museum of Zoology.

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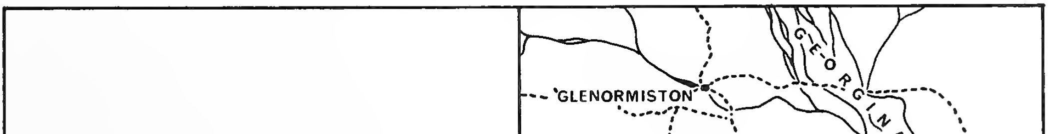
UPPER CAMBRIAN (IDAMEAN) TRILOBITES FROM WESTERN QUEENSLAND, AUSTRALIA

by R. A. HENDERSON

ABSTRACT. This paper reviews new and hitherto poorly understood trilobites from the type section of the early upper Cambrian Idamean Stage on Glenormiston Station, western Queensland. Revisions of local species of *Pseudagnostus*, *Proceratopyge*, *Eugonocare*, *Stigmatoa*, and *Pagodia* (*Idamea*) are given. Two new genera, *Aplotaspis* (Ceratopygidae) and *Prismenaspis* (Elviniidae) are established as well as the new species *Pseudagnostus curtare*, *P. margopronus*, *Proceratopyge cryptica*, *Aplotaspis mucrora*, *Aphelaspis australis*, *Eugonocare whitehousei*, *E. quadrata*, *Prismenaspis brownensis*, and *P. alta*. Representatives of *Pterocephalia*, *Yuepingia*, and *Prochuangia* are recorded from Australia for the first time. A biostratigraphic summary for the Idamean Stage and notes of its correlation are given together with discussions of the biomere concept and the significance of the basal Idamean faunal discontinuity.

THE Idamean Stage is the younger of two early upper Cambrian Stages recognized in Australia; both were introduced by Öpik (1963). The preceding Mindyallan Stage is roughly correlative with the *Agnostus pisiformis* Zone of the Swedish upper Cambrian faunal succession while the Idamean Stage approximates to the *Olenus* Zone. Together, the Australian Stages are correlative with the Dresbachian Stage and basal *Elvinia* Zone of the Franconian Stage of the North American Cambrian scale.

Trilobites described here are from some 60 sq km of Georgina Limestone cropping out south of Glenormiston Station Homestead (text-fig. 1). This area has been



TEXT-FIG. 1. Locality map with the area of Georgina Limestone comprising the Browns Creek Section from which the trilobites reported here were collected shaded.

[Palaeontology, Vol. 19, Part 2, 1976, pp. 325-364, pls. 47-51.]

a classic Australian early upper Cambrian trilobite collecting locality and reference area for biostratigraphic subdivision since the reports of Whitehouse (1936, 1939). Öpik (1963, 1967) added a number of new elements to the fauna and offered some revision of Whitehouse's taxa. In addition, he proposed a new biostratigraphic zonation for the early upper Cambrian based on faunas from many scattered outcrop areas in western Queensland among which stratigraphic relationships were poorly known. Öpik's Idamean Stage was a grouping of five zones, three of which were best represented by trilobite faunas collected south of Glenormiston Station Homestead. Hitherto, it has had no designated type section.

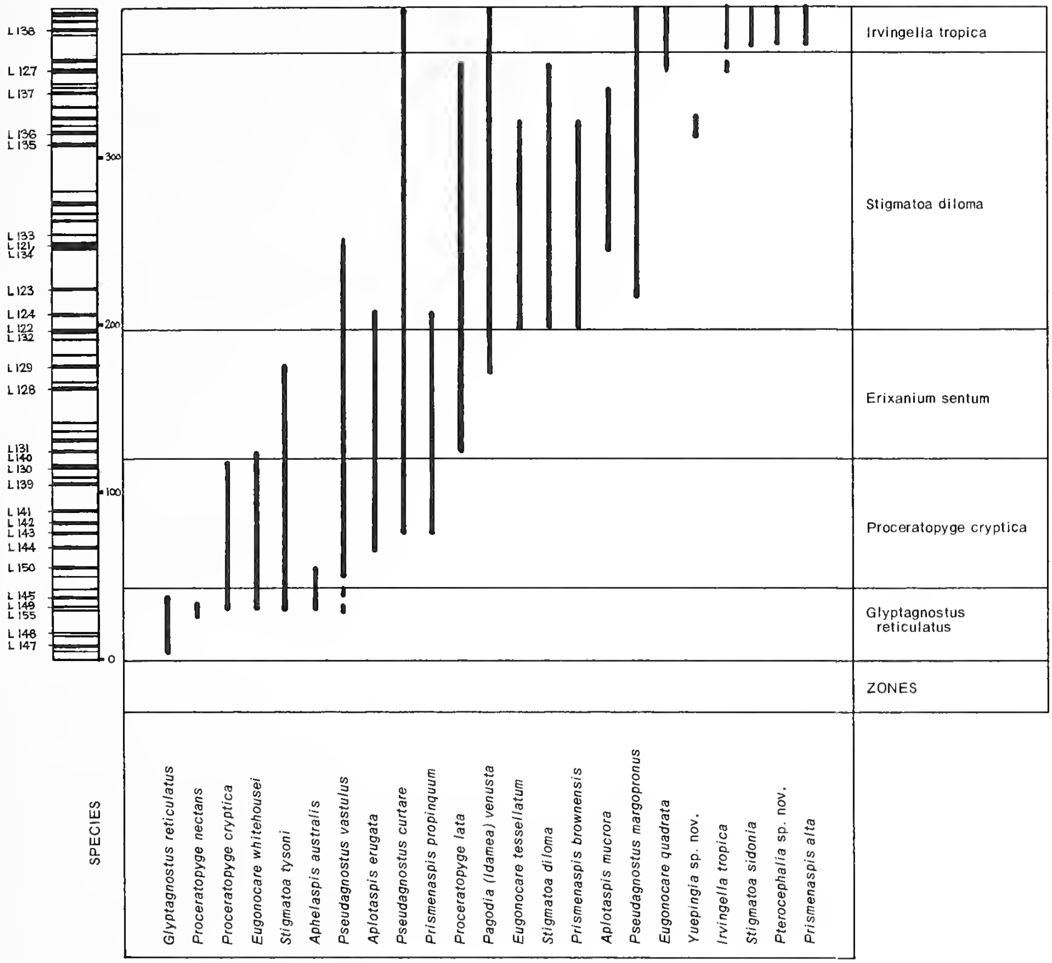
Henderson (in press) has mapped this area in detail and resolved a composite stratigraphy in spite of poor outcrop and structural complexity. The composite succession is here termed the Browns Creek Section. Extensive collections of trilobites have been made from successive limestone horizons for detailed biostratigraphic analysis. Öpik's collections can be integrated into the succession with some accuracy by virtue of their geography, but locality data for Whitehouse's collections are too generalized to allow them to be accurately placed. The revised biostratigraphy of the Browns Creek Section reveals that the entire Idamean faunal succession is represented, passing conformably down into the uppermost zone of the Mindyallan Stage (Henderson, in press). The Browns Creek Section is regarded as the type section for the Idamean Stage.

During the detailed biostratigraphic analysis, it became apparent that some taxonomic revision of the trilobites was needed. The purpose of this report is to describe several new Idamean trilobites and to revise a number of important taxa, mainly established by Whitehouse, which are poorly understood or have been misinterpreted. In addition, it is convenient at this time to give a full listing of the Idamean faunal zonation and to re-examine correlation of the Idamean Stage with biostratigraphic successions recognized elsewhere.

Collections. The study is based on faunas from twenty-seven stratigraphically controlled collection localities. These are designated by numbers, prefixed L, which refer to the Fossil Locality Register of the James Cook University of North Queensland. Complete details of the geography and stratigraphic positions of the localities is given elsewhere (Henderson, in press) and are not repeated here. A summary of their stratigraphic succession is presented in Table 1. Type and figured specimens are listed by numbers prefixed JCF which refer to the Palaeontological Collection of the same institution. Whitehouse's type specimens are curated by the University of Queensland and were consulted in the preparation of this report; specimen numbers pertaining to them are designated by the prefix UQF.

Terminology. Morphological terminology follows that given in Moore (1959) but some terms, especially those applied to agnostids, are from Öpik (1967). The term 'plectral lines' refers to weak, narrow furrows which traverse the frontal area, diverging from the anterior glabellar termination and passing smoothly into confluence with medial terminations of the anterior border furrow. They are characteristic of members of the Ceratopygidae.

TABLE 1. Range chart for Idamean trilobite species described in this report. The column summarizes stratigraphic relationships between collection localities (L140, etc.) for the Browns Creek Section. Limestone horizons are shown as black; intervening horizons are comprised of shale. Thickness scaled in metres.



SYSTEMATIC DESCRIPTIONS

Order MIOMERA Jaekel, 1909
Suborder AGNOSTINA Salter, 1864
Family DIPLAGNOSTIDAE Whitehouse, 1936
Subfamily PSEUDAGNOSTINAE Whitehouse, 1936
Genus PSEUDAGNOSTUS Jaekel, 1909

Remarks. Pseudagnostus is a long-ranging, common late Cambrian genus with considerable potential for interregional correlation. Unfortunately, species groups within it are at present poorly understood due largely to infraspecific variation and uncritical species determinations by many workers. The three species recognized here are based on substantial collections from the Browns Creek Section and are stratigraphically restricted. They are closely allied to forms of equivalent age from other regions.

Pseudagnostus vastulus Whitehouse

Plate 47, figs. 10–12

1936 *Pseudagnostus vastulus* Whitehouse, p. 99, pl. 10, figs. 3, 4.
?1967 *Pseudagnostus idalis* Öpik, p. 153, pl. 62, figs. 8, 9; pl. 63, figs. 1, 3.
?1971 *Pseudagnostus idalis* Öpik; Hill *et al.*, pl. 12, figs. 1, 2.
1971 *Pseudagnostus vastulus* Whitehouse; Hill *et al.*, pl. 12, figs. 8, 9.

Material. Holotype: UQF 3203, pygidium (figured by Whitehouse, pl. 10, fig. 4). Paratype: UQF 3202, cephalon (figured by Whitehouse, pl. 10, fig. 3). Over twenty-five specimens of each cephala and pygidia, localities L121–122, L124, L128–129, L131, L133–134, L139–144, L150.

Diagnosis. Pseudagnostus (*en grande tenue*), with strong, very broad border furrows. Preglabellar median furrow continuous. Glabella with a slight median constriction, posterior rounded to slightly pointed separating well-defined basal lobes. Pygidium with accessory furrows continuous to the border which they typically intersect well anterior to the deuterolobe termination. Pygidial spines small but distinct; located just anterior to the deuterolobe termination. Acrolobes of both cephalon and pygidium faintly constricted and faint, scrobiculate sculpture can often be discriminated on acrolobe flanks of internal moulds.

Dimensions. Cephalic lengths range from 3·0 to 5·1 mm; pygidial lengths from 2·8 to 4·2 mm.

Remarks. P. vastulus Whitehouse is based on material from the type Idamean succession. The two type specimens are associated with *Corynexochus plumula* Whitehouse on slabs of distinctive limestone that can be confidently assigned to horizons which occur at the base of the zone of *Stigmatoa diloma* at about the level of localities L121 and L134 (see Table 1). They have been recently refigured in Hill *et al.* (1971, pl. 12, figs. 8, 9). Unfortunately, the holotype pygidium (UQF 3203) is non-diagnostic because it is only partially exposed. However, the paratype cephalon

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EXPLANATION OF PLATE 47

Figs. 1–5. *Pseudagnostus curtare* sp. nov. 1, JCF 8339, paratype cephalon, L136, ×6. 2, JCF 8309, paratype pygidium, L135, ×6. 3, JCF 8430, paratype cephalon, L138, ×8. 4, JCF 8431, holotype pygidium, L138, ×6. 5, JCF 8314, paratype pygidium, L134, ×6.

Figs. 6–9. *Pseudagnostus margopronus* sp. nov. 6, JCF 8316, paratype pygidium, L133, ×6. 7, JCF 8427, disarticulated pygidium and cephalon of one specimen, holotype, L138, ×5. 8, JCF 8428, paratype pygidium, L138, ×6. 9, JCF 8429, paratype cephalon, L138, ×5.

Figs. 10–12. *Pseudagnostus vastulus* Whitehouse. 10, JCF 8218, cephalon, L122, ×5. 11, JCF 8304, cephalon, L121, ×4. 12, JCF 8454, pygidium, L122, ×6.

Figs. 13–18. *Proceratopyge nectans* Whitehouse. 13, JCF 8283, pygidium, ×3. 14, JCF 8441, free cheek, ×4. 15, JCF 8280, cranidium, ×4. 16, JCF 8285, cranidium, ×5. 17, JCF 8284, cranidium, ×4. 18, JCF 8282, pygidium, ×4. All specimens from L149.

Figs. 19–24. *Proceratopyge cryptica* sp. nov. 19, JCF 8440, paratype pygidium, L149, ×5. 20, JCF 8295, paratype free cheek, L149, ×6. 21, JCF 8439, paratype cranidium, L149, ×5. 22, JCF 8290, paratype cranidium, L150, ×5. 23, JCF 8146, paratype pygidium, L155, ×5. 24, JCF 8277, paratype cranidium, L149, ×5.


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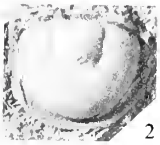
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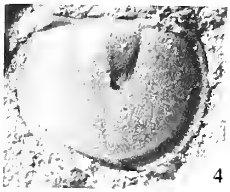
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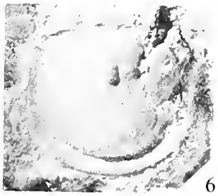
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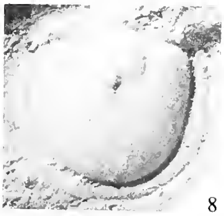
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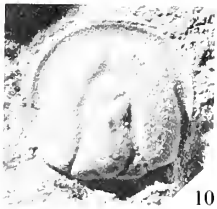
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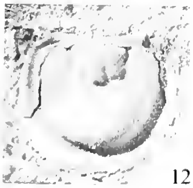
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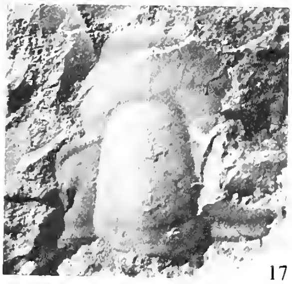
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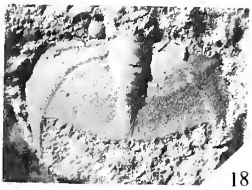
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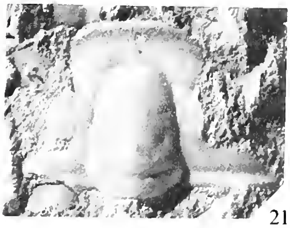
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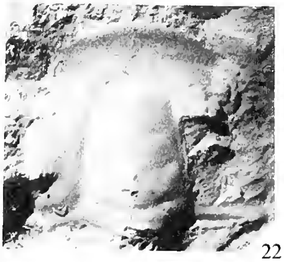
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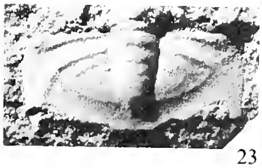
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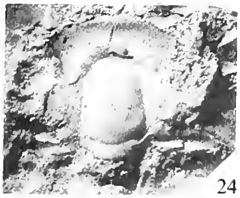
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(UQF 3202) and a pygidium from the same slab as, and likely to be conspecific with, the holotype are both conspecific with the abundant material here referred to *P. vastulus*.

P. idalis Öpik (1967) was recorded from the type Idamean succession although the type material is all from other areas. Öpik gave *idalis* to differ from *vastulus* in that the accessory furrows extend rearwards beyond the marginal spines. The termination of the accessory furrows is, however, like the strength of the furrows themselves, a variable feature in the material available. A comparison of the type cephala of *vastulus* and *idalis* suggests that the latter might be discriminated by the greater width of its border. Border lengths measured at the anterior midline, however, vary from 12% to 16% of the cephalic length on the specimens at my disposal and this difference cannot be regarded as of specific importance.

P. idalis is, therefore, tentatively considered as identical with *P. vastulus* but conclusive proof of the synonymy must await adequate preparation of the holotype of *P. vastulus*.

Pseudagnostus curtare sp. nov.

Plate 47, figs. 1-5

1936 *Pseudagnostus* cf. *cyclopyge* (Tullberg); Whitehouse, p. 100, pl. 10, fig. 8.
?1960 *Pseudagnostus communis* (Hall and Whitfield); Bell and Ellinwood *pars*, pl. 51, figs. 10, 16-18.

Material. Holotype: JCF 8431, L138; cephalon. Paratypes: JCF 8178, JCF 8189, L128; JCF 8332, JCF 8339, L136; JCF 8430, L138; JCF 8188, L139; cephala. JCF 8374, L127; JCF 8177, JCF 8190, L128; JCF 8314, L134; JCF 8309, L135; JCF 8333-8334, L136; pygidia. Additional specimens, L121, L133-134, L137, L143.

Diagnosis. Partially effaced *Pseudagnostus* characterized by a narrow glabella and narrow cephalic and pygidial borders. Pygidium short, with a length/breadth ratio of less than 0·8; it has weak accessory furrows and small spines located well forward of the deuterolobe termination.

Description. Cephalon wider than long, not strongly arched and somewhat effaced. Preglabellar median furrow weak but continuous. Glabella narrow for the genus, tapered slightly anteriorly, pointed at its posterior termination and with a straight transverse furrow. Glabellar node weak, elongate and medial in position. Border narrow with a distinct furrow and rim of approximately equal widths.

Pygidium well arched and unusually short with a length/breadth ratio of less than 0·8. Acrolobes slightly constricted. Traces of two axial rings anterior of a strong transverse furrow which is deflected posteriorly by a strong, elongate axial node. The furrow is only slightly anterior of the axis midpoint. Vestiges of a third axial ring show as two low swellings which head the lines of notulae showing on internal moulds. Anterior portion of axial furrows strong, slightly convergent, terminating in distinct pits at their intersection with the transverse furrow. Posterior axial furrows obscure. Accessory furrows weak; on some specimens they meet the border opposite the spines while on others they cannot be traced to the border. Border narrow for the genus with a broad furrow and a weak, narrow rim. A pair of weak spines are present, located well forward of the deuterolobe termination.

Dimensions. Holotype pygidium is 3·2 mm in length. Cephalic lengths range from 2·6 to 5·0 mm; pygidial lengths from 2·7 to 3·6 mm.

Remarks. The unusually short pygidium with the transverse axial furrow positioned almost half-way along the axis and the distinct pits at the termination of the anterior portion of the axial furrows set this species apart from others. *P. cyclopygeformis* (Sun 1924, p. 26, pl. 2, fig. 1*a–h*) appears to be related. Its cephalic characteristics closely resemble those of *curtare* but its pygidium has a length/breadth ratio of 0·9 or greater and thus is distinctly longer than that of the present species. *P. curtare* may well be represented among the range of forms referred to *P. communis* (Hall and Whitfield) by Bell and Ellinwood (1960). Specimens they figure in pl. 51, figs. 10, 16–18 appear to be indistinguishable from this Australian species.

Pseudagnostus margopronus sp. nov.

Plate 47, figs. 6–9

Material. Holotype: JCF 8427, L138; cephalon and pygidium from a single specimen. Paratypes: JCF 8429, L138; cephalon. JCF 8364, JCF 8369, L127; JCF 8316, L133; JCF 8428, L138; pygidia. Additional specimens, L121, L123, L136.

Diagnosis. Partially effaced *Pseudagnostus* with general morphology in common with the *communis* species group but characterized by shelf-like cephalic and pygidial borders which lack or have very poorly developed border furrows.

Description. Cephalon well domed, approximately as wide as long, slightly effaced but axial furrows distinct. Preglabellar median furrow continuous. Glabella with a slight median constriction, a distinct frontal lobe, and a pointed posterior extremity which clearly separates the basal lobes. Glabellar node elongate, just anterior of glabellar centre. Acrolobe faintly scrobiculate on some internal moulds. Border broad, shelf-like, border furrow lacking or very poorly developed.

Pygidium distinctly wider than long, well domed. Acrolobes slightly constricted; anterior portions of the axial furrows clear and converging slightly posteriorly. Two vestigial anterior axial lobes distinguishable, terminated by a transverse furrow of variable strength which is deflected posteriorly by an elongate axial node. Third ring of axial lobe vestigially represented by a pair of low swellings and these are followed on internal moulds by rows of notulae. Posterior axial furrows obscure, weakly convex laterally; posterior axial segment narrow. Accessory furrows generally clear, obliquely angled to reach the border well forward of the axis termination. A small terminal node can be distinguished. Border broad, shelf-like, lacking a border furrow or almost so. Marginal spines minute, located just anterior to the deuterolobe termination.

Dimensions. Holotype cephalon length is 3·9 mm; holotype pygidial length 4·0 mm. Cephalic lengths range from 3·9 to 4·3 mm; pygidial lengths from 3·0 to 4·0 mm.

Remarks. P. margopronus resembles *P. vastulus* Whitehouse but is somewhat effaced in comparison to this species and lacks its characteristic border furrow. In most characters *P. margopronus* resembles members of the *P. communis* species group listed by Palmer (1968, p. 30) but the shelf-like nature of its cephalic and pygidial borders, which at best have very faint border furrows, allows discrimination. *P. sentosus* Grant (1965, p. 108, pl. 9, figs. 2, 3, 5) also appears to be allied but the same distinction applies.

Family GLYPTAGNOSTIDAE Whitehouse, 1936

Genus GLYPTAGNOSTUS Whitehouse, 1936

Glyptagnostus reticulatus (Angelin)

Material. Twelve cranidia and ten pygidia; localities L145, L147–149, L155.

Remarks. Glyptagnostus reticulatus has been thoroughly described by Palmer (1962) and Öpik (1961*a*, 1963); a full synonymy was compiled by Palmer (1968), the only subsequent addition being that of Jago (1974). It has a world-wide distribution and is thus a most important species for intercontinental correlation. Palmer (1962) has documented an evolutionary sequence involving two subspecies of *reticulatus* discriminated by the length of the terminal bulb of the pygidial axis which is significantly longer in younger populations. It is worth recording that the few pygidia from the Browns Creek Section appear to confirm this trend.

Order PTYCHOPARIIDA Swinnerton, 1915

Suborder PTYCHOPARIINA Richter, 1933

Family CERATOPYGIDAE Linnarsson, 1869

Genus PROCERATOPYGE Wallerius, 1895

1895 *Proceratopyge* Wallerius, p. 56.
?1935 *Kogenium* Kobayashi, p. 273.
1937 *Lopnorites* Troedsson, p. 34.

Type species. Proceratopyge conifrons Wallerius.

Diagnosis. Ceratopygidae with the cephalon comprising about one-third of the total exoskeleton length. Glabella with subparallel sides or tapering anteriorly; surrounded by clearly defined axial furrows and possessing poorly defined lateral glabellar furrows. Thorax comprising nine segments. Pygidial spines subtended from the first segment.

Remarks. A wide range of morphological variation is shown among the some twenty-two nominate species of *Proceratopyge* but useful subgeneric groupings are not as yet apparent. Troedsson (1937) introduced *Lopnorites*, type species *L. rectispinatus* Troedsson, to include species distinguished from *Proceratopyge* (s.s.) by possessing eye ridges. Westergaard (1947), however, described eye ridges from the type species of *Proceratopyge*, *P. conifrons*, thus eliminating the original basis for *Lopnorites*. Later Kobayashi and Ichikawa (1955) recognized *Lopnorites* as a subgeneric category set apart from *Proceratopyge* (s.s.) in possessing a subparallel-sided glabella. Öpik (1963) considered that *Lopnorites* might be best characterized by the number of axial rings of the pygidium. Accordingly, species with six or more axial rings may be grouped in *Lopnorites* while those with less than six may be referred to *Proceratopyge* (s.s.). However, glabella shape and the number of axial rings are but two of a number of characters which vary among species of *Proceratopyge* and division on either of these criteria does not result in the grouping of closely allied species.

Further, intraspecific variation in the Australian species *P. lata* embraces the characteristics of both *Proceratopyge* and *Lopnorites* in terms of either glabella shape (see Pl. 48, figs. 8, 10) or the number of axial rings (Pl. 48, figs. 9, 11). *Lopnorites* is here regarded as a valueless taxon best treated as synonymous with *Proceratopyge*.

Kogenium Kobayashi, based on *K. rotundum* Kobayashi (1935, p. 274, pl. 17, figs. 6-9) is of uncertain status. As noted by Öpik (1963, p. 97), pygidia of *K. rotundum* cannot be distinguished from those of *Proceratopyge* but cranidia appear to have been mismatched and apparently represent a stock of trilobites unrelated to the Ceratopygidae. Cranidia of different morphology were subsequently assigned to *K. rotundum* by Kobayashi (1962, p. 120) but these closely resemble cranidia of *Aplotaspis* gen. nov. established herein. *K. rotundum* is based on pygidial characters (Kobayashi 1962, p. 119). The same is therefore true for *Kogenium* which is best regarded as a tentative synonym of *Proceratopyge*.

Proceratopyge ranges as low as the zone of *Lejopyge laevigata* in Sweden (Westergaard 1947), the zone of *Agnostus pisiformis* in Kazakhstan (Ivshin and Pokrovskaya 1968), and the zone of *Blackwelderia* and *Drepanura* in southern China (Jegorova *et al.* reported in Kobayashi 1971) but the available evidence suggests it to range no lower than the zone of *G. reticularis* in Alaska (Palmer 1968) and Australia. In Australia its range extends upwards to the base of the local zone of *Irvingella tropica* and it is a characteristic element of the Idamean Stage being represented at almost every locality in the Browns Creek Section.

Two of the Australian species recognized by Whitehouse (1939) must now be discarded. The holotype of *P. rutellum* figured by Whitehouse (1939, pl. 25, fig. 9) cannot be located but appears to represent *Aplotaspis erugata* (Whitehouse) in the poor definition of the glabella from the exceedingly narrow fixed cheeks and the near absence of lateral glabellar furrows. A paratype cranidium, UQF 3389, figured by Whitehouse (1939, pl. 25, fig. 10) is identical with *A. erugata*. The two species are here regarded as synonymous. *P. polita* Whitehouse (1939, p. 251, pl. 25, fig. 14) does not belong in *Proceratopyge*. It is known only from a cranidium which superficially resembles that of *Proceratopyge* but which lacks the characteristic glabellar tubercle. In its observable characteristics *P. polita* resembles *Mapania*, cephala of which are distinguished from *Proceratopyge* primarily by lacking a glabellar node (Öpik 1961*b*, p. 166). Other trilobites from near Polly's Lookout, the type locality of *P. polita*, indicate a pre-Idamean age (Henderson, in press).

Proceratopyge nectans Whitehouse

Plate 47, figs. 13-18

1939 *Proceratopyge nectans* Whitehouse, p. 249, pl. 25, fig. 8*a*, *non* fig. 8*b*.

Material. Holotype: UQF 3386, cranidium, 16 miles south of Glenormiston Homestead (figured by Whitehouse, pl. 25, fig. 8*a*). Thirty cranidia, twenty-five pygidia, five free cheeks, and numerous fragments, L149.

Diagnosis. Cranidium with a gently tapering glabella showing indistinct lateral glabellar furrows; posterior borders narrow and strap-like. Frontal area elongate for the genus, about one-third of the cranidial length. It is gently concave and possesses distinct plectral lines. Pygidium and free cheeks with unusually broad borders. Axial lobe of pygidium with four or five axial rings.

Description. Frontal area gently concave, about one-third of the cranidial length. Anterior border broad, gently upturned and with an arcuate anterior margin. Border furrow distinct, confluent with diverging plectral lines which extend from the glabellar termination to the border furrow. Glabella gently tapering, lateral glabellar furrows lacking or obscure. Palpebral lobes short, about 35% of the glabellar length and terminating posteriorly opposite the glabellar node. Eye ridges distinct. Posterior cranidial limbs narrow, strap-like. Free cheek with a broad border and a narrow, elongate genal spine. Pygidial border flattened and exceptionally broad, its span being approximately equal to the length of the pleural field. Axis narrow, tapering and extending on to the border; axial rings are poorly defined and number four or rarely five. Pygidial spines elongate.

Dimensions. Cranidial lengths range from 2·1 to 8·8 mm; lengths of pygidial axes from 3·2 to 5·6 mm.

Remarks. The pygidium figured as *P. nectans* by Whitehouse (1939, pl. 25, fig. 8*b*) has a narrow border and belongs to *P. cryptica* sp. nov. which is contemporary with *nectans* in the lower portion of its range. *P. nectans* is a distinctive species of *Proceratopyge*, characterized by the very broad borders of its pygidium and free cheeks. Cranidia have elongate frontal areas which in general allow separation from cranidia of *P. cryptica* sp. nov. (see text-fig. 2) which are otherwise very similar. This difference is statistically significant; the statistic 'z' evaluating differences in slope of the regressions given in text-fig. 2 is 3·97 (see Imbrie 1956, p. 235).

Rare specimens allied to, but specifically distinct from, *P. nectans* occur higher in the Idamean succession but the species are as yet incompletely known and unnamed. The cranidium described by Öpik (1963, p. 99, pl. 5, fig. 5A, text-fig. 37) as *P.* cf. *chuhsiensis* Lu from the zone of *I. tropica* is such a form and shows the characteristic elongate frontal area. Pygidia have a broad border like *P. nectans*. *P. chuhsiensis* Lu (1956*a*, p. 280, pl. 1, figs. 1–6) may indeed be allied to these forms as Öpik suggested.

It is evident that two species groups are represented among Australian *Proceratopyge*, one comprised of *P. nectans* and its offshoots and the other the partial lineage of *P. cryptica* sp. nov. and *P. lata* Whitehouse.

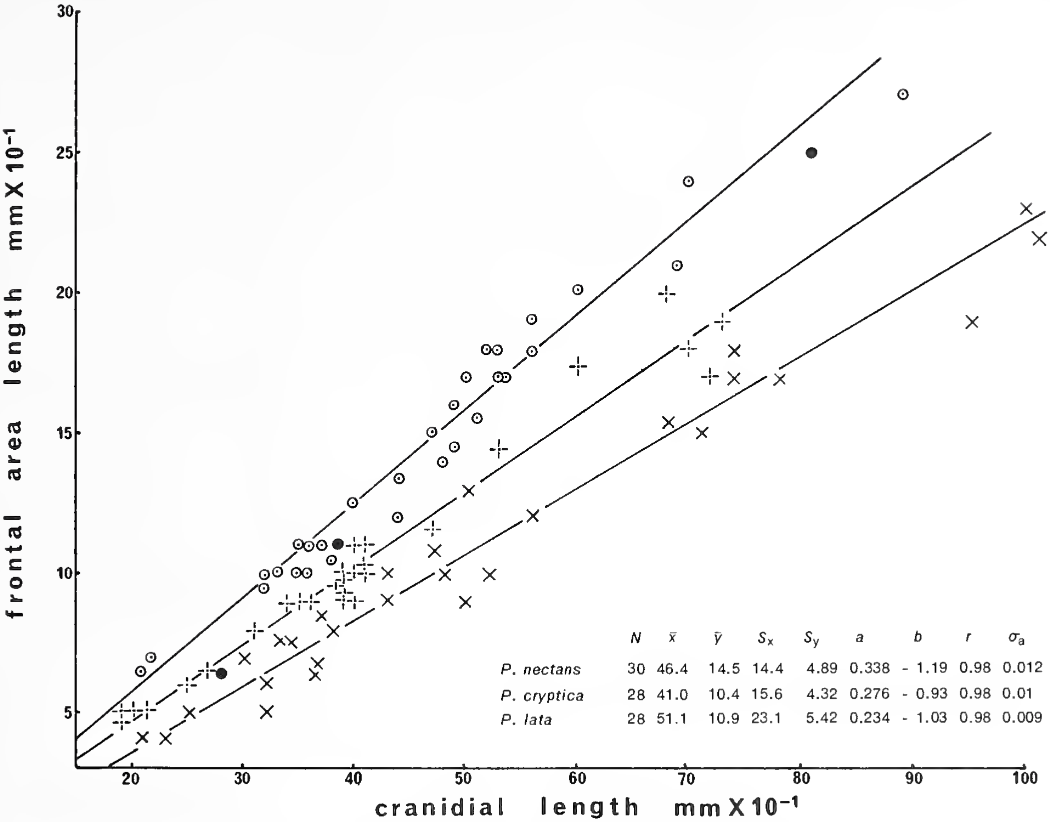
Proceratopyge cryptica sp. nov.

Plate 47, figs. 19–24; Plate 48, figs. 1–3

1939 *Proceratopyge nectans* Whitehouse *pars*, pl. 25, fig. 8*b*.
1968 *Proceratopyge* cf. *P. chuhsiensis* Lu; Palmer, p. 55, pl. 10.

Material. Holotype: JCF 8278, L149; cranidium. Paratypes: JCF 8200, JCF 8269, L130; JCF 8151, L142; JCF 8195, JCF 8277, JCF 8439, L149; JCF 8290–8292, JCF 8294, JCF 8442, L150; cranidia. JCF 8275, JCF 8440, L149; JCF 8293, L150; JCF 8146, L155; pygidia. JCF 8295, L149; free cheek. Additional specimens, L130, L141–142, L144–145, L149–150.

Diagnosis. Frontal area a little more than a quarter of the cranidial length, with a gently upturned border and distinct plectral lines. Glabella gently tapering with weak, variable glabellar furrows. Palpebral lobes short and the posterior cranidial



	N	$\bar{x}$	$\bar{y}$	S_x	S_y	a	b	r	σ_a
P. nectans	30	46.4	14.5	14.4	4.89	0.338	- 1.19	0.98	0.012
P. cryptica	28	41.0	10.4	15.6	4.32	0.276	- 0.93	0.98	0.01
P. lata	28	51.1	10.9	23.1	5.42	0.234	- 1.03	0.98	0.009

TEXT-FIG. 2. Reduced major axis regressions of frontal area length plotted against cranidial length for Idamean species of *Proceratopyge*. The following standard symbols are employed in the tabulated statistics: N—number of specimens; $\bar{x}$—mean of x; $\bar{y}$—mean of y; Sx—standard deviation of x; Sy—standard deviation of y; a—growth ratio; b—initial growth index; r—correlation coefficient; σ_a—standard error of slope.

limbs narrow and strap-like. Free cheeks with narrow borders. Pygidium twice as wide as long, with five or six axial rings.

Description. Frontal area a little over a quarter of the cranidial length, very gently concave and with an arcuate margin. Anterior border gently upturned, narrow; border furrow distinct, confluent with divergent plectral lines which extend from the glabellar termination. Glabella gently tapering, lateral glabellar furrows variably developed but commonly two pairs are distinguishable, the posterior pair invariably with their strongest indentation sagittally orientated. Eye ridges are discernible. Palpebral lobes short, little more than a third of the glabellar length and terminating posteriorly opposite the glabellar node. Posterior limbs narrow, strap-like. Free cheeks with a narrow border and a long genal spine. Pygidium about twice as wide as long with the maximum span of the concave border less than half the length of the pleural fields. Axis strong, tapering, with five or six rings and a pointed terminus. Lateral spines long and narrow.

Dimensions. Holotype cranidium is 7·2 mm in length. Cranidial lengths range from 1·9 to 7·2 mm; lengths of pygidial axes from 1·6 to 4·5 mm.

Remarks. P. cryptica shows a striking resemblance to the Alaskan species described as *P.* cf. *chuhsiensis* Lu by Palmer (1968). The only distinction is in the relative length of the frontal area, the two larger Alaskan specimens plotting at the extreme edge of variation in *P. cryptica* (text-fig. 2). This difference is regarded as intraspecific and the two species united. *P. chuhsiensis* Lu (1956*a*, p. 280, pl. 1, figs. 1–6) although established on poorly preserved material appears to be distinct as its palpebral lobes measure about half the glabellar length. *P. cryptica* is allied to *P. liaotungensis* Kobayashi and Ichikawa (1955). The cephalic characteristics of the Manchurian species are not well documented but the glabella appears to be more squat than that of *P. cryptica.* Pygidia of the two species are indistinguishable.

Proceratopyge lata Whitehouse

Plate 48, figs. 4–11

1939 *Proceratopyge lata* Whitehouse, p. 248, pl. 25, figs. 12, 13.
1963 *Proceratopyge lata* Whitehouse; Öpik, p. 98, pl. 4, figs. 9, 10; pl. 5, figs. CC, EF, GF.
1971 *Proceratopyge lata* Whitehouse; Hill *et al.*, pl. 8, figs. 2, 3.

Material. Holotype: UQF 3391, a cranidium, 5 miles north of Twenty Mile Bore, Glenormiston (figured by Whitehouse, pl. 25, fig. 12). Thirty-five cranidia, nineteen pygidia, six free cheeks, localities L121–124, L127, L129, L134–137.

Diagnosis. Proceratopyge closely allied to *P. cryptica* sp. nov. but differing in the nature of the anterior border of the cranidium which is less than 25% of the cranidial length and is sharply upturned to the anterior margin. Pygidium with five or six axial rings.

Description. Frontal area short, less than 25% of the cranidial length. Anterior border distinct, confluent with plectral lines which diverge from the glabellar termination. Anterior portion of the border sharply upturned to a flattened anterior margin. Glabella gently tapering with variably developed lateral glabellar furrows. On some specimens three pairs can be distinguished while on others, even from the same locality, only a single pair is discernible. The posterior pair have their strongest

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EXPLANATION OF PLATE 48

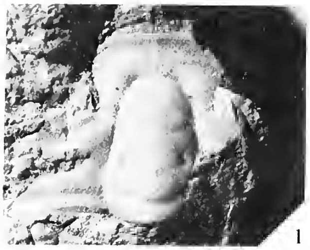
Figs. 1–3. *Proceratopyge cryptica* sp. nov. 1, JCF 8278, holotype cranidium, L149, ×3. 2, JCF 8293, paratype pygidium, L150, ×5. 3, JCF 8275, paratype pygidium, L149, ×4.

Figs. 4–11. *Proceratopyge lata* Whitehouse. 4, JCF 8287, cranidium, L129, ×6. 5, JCF 8258, cranidium, L122, ×4. 6, JCF 8448, free cheek, L136, ×3. 7, JCF 8435, cranidium, L137, ×8. 8, JCF 8446, cranidium, L136, ×4. 9, JCF 8267, pygidium, L122, ×6. 10, JCF 8452, cranidium, L137, ×8. 11, JCF 8329, pygidium, L136, ×3.

Fig. 12. *Yuepingia* sp. nov. JCF 8353, cranidium, L136, ×6.

Figs. 13–14. *Aplotaspis mucrora* gen. et sp. nov. 13, JCF 8234, paratype cranidium, L121, ×3. 14, JCF 8232, holotype pygidium, L121, ×2.

Figs. 15–19. *Aplotaspis erugata* (Whitehouse). 15, JCF 8250, free cheek, L130, ×4. 16, JCF 8254, cranidium, L144, ×5. 17, JCF 8247, cranidium, L130, ×5. 18, JCF 8257, cranidium, L139, ×5. 19, JCF 8471, pygidium, L130, ×4.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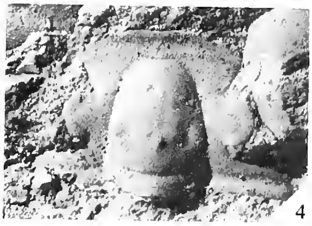
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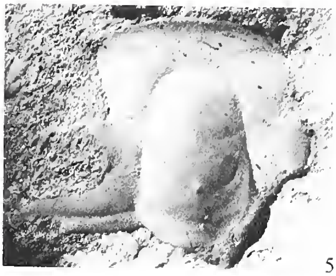
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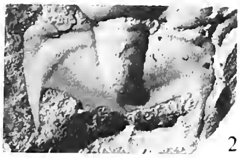
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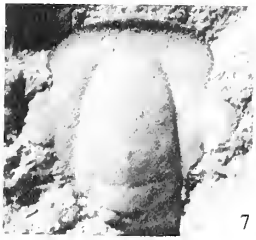
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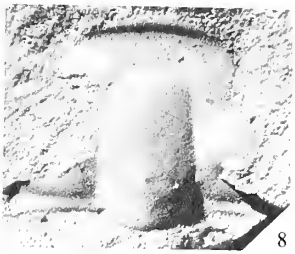
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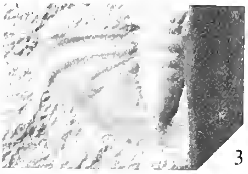
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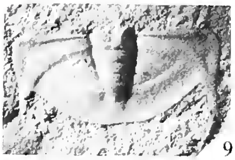
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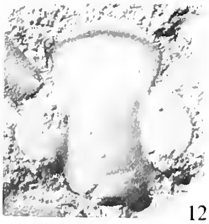
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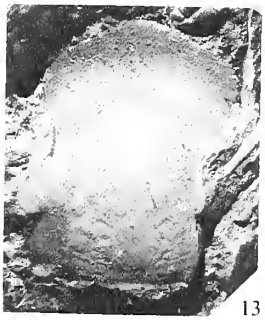
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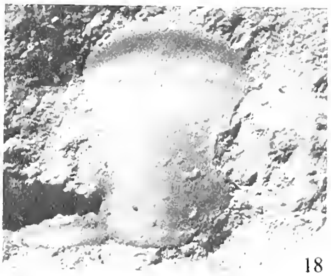
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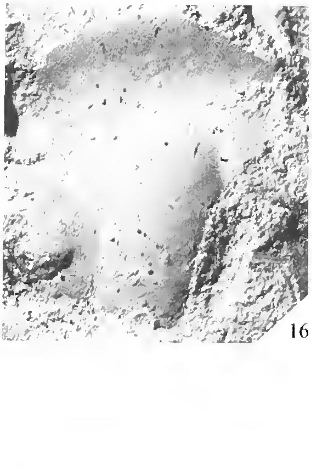
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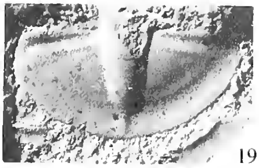
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HENDERSON, Cambrian trilobites

indentation sagittally oriented. Palpebral lobes very short, 25–30% of the glabellar length, typically terminating just anterior of the glabellar node. Free cheek with a narrow border, a strong border furrow and a long, slender, pleated genal spine. Pygidium twice as wide as long with a distinct, narrow, concave border. Axis strong, tapering with five to seven rings. Lateral spines delicate and elongate, nearly as long as the pygidium is wide.

Dimensions. Cranidial lengths range from 2·1 to 10·1 mm; lengths of pygidial axes from 2·1 to 6·0 mm.

Remarks. P. lata is a variable species even among material from a single locality. It also shows systematic morphological change in time. Cranidia from lower horizons in general have less steeply upturned zones of the anterior border, are less flattened along their anterior margins, and their frontal areas are a little more elongate (compare early specimens illustrated in Pl. 48, figs. 4, 5 with late specimens illustrated in figs. 7, 8, 10).

P. lata is closely allied to *P. cryptica* and the two species probably comprise a bioseries. Their ranges abut in the Browns Creek Section, but an evolutionary transition is not recorded, and an abrupt change in cranidial morphology occurs where their ranges meet. The two species are discriminated on the relative lengths of their frontal areas as shown in text-fig. 2. Discrimination of the slopes of the calculated regression lines is statistically valid with the statistic 'z' having the value of 3·26 (see Imbrie 1956, p. 235). The stronger reflection of the anterior border, the more flattened anterior margin, and the slightly shorter palpebral lobes of the cranidia of *P. lata* also serve to distinguish it from *P. cryptica*. Pygidia of the two species cannot be separated with confidence, especially when specimens from low in the range of *P. lata* are involved (see Pl. 48, figs. 2, 3, 9).

Genus YUEPINGIA Lu, 1956*b*

Yuepingia sp. nov.

Plate 48, fig. 12

Material. JCF 8335–8336, JCF 8353; cranidia; locality L136.

Description. Cranidium with a gently tapering glabella which lacks lateral glabellar furrows and bears a small posterior glabellar tubercle. Occipital furrow distinct and narrow; occipital lobe flattened. Fixed cheeks comprised almost entirely of large, subhorizontal, semicircular palpebral lobes which measure a little over half the glabellar length and which are located opposite the glabellar midpoint. Weak palpebral furrows can be distinguished. Frontal area about 40% of the glabellar length; border furrow very faint passing into confluence with equally faint plectral lines which diverge from the anterior glabellar termination. The border is initially flattened and slightly declined but is gently turned up into a narrow lip at the periphery.

Dimensions. Cranidial lengths range from 2·7 to 3·8 mm.

Remarks. Hitherto *Yuepingia* has been known only from the southwestern Chinese type species *niobiformis* Lu (1956*b*, p. 378, pl. 1, figs. 6–13) and *Y. glabra* Palmer (1968, p. 56, pl. 13, figs. 9, 12–16) from Alaska. The Australian cranidia shows good agreement with these species in major characteristics but differs in possessing a slightly more elongate frontal area with a more distinct border lip and in the more posterior position of the palpebral lobes. It clearly represents a new species but formal naming must wait the collection and description of further material.

Genus APLOTASPIS nov.

Type species. Aplotaspis erugata (Whitehouse).

Diagnosis. Partially effaced Ceratopygidae lacking pygidial spines. Glabella tapering anteriorly, with poorly defined axial furrows. Lateral glabellar furrows lacking or indistinct. Frontal area elongate, measuring almost half the glabellar length, and comprised largely of the anterior border. Palpebral lobes short, about a quarter of the glabellar length. Thorax comprises eight segments. Pygidium and free cheeks with well-defined, broad, concave borders.

Description. Cephalon opisthoparian, semicircular. Glabella inflated, arched in the sagittal plane, passing smoothly into the flattened cheeks and the frontal area; axial furrows indistinct. Frontal area very long, almost half the glabellar length, concave and rising anteriorly. The border furrow lies just anterior to the glabellar termination and is interrupted by a broad plectrum. Facial sutures divergent, initially straight but later passing into the curvature of the anterior margin. Glabellar furrows lacking or almost so; a small posterior glabellar node is present. A narrow occipital lobe is just discernible, divided from the glabella by a very weak occipital furrow. Fixed cheeks about half the glabellar width, largely comprised of slightly raised, strongly curved palpebral lobes which are located just anterior of the glabellar midpoint and are a little over a quarter of the glabellar length. Palpebral furrows distinct. A weak eye ridge slopes forward to the glabella which it joins some distance before the glabellar termination. Posterior limbs narrow, elongate, strap-like. Free cheek initially convex but sloping out to a very broad, concave border; its anterior termination is pointed and there is a short genal spine. Thorax of eight segments, each with distinct axial furrows and pleurae which are sharply turned downwards towards the periphery and have broad, distinct pleural grooves. Pygidium semicircular with the axis weakly convex, tapering posteriorly; up to five poorly defined axial rings can be differentiated. Pleural fields dropping gently to a broad, flattened border and reflected at their leading edges into a lip which terminates distally in distinct articulating facets. Three very faint, narrow pleural ribs may be distinguished.

Remarks. Whitehouse (1939, p. 239) incorrectly interpreted *erugata* as possessing a narrow frontal area and referred the species to *Charchaqia* Troedsson as a result. In fact the single specimen available to Whitehouse is misleading in that its frontal area is not fully exposed. The true cranidial morphology of *erugata* described here show it to represent a new genus, *Aplotaspis* nov., for which it is designated the type species.

Aplotaspis belongs to the Ceratopygidae Linnarsson, other members of which have a large frontal area, a glabella with subparallel sides, poorly defined glabellar furrows, a post-central glabellar node and a semicircular pygidium with a tapering axis, weak pleural ribs, and a well-defined border. The number of thoracic segments lies within the range shown by the Ceratopygidae. Its closest relative is *Yuepingia* Lu (1956*b*,

p. 377) recently reviewed by Palmer (1968, p. 56). *Aplotaspis* is, however, readily discriminated by its much shorter palpebral lobes, much larger frontal area, and its very clear pygidial border.

Among previously described taxa the unclassified Alaskan pygidium of Franconian age listed by Palmer (1968, p. 103, pl. 13, fig. 10) resembles *Aplotaspis* as does the unclassified pygidium from the *Irvingella tropica* Zone listed in Öpik (1963, p. 100, pl. 5, fig. BB). Cranidia assigned to the type species of *Kogenium* Kobayashi, *K. rotundum*, by Kobayashi (1962, p. 120) appear to be indistinguishable from *Aplotaspis*. However, *K. rotundum* was established by Kobayashi (1935, p. 274, pl. 17, figs. 6–9) for pygidia of *Proceratopyge* morphology and mismatched cranidia which are unrelated to the Ceratopygidae. *Kogenium* is not, therefore, a senior synonym of *Aplotaspis*.

Aplotaspis erugata (Whitehouse)

Plate 48, figs. 15–19; Plate 49, figs. 1–4

1939 *Charchaqia erugata* Whitehouse, p. 239, pl. 25, figs. 6, 7*a*.
1939 *Proceratopyge rutellum* Whitehouse, pl. 25, figs. ?9, 10.
1971 *Charchaqia erugata* Whitehouse; Hill *et al.*, pl. 6, fig. 7.

Material. Holotype: UQF 3369, a whole specimen about 4 miles north of Twenty Mile Bore, Glenormiston (figured by Whitehouse, pl. 25, figs. 6, 7*a*). Twenty-five of each cranidia and pygidia, localities L122, L124, L128–130, L139–141, L143–144.

Diagnosis. Aplotaspis with the anterior margin of cranidia uniformly arched or indistinctly pointed. Span of the pygidial border distinctly shorter than the anterior width of the pleural fields.

Dimensions. Cranidial lengths range from 3·0 to 7·4 mm; pygidial lengths from 2·0 to 4·5 mm.

Remarks. A. erugata is a common species in the upper *P. cryptica* Zone and in the *Erixanium sentum* Zone and is somewhat variable in its definitive characters. The width of the pygidial border is variable (Pl. 48, fig. 19; Pl. 49, figs. 1, 3, 4) but is never as broad as that of *A. mucrora*. Likewise the anterior cranidial margin may be evenly arched (Pl. 48, fig. 18) or slightly pointed (Pl. 48, fig. 16) but never displays the straight limbs and clear point of *A. mucrora*.

EXPLANATION OF PLATE 49

Figs. 1–4. *Aplotaspis erugata* (Whitehouse). 1, JCF 8253, pygidium, L144, ×5. 2, JCF 8248, cranidium, L130, ×5. 3, JCF 8249, pygidium, L130, ×5. 4, JCF 8252, pygidium, L144, ×5.

Figs. 5–7. *Aphelaspis australis* sp. nov. 5, JCF 8126, holotype cranidium, ×5. 6, JCF 8127, paratype cranidium, ×6. 7, JCF 8131a, paratype pygidium, ×4. All specimens from L155.

Figs. 8–14. *Eugonocare quadrata* sp. nov. 8–9, JCF 8410, paratype cranidium, L138, ×2. 10, JCF 8357, paratype free cheek, L127, ×2·5. 11, JCF 8417, paratype cranidium, L138, ×2. 12, JCF 8415, paratype cranidium, L138, ×3. 13, JCF 8361, paratype pygidium, L127, ×4. 14, latex peel from JCF 8414, holotype pygidium, L138, ×3.

Figs. 15–19. *Eugonocare whitehousei* sp. nov. 15, JCF 8157, paratype pygidium, L144, ×4. 16–17, JCF 8262, paratype cranidium, L130, ×2. 18, JCF 8159, holotype pygidium, L149, ×3. 19, JCF 8161, paratype cranidium, L149, ×2·5.

PLATE 49


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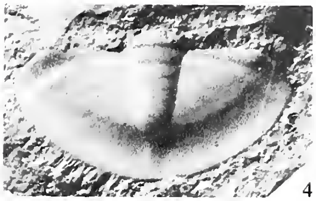
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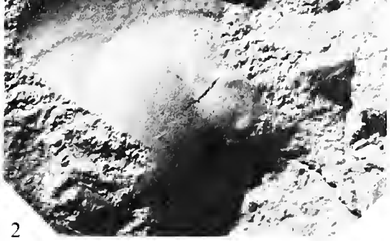
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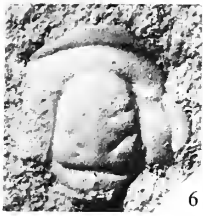
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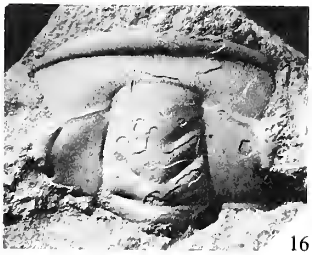
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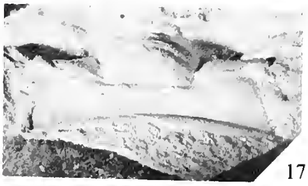
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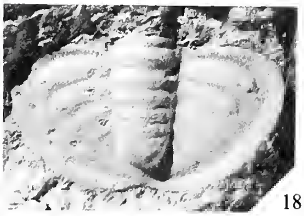
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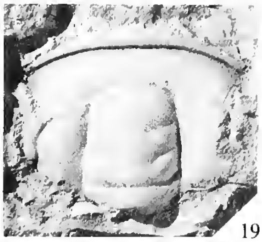
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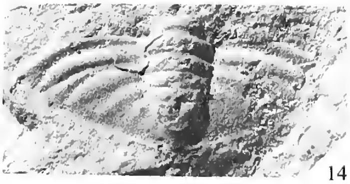
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HENDERSON, Cambrian trilobites

Aplotaspis mucrora sp. nov.

Plate 48, figs. 13–14

?1939 *Eugonocare tessellatum* Whitehouse *pars*, pl. 23, fig. 16.

Material. Holotype: JCF 8232, L121; pygidium. Paratypes: JCF 8234–8235, L121; JCF 8236–8237, L136; cranidia. JCF 8231, JCF 8233, JCF 8303, L121; JCF 8311, L133; pygidia.

Diagnosis. Aplotaspis with the anterior margin of cranidium distinctly pointed. Span of the pygidial border measuring about the same as the anterior width of the pleural fields.

Dimensions. Holotype cranidium is 9·4 mm in length. Cranidial lengths range from 6·3 to 9·4 mm; pygidial lengths from 4·1 to 9·4 mm.

Remarks. A. mucrora is an uncommon species in the zone of *Stigmatoa diloma.* The pygidium figured by Whitehouse (1939, pl. 23, fig. 16) and referred to *Eugonocare tessellatum* Whitehouse, now numbered UQF 3366 in the University of Queensland collections, appears to belong to this species.

Family PTEROCEPHALIIDAE Kobayashi, 1935
Subfamily APHELASPIDINAE Palmer, 1960
Genus APHELASPIS Resser, 1935

Aphelaspis is a characteristic early upper Cambrian North American genus commonly employed as a zonal index (see Palmer 1965*b*, p. 5). Records of it from other areas are, however, rare; they include western Antarctica (Webers 1972), southern China (Jegorova *et al.* reported in Kobayashi 1971), Kazakhstan (Ivshin 1956), northern Siberia (Rosova 1968; Pokrovskaya 1961), and Australia (Thomas and Singleton 1956).

Aphelaspis australis sp. nov.

Plate 49, figs. 5–7

Material. Holotype: JCF 8126, L155; cranidium. Paratypes: JCF 8132, L149; JCF 8127–8130, L155; cranidia. JCF 8443, L150; JCF 8131, L155; pygidia.

Diagnosis. Aphelaspis characterized by a short frontal area measuring about 40% of the glabellar length, elongate palpebral lobes, and a pygidium which is twice as long as wide.

Description. Cranidium with the glabella curved sagittally, distinctly tapering, bluntly rounded anteriorly, and with two pairs of weak, posteriorly directed lateral glabellar furrows. Occipital furrow well marked, occipital lobe narrow with a small median tubercle. Frontal area about 40% of the glabellar length, unequally divided by a strong border furrow into a broader, convex, downsloping preglabellar field and a narrower, convex border. Fixed cheeks a little wider than half the maximum glabellar width, convex and rising slightly to the long, gently curved palpebral lobes, which are positioned a little anterior to the glabellar midpoint. Narrow eye ridges and palpebral furrows are well marked. The posterior limbs are short, narrow, and with strong furrows. Pygidium semicircular in outline, about twice as wide as long. Axis strong, gently tapering to a blunt terminus and with five rings. Pleural fields with three pairs of broad, rounded ribs on which interpleural grooves can just be recognized. The border is well marked, narrow, and flattened.

Dimensions. Holotype cranidium is 4·5 mm in length. Cranidial lengths range from 3·1 to 7·3 mm; pygidial lengths from 3·0 to 3·4 mm.

Remarks. The nearest match for *A. australis* is with *A. brachyphasis* Palmer (1962, p. 33, pl. 4, figs. 1–19) and *A. subditus* Palmer (1962, p. 35, pl. 4, figs. 20–22, 25) but it is set apart from these and other species of *Aphelaspis* by its short frontal area and semicircular pygidium with a narrow, flattened border.

Genus EUGONOCARE Whitehouse, 1939

1939 *Eugonocare* Whitehouse, p. 224.
1967 *Eugonocare* Öpik, p. 202.

Type species. Eugonocare tessellatum Whitehouse 1939.

Diagnosis. Aphelaspidinae characterized by a subquadrate cranidium in which the interocular width clearly exceeds the cranidial length. Free cheeks with a long, slender genal spine. Pygidium lacking spines.

Description. Aphelaspidinae with a squat, subquadrate cranidium such that the interocular width clearly exceeds the cranidial length. Glabella gently tapering to subquadrate with an abruptly rounded anterior termination and two pairs of well-marked posteriorly directed lateral glabellar furrows. A third pair of lateral glabellar furrows is just discernible near the anterior glabellar termination. Occipital lobe clearly demarcated, possessing a small occipital node. Palpebral lobes set opposite the glabellar midpoint and measure about one-third its length. Fixed cheeks weakly convex, subhorizontal, and broad; about 65% of the glabellar width measured on the same line. Eye ridges distinct, joining the glabella near its termination. Preglabellar field convex with a delicate, venulose ornamentation, downsloping to a well-developed border furrow. Anterior border convex, narrow, sharply reflected into the border furrow. Free cheeks with venulose ornament, a very long, slender genal spine, and a well-developed border furrow. Most of the border is convex but there is a distinct zone of concavity adjacent to the margin.

Pygidium transversely subovate; axis strongly arched, gently tapering, reaching almost to the border and with five or six well-marked rings. Pleural areas weakly convex, with three or four broad, weak ribs bearing distinct pleural grooves. Border narrow, flattened, lacking spines.

Remarks. Öpik (1967) regarded *Eugonocare* as a probable junior synonym of *Proaulacopleura* Kobayashi (1936, p. 93) which is based on *P. buttsi* Kobayashi. Recent reports by Palmer (1962, 1965*b*) show, however, that *P. buttsi* is best referred to *Aphelaspis*. Cranidia of *Eugonocare* are set apart from *A. buttsi* and other species of *Aphelaspis* by their squat, subquadrate shape with the interocular width distinctly exceeding the cranidial length. In *Aphelaspis* these two measurements are subequal. The cranidia of some species of *Olenaspella*, for example *O. regularis* Palmer (1962, p. 38, pl. 5, figs. 1–3), are inseparable from *Eugonocare* but this genus is set apart by virtue of its pygidial spines.

Whitehouse's concept of *Eugonocare* is now known to have been partially in error because most of the pygidia and the single free cheek which he figured as representative of the genus were misidentified.

Eugonocare is a characteristic element of Idamean faunas in north-western Queensland and is abundantly represented in collections from the Browns Creek Section. It has also been recorded from Victoria, Australia (Thomas and Singleton 1956) and doubtfully from western Antarctica (Webers 1972). The Kazakhstan species *O. evansiformis* Ivshin (1962, p. 70, pl. 4, figs. 11–18; text-fig. 17) is known from cranidia alone and may well represent *Eugonocare*. It occurs with *Irvingella* and is, therefore, probably younger than American *Olenaspella* which are restricted to pre-*Dunderbergia* zones of the Dresbachian Stage (Palmer 1965*b*) whereas *Irvingella* is a characteristic member of the American *Elvinia* Zone assemblage. As noted by Öpik (1963, p. 88), *Eugonocare*(?) sp. recorded by Lu (1956*b*) from Kueichou, China is more likely to be a representative of *Stigmatoa* Öpik.

The three species recognized here are closely allied and are discriminated essentially on pygidial shape (text-fig. 3).

Eugonocare tessellatum Whitehouse

Plate 50, figs. 1–5

1939 *Eugonocare tessellatum* Whitehouse, p. 226, pl. 23, figs. 15, 17 (*non* figs. 16, 18); pl. 25, fig. 7*b*.

Material. Holotype: cephalon UQF 3370*a*, *b* from *c*. 4½ miles north of Twenty Mile Bore, Glenormiston (figured by Whitehouse, pl. 23, fig. 15; pl. 25, fig. 7*b*). Fifteen cranidia, ten pygidia, eight free cheeks; localities L121–122, L132–136.

Diagnosis. Anterior cranidial border narrow, convex. Pygidium of moderate width (text-fig. 3) with five axial rings and pleural grooves which are not strongly oblique, reaching almost to the axial furrows.

Dimensions. Cranidial lengths range from 6·5 to 12·0 mm; pygidial lengths from 4·7 to 8·8 mm.

Remarks. The free cheek figured by Whitehouse (1939, pl. 23, fig. 18) cannot be located in the University of Queensland collections. It appears to be from a *Pagodia* (*Idamea*). Likewise the pygidium (UQF 3366) figured in plate 23, fig. 16 was misidentified and probably represents *Aplotaspis mucrora* sp. nov. The second figured pygidium (UQF 3365a, pl. 23, fig. 17) is only a fragment but appears to have been correctly identified.

EXPLANATION OF PLATE 50

Figs. 1–5. *Eugonocare tessellatum* Whitehouse. 1, JCF 8259, cranidium, L132, ×3. 2, JCF 8317, pygidium, L136, ×2·5. 3, JCF 8260, pygidium, L132, ×3. 4, JCF 8271, pygidium, L122, ×3. 5, JCF 8350, free cheek, L136, ×4.

Figs. 6–13. *Prismenaspis propinquum* (Whitehouse). 6, JCF 8265, cranidium, L130, ×4. 7, JCF 8244, cranidium, L139, ×3. 8–9, JCF 8264, pygidium, L130, ×3. 10–11, JCF 8263, L130, ×3. 12, JCF 8246, pygidium, L139, ×3. 13, JCF 8445, free cheek, L139, ×3.

Figs. 14–19. *Prismenaspis brownensis* gen. et sp. nov. 14–15, JCF 8299, holotype pygidium, L121, ×2. 16, JCF 8306, paratype free cheek, L121, ×3. 17, JCF 8307, paratype cranidium, L135, ×1·5. 18, JCF 8345, paratype cranidium, L136, ×2·5. 19, JCF 8300, paratype pygidium, L121, ×2.


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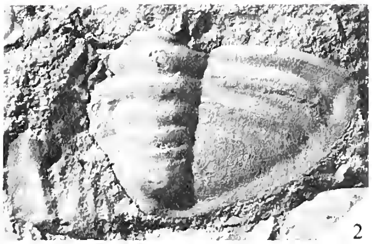
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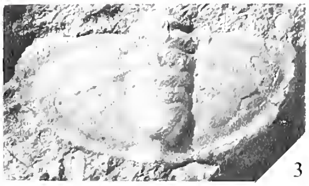
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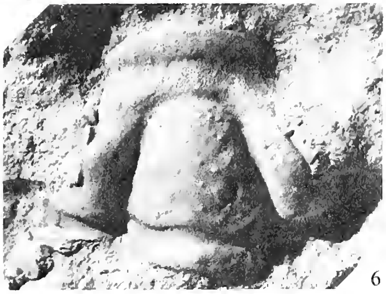
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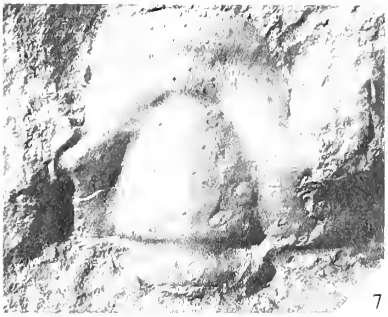
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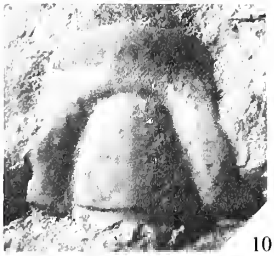
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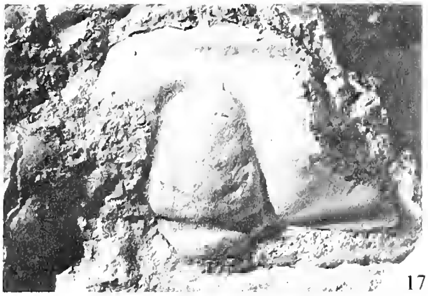
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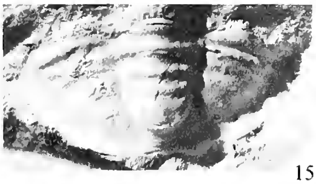
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19

HENDERSON, Cambrian trilobites

The cranidial characteristics of *E. tessellatum* as redefined in this report are inseparable from those of the stratigraphically lower species *E. whitehousei* sp. nov. and the two species are differentiated by their pygidia. Since the holotype of *E. tessellatum* is a cranidium, a difficult situation arises. The cranidium is associated in the same slab with *A. erugata* (Whitehouse) but the range of that species overlaps those of both *E. tessellatum* and *E. whitehousei*. However, the type locality of *E. tessellatum* is given by Whitehouse as 4½ miles north of Twenty Mile Bore, Glenormiston where mapping suggests that strata predating the range of *E. tessellatum* are lacking (Henderson, in press). This conclusion is substantiated by other taxa among the collections which Whitehouse recorded from the type locality and it can be assumed that the holotype cephalon is contemporary with pygidia on which the species is now recognized.

Eugonocare whitehousei sp. nov.

Plate 49, figs. 15–19

Material. Holotype: JCF 8159, L149; pygidium. Paratypes: JCF 8262, L130; JCF 8154, L139; JCF 8168, L140; JCF 8158, L144; JCF 8161, L149; cranidia. JCF 8199, JCF 8266, JCF 8270, L130; JCF 8175, L131; JCF 8155–8157, L144; JCF 8160, L149; pygidia. Additional specimens, L141–143, L145, L150.

Diagnosis. Glabella distinctly tapering, anterior border narrow, convex. Pygidium elongate for the genus (text-fig. 3), with pleural grooves which are not oblique and reach to the axial furrows.

Dimensions. Holotype pygidium is 7·0 mm in length. Cranidial lengths range from 6·0 to 12·0 mm; pygidial lengths from 2·5 to 9·1 mm.

Remarks. Cranidia of *E. whitehousei* are indistinguishable from those of the type species, *E. tessellatum*. Thus the immature cranidia referred to in Öpik (1967, p. 203, pl. 8, fig. 2) as *E. tessellatum* could belong to either species. Pygidia exceeding 5·0 mm in length are however readily distinguishable by shape (text-fig. 3) but smaller pygidia are subject to confusion due to crossing of the growth trends.

Eugonocare quadrata sp. nov.

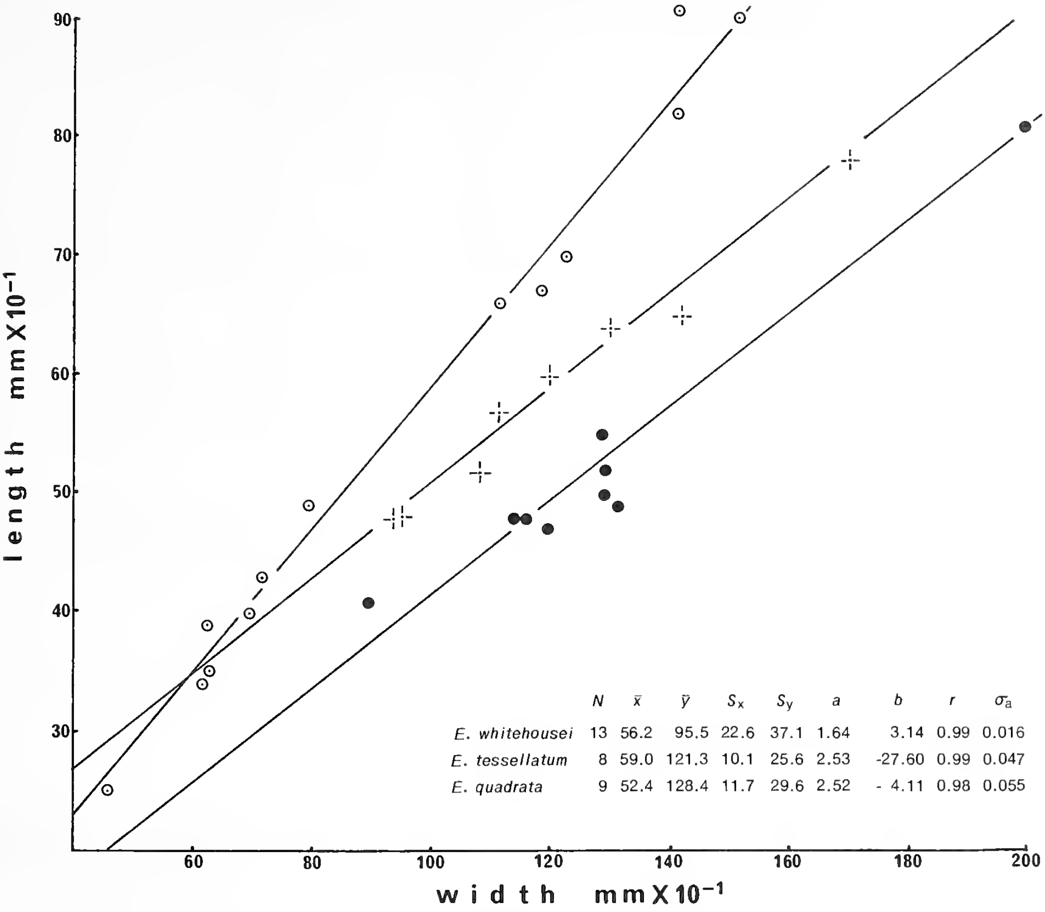
Plate 49, figs. 8–14

Material. Holotype: JCF 8414, mould of pygidium, L138. Paratypes: JCF 8358, JCF 8365, JCF 8376–8377, JCF 8383–8385, L127; JCF 8371, JCF 8409–8410, JCF 8412–8413, JCF 8415, JCF 8417, L138; cranidia. JCF 8359–8362, L127; JCF 8408, L138; pygidia. JCF 8357, JCF 8381–8382, L127; JCF 8411, L138; free cheeks.

Diagnosis. Glabella subquadrate, barely tapering. Anterior border broad for the genus, convex near the border furrow but flattened or slightly concave adjacent to the anterior margin. Pygidium short (text-fig. 3) with five axial rings and oblique pleural grooves which do not reach to the axial furrows.

Dimensions. Holotype pygidium is 5·7 mm in length. Cranidial lengths range from 4·1 to 15·5 mm; pygidial lengths from 4·1 to 8·2 mm.

Remarks. A well-preserved free cheek illustrated in Plate 49, fig. 10 shows the long, delicate genal spine characteristic of the genus. Pygidial characteristics serve best to distinguish *E. quadrata* from the two species which precede it in north-western Queensland but its cranidial characteristics are also unique.



	N	$\bar{x}$	$\bar{y}$	S_x	S_y	a	b	r	σ_a
E. whitehousei	13	56.2	95.5	22.6	37.1	1.64	3.14	0.99	0.016
E. tessellatum	8	59.0	121.3	10.1	25.6	2.53	-27.60	0.99	0.047
E. quadrata	9	52.4	128.4	11.7	29.6	2.52	- 4.11	0.98	0.055

TEXT-FIG. 3. Reduced major axis regressions of pygidial width plotted against pygidial length for Idamean species of *Eugonocare*. Symbols for tabulated statistics are as for text-fig. 2.

Subfamily PTEROCEPHALIINAE Kobayashi, 1935

Genus PTEROCEPHALIA Roemer, 1849

Pterocephalia sp. nov.

Plate 51, fig. 10

Material. JCF 8418, JCF 8426, L138; fragmentary cranidia.

Description. Cranidia effaced for the genus. Glabella gradually tapering and gently convex with a distinct axial crest. It has barely discernible lateral glabellar furrows between which some four, very poorly defined, glabellar lobes can be distinguished. Occipital lobe and furrow poorly defined. Posterior limb elongate with a narrow furrow. Fixed cheeks narrow, sloping gently upward; palpebral lobe short and positioned opposite the glabellar midpoint. Frontal area gently concave and lacking a border furrow. It has the overlapping, terraced ornament and strongly curved anterior margin characteristic of the genus.

Dimensions. Cranidial lengths range from 20·5 to 23·0 mm.

Remarks. The effaced character of this species and its lack of a distinguishable border furrow appear to separate it from other described *Pterocephalia*.

Family ELVINIIDAE Kobayashi, 1935

Genus PRISMENASPIS nov.

Type species. Prismenaspis propinquum (Whitehouse).

Diagnosis. Cranidium pustulose, tumid; glabella with four pairs of lateral glabellar furrows. Frontal area elongate and containing a broad border furrow. Internal moulds of the preglabellar field show a distinctive coarse punctation. Free cheeks with a short, stout spine. Pygidium possesses strong axial rings and inflated pleural fields with strong, broad ribs.

Description. Cranidium large, pustulose, with strong axial and preglabellar furrows. Glabella tumid, sagittally arched, tapering forward with four pairs of very weak lateral glabellar furrows; glabellar lobes decline in size anteriorly. Occipital lobe and furrow strong; prominant occipital node. Fixed cheeks tumid, inclined upward, about half the posterior glabellar width. Palpebral lobes short, about 30% of the glabellar length, set a little anterior to the glabellar midpoint. Palpebral rim well developed and wide for the family. Eye ridges narrow, distinct, sloping obliquely forward, and joining to the first glabellar furrow. Facial sutures anterior to the eye subparallel. Frontal area relatively broad, comprised of a weakly convex preglabellar field set at an angle to a weakly convex border of approximately equal width. The border furrow is clear, but not sharply defined. Preglabellar field with a distinctive, coarsely punctate ornament on internal moulds. Posterior limbs elongate, triangular with furrows expanding laterally. Free cheek with a projecting pointed tip, a short, stout spine, and a broad, weakly convex border.

Pygidium tumid, semicircular in outline. Axis broad slightly tapering, with four strong rings; terminus broadly rounded, vertically truncate, and reaching almost to the periphery. Pleurae narrow, inflated and downsloping, bearing up to four broad ribs each with a pleural groove. Border narrow and weakly convex or broad and flattened. Border furrow lacking.

EXPLANATION OF PLATE 51

Figs. 1–4. *Prismenaspis alta* gen. et sp. nov. 1–2, JCF 8420, paratype cranidium, ×2·5. 3, JCF 8419, holotype cranidium, ×2·5. 4, JCF 8421, paratype pygidium, ×3. All specimens from L138.

Figs. 5–7. *Stigmatoa diloma* Öpik. 5, JCF 8349, cranidium, ×4. 6, JCF 8348, cranidium, ×4. 7, JCF 8328, pygidium, ×2·5. All specimens from L136.

Figs. 8–9. *Stigmatoa tysoni* Öpik. 8, JCF 8453, cranidium, L143, ×4. 9, JCF 8279, pygidium, L149, ×2·5.

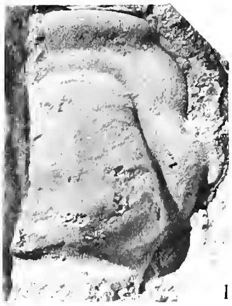
Fig. 10. *Pterocephalia* sp. nov. JCF 8418, cranidium, L138, ×2.

Figs. 11–14. *Pagodia* (*Idamea*) *venusta* Whitehouse. 11, JCF 8394, free cheek, ×3. 12, JCF 8392, cranidium, ×2·5. 13, JCF 8407, pygidium, ×4. 14, JCF 8473, cranidium, ×4. All specimens from L138.

Figs. 15–16. *Stigmatoa sidonia* Öpik. 15, JCF 8391, cranidium, ×4. 16, JCF 8390, cranidium, ×4. Both specimens from L138.

Figs. 17–18. *Irvingella tropica* Öpik. 17, JCF 8388, cranidium, ×2·5. 18, JCF 8389, cranidium, ×2·5. Both specimens from L138.

Fig. 19. *Prochuangia* sp. JCF 8366, pygidium, L127, ×3.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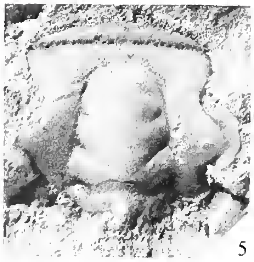
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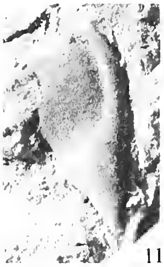
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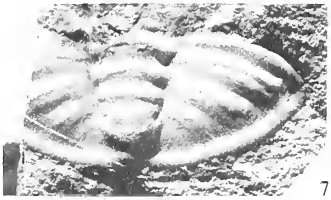
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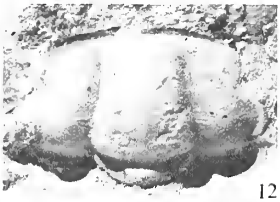
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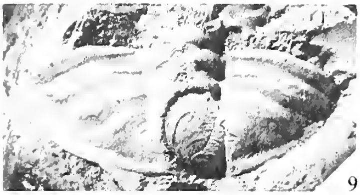
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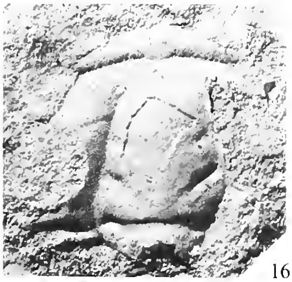
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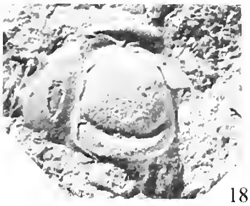
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19

HENDERSON, Cambrian trilobites

Remarks. Prismenapsis is most closely allied to the imperfectly known genus *Protemnites* Whitehouse (1939, p. 209) which itself requires some comment and clarification. It is based on a single species, *P. elegans* Whitehouse (1939, p. 210, pl. 22, fig. 12*a*, *b*, *non* fig. 13), known from two cranidia on a chert slab. Whitehouse refers to two pygidia on the same slab in his description, but the figured pygidium (UQF 3331) is from a separate slab and represents *Pagodia*, presumably *P.* (*Idamea*) *superstes* Whitehouse which occurs at the same locality. The two unfigured pygidia are probably conspecific with the associated cranidia. They have a strongly arched axis with four well-marked rings, flattened pleural fields with four, low, rounded ridges each of which bears a weak pleural groove and what appears to be a wide, flat border.

The age of *Protemnites* is in doubt. It is recorded by Whitehouse as from 'beds at the base of a hill immediately west of Tyson's bore on Glenormiston' in association with *Idamea superstes* Whitehouse, *Aspidagnostus parmatus* Whitehouse, *Pseudagnostus nuperus* Whitehouse, and '*Elathriella*' *plebeia* Whitehouse. Most of these species are poorly defined and none are known from other localities. Current data suggest that the ranges of *Idamea* and *Aspidagnostus* do not overlap, indicating that the collection is probably of mixed age. The *Protemnites* slab contains cranidia referable to either *Hypagnostus* or *Kormagnostus*, genera known to range no higher than the Australian Mindyallan Stage and its equivalent elsewhere.

Prismenapsis is distinguished from *Protemnites* by possessing an additional pair of lateral glabellar furrows and by the weak impression of all four pairs of furrows. It is further distinguished by the obliquity of its eye ridges and by the inflated pleural regions of its pygidium. In all other features, including details of cranidial ornamentation, *Prismenapsis* and *Protemnites* are alike. Both are best referred to the family Elviniidae in the sense of Palmer (1965*b*, p. 32) and are here considered to be allied to the characteristic North American genus *Dunderbergia*. *Prismenaspis* differs from *Dunderbergia* in its broader, less convex anterior border and less sharply defined anterior border furrow.

Three post-Idamean north Siberian genera, *Ketyna*, *Mansiella*, and *Nyaya* established by Rosova (1963, 1968) appear to be affiliated with *Prismenaspis*. All three have pygidial morphology of the *Prismenaspis* style but their cranidia possess fewer than four glabellar furrows and appear to have distinctly less elongate posterior limbs.

Prismenaspis propinquum (Whitehouse)

Plate 50, figs. 6–13

1936 *Eugonocare propinquum* Whitehouse *pars*, p. 227; pl. 23, fig. 19, *non* fig. 20.

Material. Holotype: pygidium, UQF 3392, 5 miles north of Twenty Mile Bore, Glenormiston (figured by Whitehouse, pl. 23, fig. 19). Twenty-one cranidia, ten pygidia, and four free cheeks; localities L122, L124, L128–130, L139–140, L143.

Diagnosis. Cranidium inflated with a strongly arched glabella and fixed cheeks. Like that of *P. brownensis* but the preglabellar field is fractionally longer and the angle made by the preglabellar field and the anterior border is more distinct. Anterior border inclined upwards with respect to the glabella and with the anterior margin strongly arched as viewed from the front. Pygidium with an axis which is about the same width as the pleural fields. Pleural grooves weak, barely distinguishable on some specimens. Border narrow, weakly convex.

Dimensions. Cranidial lengths range from 7·5 to 12·5 mm; pygidial lengths from 4·4 to 7·8 mm.

Remarks. Whitehouse mistakenly associated pygidia of *P. propinquum* with cranidia of *Eugonocare* believing that the pygidial characteristics were sufficient to discriminate the new species, *propinquum.* He designated his figured pygidium (now numbered UQF 3392) as the holotype. The paratype cephalon is missing from the University of Queensland collections but evidently represents either *E. tessellatum* Whitehouse or *E. whitehousei* sp. nov.

Prismenaspis brownensis sp. nov.

Plate 50, figs. 14–19

Material. Holotype: JCF 8299, L121; pygidium. Paratypes: JCF 8201, JCF 8239, L122; JCF 8307, JCF 8354, JCF 8356, L135; JCF 8342–8346, L136; cranidia. JCF 8300, L121; JCF 8355, L135; JCF 8338, L136; pygidia. JCF 8306, L121; free cheek. Additional specimens, L122–123, L133.

Diagnosis. Cranidium inflated with strongly arched glabella and fixed cheeks. Anterior border not inclined upward with respect to the glabella. Anterior border and the preglabellar field meet in less of an angle and the anterior margin is less strongly arched as viewed from the front than in *P. propinquum.* Pygidium with an axis which is about the same width as the pleural fields. Pleural ribs broad and weak with distinct pleural grooves. Border flat and broad.

Dimensions. Holotype pygidium is 8·2 mm in length. Cranidial lengths range from 5·8 to 19·2 mm; pygidial lengths from 7·2 to 8·2 mm.

Remarks. Cranidia of both *P. brownensis* and *propinquum* are variable in a similar fashion. The axial furrows may be nearly straight or distinctly curved and the glabella may be truncated or with a rounded anterior termination. In both species the preglabellar field can be a little longer than the anterior border or vice versa, and in both there is variation in the angular relationship of the preglabellar field and the anterior border. Some individual variants among cranidia cannot be referred to either species with confidence and it is the nature of the pygidium which allows clear specific discrimination.

These two species are closely related and may comprise a local bioseries. The collection at L122 is from a stratigraphic horizon when their ranges abut. Here cephala resemble *brownensis*, but two fragmentary pygidia are of the *propinquum* style with one having a broader border than typical of that species. These specimens could represent a fragment of an intermediate population but are too few in number to give an adequate indication. For the time being both species are listed from this locality.

Prismenaspis alta sp. nov.

Plate 51, figs. 1–4

Material. Holotype: JCF 8419, L138; cranidium. Paratypes: JCF 8420–8425, L138; cranidia. JCF 8421, L138; pygidium.

Diagnosis. Cephalon effaced for the genus with the glabella not strongly arched either sagittally or transversely and the fixed cheeks weakly convex and inclined slightly upward. Frontal area short for the genus and the preglabellar field is distinctly shorter than the border with which it makes but a slight angle. Pygidium with an axis which is distinctly broader than the pleural fields, weak pleural ribs and a rather broad, flat border.

Dimensions. Holotype cranidium is 14·2 mm in length; cranidial lengths range from 11·5 to 15·5 mm; the single pygidium is approximately 6·0 mm in length.

Remarks. Cranidia which represent *P. alta* are distinctive. The length of the frontal area in *P. alta* is 28%–30% of the glabellar length, and the preglabellar field is distinctly shorter than the anterior border. In *P. brownensis* and *P. propinquum* the frontal area is never less than 35% of the glabellar length and the preglabellar field and border are of approximately equal lengths. In addition, cranidia of *P. alta* are effaced and less inflated compared to those of the other two species. The pygidium of *P. alta* resembles that of *P. brownensis* in the nature of the pleural ribs and border but is readily distinguished by its broad axis.

Genus IRVINGELLA Ulrich and Resser, 1924

Irvingella tropica Öpik

Plate 51, figs. 17–18

1963 *Irvingella tropica* Öpik, p. 96, pl. 4, figs. 5–8; text-fig. 36.

Material. Four cranidia, L138; one doubtful cranidium, L127.

Diagnosis. Irvingella with a frontal area some 20% of the glabellar length, comprised of a narrow, convex border and a slightly longer preglabellar field which are separated by a distinct border furrow. Glabella broad, tapering gently forward, with a rounded anterior termination. Fixed cheeks some 60% of basal glabellar width; palpebral lobes gently and evenly curved.

Dimensions. Cranidial lengths range from 7·1 to 9·5 mm.

Remarks. I. tropica is allied to *I. angustilimbatus* Kobayashi which was redescribed by Palmer (1968, p. 46, pl. 6, figs. 17–18, 21–23) and is characterized by its distinctly tapering glabella. Indeed, a single cranidium described by Palmer as an extreme variant of *I. angustilimbatus* was regarded by him as indistinguishable from *I. tropica*. Among American *Irvingella*, only *angustilimbatus* has a well-developed cranidial border and it is the oldest of the American species (Palmer 1968).

Hitherto *Irvingella* has been recorded from a single locality in Australia, near Mistake Bore, Chatsworth Station 180 km to the north-east of the Browns Creek Section (Öpik 1963).

Family EULOMATIDAE Kobayashi, 1955

Genus STIGMATOA Öpik, 1963

1963 *Stigmatoa* Öpik, p. 87.

Type species. Stigmatoa diloma Öpik.

Diagnosis. Glabella uniformly tapering with three pairs of straight lateral glabellar furrows which progressively increase in length and strength posteriorly. Occipital lobe well defined and bearing a stout, elongate spine. The preglabellar field is steeply declined to a well-defined border and border furrow which bears 20–30 regularly spaced pits. Fixed cheeks strongly convex, terminating in large palpebral lobes set opposite the glabellar midpoint. Eye ridges clear, anteriorly directed; anterior facial sutures divergent. Pygidium twice as wide as long with a smoothly curved posterior margin. Border narrow, convex; border furrow poorly defined. Axis tumid with four rings and the convex pleural fields each bear four broad ribs with weak interpleural grooves.

Remarks. Öpik established the genus on cranidial characteristics; the single pygidium he figured as *S. diloma* (Öpik 1963, text-fig. 32) is unrelated and of undetermined affinities. Pygidia of two species figured here are almost identical and of little use in species discrimination. In spite of abundant cranidial material in the collections reported here, no free cheeks have been identified.

Stigmatoa has recently been reported from northern Victoria Land, Antarctica by Shergold *et al.* (1976). It also appears in faunal lists given for the Cambrian succession of Altay, U.S.S.R. by Poletaeva and Romanenko (1970) but this record must be treated with caution as the associated assemblage is of middle Cambrian age.

Stigmatoa diloma Öpik

Plate 51, figs. 5–7

1963 *Stigmatoa diloma* Öpik, p. 89, pl. 4, fig. 2; text-fig. 31; *non* text-fig. 32.

Material. Twelve cranidia and three pygidia; localities L121–122, L127, L136.

Diagnosis. Glabella elongate, length of frontal area less than one-third that of the glabella. Interocular span about one-third of the glabellar width measured on the same line. Anterior border slightly concave adjacent to the anterior margin. Preglabellar field with venulose ornament.

Dimensions. Cranidial lengths range from 5·5 to 11·0 mm; pygidial lengths from 7·5 to 8·4 mm.

Remarks. The pygidium of *S. diloma* is indistinguishable from that of *S. tysoni* in spite of substantial differences in cranidial morphology between the two species. The slight, anterior concavity of the anterior border is a consistent feature of the cranidia examined and can be taken as a reliable characteristic for the discrimination of *S. diloma* from *S. sidonia.*

Stigmatoa sidonia Öpik

Plate 51, figs. 15–16

1963 *Stigmatoa sidonia* Öpik, p. 91; pl. 4, fig. 1; text-fig. 34.

Material. Five fragmentary cranidia, L138.

Diagnosis. Cranidial characteristics identical to *S. diloma* except that the anterior border is convex right to the anterior margin and the venulose ornament appears to be lacking from the preglabellar field.

Dimensions. Cranidial lengths range from 6·5 to 9·3 mm.

Remarks. S. sidonia is probably derived from *S. diloma* which it so closely resembles.

Specimens from the present collection like Öpik's single specimen, are associated with *I. tropica* and lie stratigraphically above *S. diloma*. The range of *I. tropica*, however, appears to extend a little below that of *S. sidonia* as at L127 a poor specimen which probably represents *I. tropica* is associated with *S. diloma*.

Stigmatoa tysoni Öpik

Plate 51, figs. 8–9

1963 *Stigmatoa tysoni* Öpik, p. 92, pl. 4, fig. 3.

Material. Three fragmentary cranidia and one pygidium; localities L130, L143, L145, L149.

Diagnosis. Glabella squat, length of frontal area more than one-third of glabellar length. Preglabellar field lacking venulose ornament. Fixed cheeks narrow; interocular span about half the width of the glabella measured on the same line. Anterior border convex right to the anterior margin.

Dimensions. Cranidial lengths range from 6·7 to 7·4 mm; the single pygidium is 6·5 mm in length.

Remarks. The occipital spine shows well on JCF 8453 and is bent posteriorly with the distal portion orientated parallel to the glabellar crest. *S. tysoni* is allied to *Stigmatoa* sp. recorded by Shergold *et al.* (1976) from northern Victoria Land, Antarctica.

Family KAOLINSHANIIDAE Kobayashi, 1935

Genus PROCHUANGIA Kobayashi, 1935

Prochuangia sp.

Plate 51, fig. 19

Material. JCF 8366, JCF 8469, L127; pygidia.

Description. Pygidium semicircular with an inflated axis tapering gently, reaching almost to the posterior margin and bearing six rings. Pleural fields convex, lacking ribs, with their anterior margins raised into prominent ridges. A pair of strong, diverging spines originate from the midpoints of pleural margins. Shell surface with well-developed pustules on both the pleural fields and the axis.

Dimensions. The two pygidia range from 1·7 to 6·0 mm in axial length.

Remarks. The figured specimen is an internal mould and does not show the pustulose ornamentation of the shell surface. The specimens are indistinguishable from *Prochuangia granulosa* Lu (1956*b*, p. 376, pl. 1, fig. 5), which is known from a single pygidium from the Yüping district, eastern Kueichou Province, China. They may well be conspecific with the Chinese species but, bearing in mind the specific provinciality of Australian Idamean polymerid taxa, it would be premature to record them so until cranidia are known.

Family LEIOSTEGIIDAE Bradley, 1925
Subfamily PAGODIINAE Kobayashi, 1935
Genus PAGODIA Walcott, 1905
Subgenus IDAMEA Whitehouse, 1939

The status of *Pagodia* (*Idamea*) has been exhaustively treated by Öpik (1967) who also substantially clarified its morphology. As discussed below, *P.* (*I.*) *baccata* Öpik and the type species *P.* (*I.*) *venusta* Whitehouse are the only two species constituting the subgenus and they may themselves prove to be synonymous.

Pagodia (*Idamea*) *venusta* Whitehouse

Plate 51, figs. 11–14

1939 *Idamea venusta* Whitehouse, p. 232, pl. 24, figs. 4–5, *non* pl. 24, fig. 6.
1967 *Pagodia* (*Idamea*) *venusta* Whitehouse; Öpik, p. 260, pl. 18, fig. 6*a–c*; text-fig. 88.
1967 *Pagodia* (*Idamea*) *extricans* Öpik, p. 261, pl. 18, figs. 4, 5.

Material. Twenty-six cranidia, twenty-one pygidia, and twelve free cheeks; localities L121–122, L127, L138.

Diagnosis. P. (*Idamea*) possessing non-granulose or weakly granulose cranidial and pygidial surfaces.

Description. Cranidium distinctly wider than long with broad, convex fixed cheeks measuring from 60 to 75% of the glabellar width. Glabella tapering gently forward, often with slight constriction anterior to the midpoint, truncate against the border furrow. Four pairs of weak lateral glabellar furrows; the first are located adjacent to the eye ridges and the last extend a little closer to the glabellar midline than the others with each of the pair enclosing a distinct median bulge. Palpebral lobes gently curved, posterior in position, margined by quite strong palpebral furrows and measuring almost half the glabellar length. Eye ridges distinct and forward sloping. Anterior border a narrow, steeply upturned lip separated from the glabella by a deep, narrow border furrow. Its anterior margin bears delicate, subparallel terrace lines. Occipital lobe, furrow, and node well developed. Posterior limbs strongly furrowed, barely extending beyond the palpebral lobes. Free cheek rather tumid with a strongly convex border passing into confluence with a broad-based, squat, convex genal spine.

Pygidium semicircular with well-developed, widely spaced articulating facets and a broad, convex border. Axis strongly arched, gently tapering with four or five rings. Pleural fields weakly convex with three or four broad, weak ribs.

Test surfaces of both pygidia and cranidia may be smooth except for fine puncta or bear small, scattered granules.

Dimensions. Cranidial lengths range from 3·5 to 8·5 mm; pygidial lengths from 2·9 to 6·0 mm.

Remarks. P. (*I.*) *venusta* was established from silicified material and another silicified cranidium was later referred to the species by Öpik. As noted by Öpik (1967, p. 259) the single pygidium referred to *P.* (*I.*) *venusta* by Whitehouse is unrelated. The cranidial proportions of *P.* (*I.*) *extricans* Öpik are identical with those of *venusta* which is given by Öpik as distinguished by its impunctate test and lack of external eye ridges. *P.* (*I.*) *extricans* was, however, described from shelly material and these distinctions are almost certainly due to differing modes of preservation. Only a single species of nongranulose or weakly granulose *P.* (*Idamea*) can be discriminated in the Browns Creek Section; the lower part of its range overlaps with that of *Corynexochus plumula* and is consistent with the association of *venusta* and *C. plumula* reported by Öpik from Mount Idamea 20 km to the north-west. The single locality from which *extricans* is known corresponds to a horizon at the base of the range of the comparable species in the Browns Creek Section (see Henderson, in press). The ages of *P.* (*I.*) *venusta* and *extricans* are, therefore, not widely discrepant as Öpik thought and they lie within the lower portion of the range of a single comparable species collected in this project. *P.* (*I.*) *venusta* and *P.* (*I.*) *extricans* are here regarded as synonymous and identical with the material described here.

P. (*I.*) *baccata* Öpik (1967, p. 262, pl. 17, figs. 1–8; pl. 18, figs. 1–3; text-fig. 89) is given as distinguished from *P.* (*I.*) *venusta* by its granulose surface ornament, but may prove to be an extreme variant of *P.* (*I.*) *venusta.* The material available includes a number of specimens which show incipient granulation (see Pl. 51, fig. 14) and which otherwise encompass in their variation the morphology of *P.* (*I.*) *baccata.* Only a single specimen shows a granulation as strong as the types of *baccata* but a precise discrimination of this species from *venusta* is not at present clear.

BIOSTRATIGRAPHY

Henderson (in press) has recognized five assemblage zones in the Browns Creek Section of the Idamean Stage, each being named for its characteristic species. Ranges of those species discussed in the systematic descriptions are illustrated in Table 2. The full zonal assemblages, including four species recorded from other areas by Öpik (1963, 1967), are listed below.

Glyptagnostus reticulatus *Zone*

Aspidagnostus strictus Öpik, *Innitagnostus inexpectans* (Kobayashi), *Peratagnostus nobilis* Öpik, *Glyptagnostus reticulatus* (Angelin), ?*Pseudagnostus vastulus* Whitehouse, *Olenus ogilviei* Öpik, *Proceratopyge nectans* Whitehouse, *Aphelaspis australis* sp. nov., and *Blountia* (*Mindycrusta*) *advena* Öpik.

Proceratopyge cryptica *Zone*

Peratagnostus nobilis Öpik, *Pseudagnostus vastulus* Whitehouse, *P. curtare* sp. nov., *Corynexochus plumula* Whitehouse, *Proceratopyge cryptica* sp. nov., *Aplotaspis erugata* (Whitehouse), *Aphelaspis australis* sp. nov., *Eugonocare whitehousei* sp. nov., *Stigmatoa tysoni* Öpik, and *Prismenaspis propinquum* (Whitehouse).

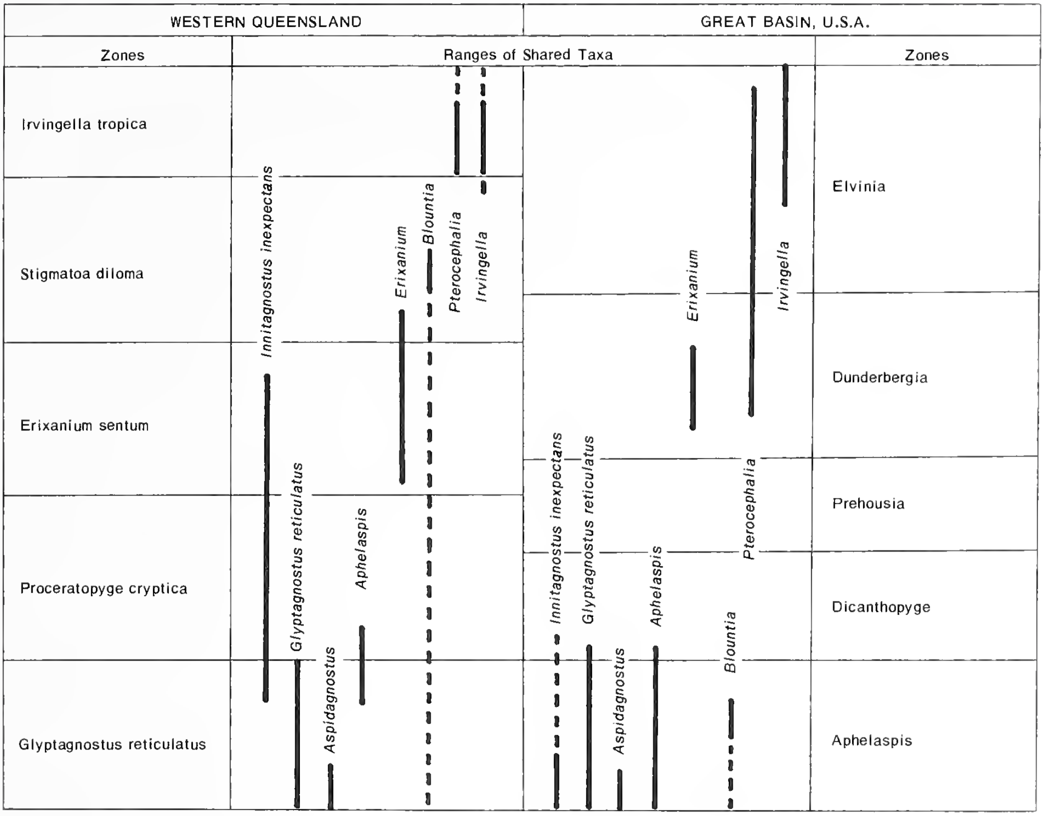
Erixanium sentum *Zone*

Peratagnostus nobilis Öpik, *Innitagnostus inexpectans* (Kobayashi), *Pseudagnostus vastulus* Whitehouse, *P. curtare* sp. nov., *Corynexochus plumula* Whitehouse, *Proceratopyge lata* Whitehouse, *Aplotaspis erugata* (Whitehouse), *Eugonocare tessellatum* Whitehouse, *Erixanium sentum* Öpik, *Stigmatoa tysoni* Öpik, *Prismenaspis propinquum* (Whitehouse), and *Pagodia* (*Idamea*) *baccata* Öpik.

Stigmatoa diloma *Zone*

Peratagnostus nobilis Öpik, *Pseudagnostus vastulus* Whitehouse, *P. curtare* sp. nov., *P. margopronus* sp. nov., *Corynexochus plumula* Whitehouse, *Proceratopyge lata* Whitehouse, *Aplotaspis mucrora* sp. nov., *Yuepingia* sp. nov., *Eugonocare tessellatum* Whitehouse, *E. quadrata* sp. nov., *Blountia* (?*Mindycrusta*) *georginae* Öpik, *Asilluchus nanus* Öpik, *Erixanium strabum* Öpik, *E. alienum* Öpik, *Stigmatoa diloma* Öpik, *Prismenaspis brownensis* sp. nov., *Prochuangia* sp. nov., and *Pagodia* (*Idamea*) *venusta* Whitehouse.

TABLE 2. Chart showing the ranges of taxa shared between the Pterocephaliid Biomere and the Idamean Stage and the best match of zonations for these two divisions.



Irvingella tropica *Zone*

Agnostotes inconstans Öpik, *Pseudagnostus curtare* sp. nov., *P. margopronus* sp. nov., *Olenus delicatus* Öpik, *Proceratopyge lata* Whitehouse, *Eugonocare quadrata* sp. nov., *Pterocephalia* sp. nov., *Stigmatoa sidonia* Öpik, *Prismenaspis alta* sp. nov., *Irvingella tropica* Öpik, *Pagodia* (*Idamea*) *venusta* Whitehouse, and *Hercantyx rudis* Öpik.

NOTES ON IDAMEAN CORRELATIVES

Glyptagnostus reticulatus, characteristic of the lowest zone of the Idamean Stage, and *Irvingella*, characteristic of the highest, are widely distributed taxa on a global basis and provide a means of reasonably accurate correlation of the Idamean Stage with biostratigraphic units recognized in many other regions. Only five Idamean genera, *Eugonocare* Whitehouse, *Asilluchus* Öpik, *Hercantyx* Öpik, *Aplotaspis* gen. nov., and *Prismenaspis* gen. nov. are presently unknown outside Australia; many of the others are useful in correlation.

North America

The most complete and thoroughly documented Idamean equivalent in North America comprises the Pterocephaliid Biomere of the Great Basin region described

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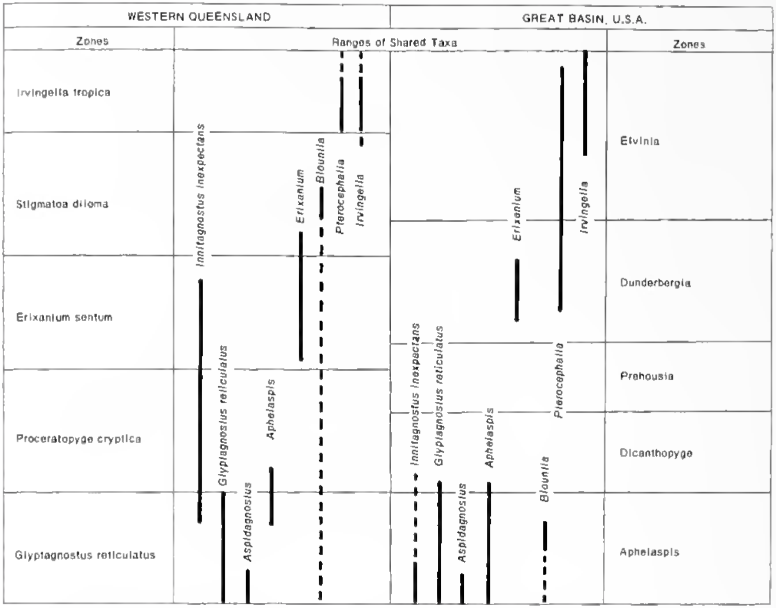

Irvingella tropica *Zone*

Agnostotes inconstans Öpik, *Pseudagnostus curtare* sp. nov., *P. margopronus* sp. nov., *Olenus delicatus* Öpik, *Proceratopyge lata* Whitehouse, *Eugonocare quadrata* sp. nov., *Pterocephalia* sp. nov., *Stigmatoa sidonia* Öpik, *Prismenaspis alta* sp. nov., *Irvingella tropica* Öpik, *Pagodia* (*Idamea*) *venusta* Whitehouse, and *Hercantyx rudis* Öpik.

NOTES ON IDAMEAN CORRELATIVES

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North America

The most complete and thoroughly documented Idamean equivalent in North America comprises the Pterocephaliid Biomere of the Great Basin region described by Palmer (1965*b*). The biomere lies within the familiar Dresbachian and Franconian Stage divisions established in the upper Mississippi Valley region and widely employed in North America. The boundary between the two stages is generally taken at the base of the *Elvinia* Zone which is the uppermost of five zones recognized in the biomere. While the utility of the biomere as a biostratigraphic concept may be disputed, the zonation recognized by Palmer has been established beyond doubt and can be successfully applied to Cambrian successions throughout North America with the exception of the restricted province of Baltic aspect located on south-eastern Newfoundland, Cape Breton Island, and eastern New England (see North 1971). *G. reticulatus* occurs at the base of the biomere sequence and *Irvingella* towards the top. Prominent faunal discontinuities mark its boundaries, similar to that at the base of the Idamean Stage. Ranges of common genera, with the exception of *Pseudagnostus* which ranges well beyond the limits of the Idamean Stage and its equivalents, and the best match of the Pterocephaliid Biomere zonation with that of the Idamean Stage is presented in Table 2.

In terms of evolutionary aspect, the Pterocephaliid and Idamean faunas show striking similarities in spite of possessing dissimilar taxonomic complements. In both, some species groups can be identified which undoubtedly comprise segments of individual bioseries. Among Idamean faunas there are series of *Eugonocare* (three species), *Stigmatoa* (three species), *Prismenaspis* (three species), *Aplotaspis* (two species), and *Proceratopyge* (two species). Similar trends in quite different genera, involving up to five species are reported from Great Basin sequences by Palmer (1965*b*).

Data on Alaskan faunas presented by Palmer (1968) are of interest because some taxa are shared with Australia but are unknown elsewhere in North America. These include *Proceratopyge cryptica* sp. nov. with *Peratagnostus* (Franconian-1 fauna of Palmer) and *Corynexochus plumula* Whitehouse (Dresbachian-2 fauna of Palmer). The Franconian-1 fauna, judging from the Australian ranges of the shared taxa, is probably of Dresbachian age and best regarded as correlative with a horizon within the *Prehousia–Dicanthopyge* zonal interval. Alaskan *Yuepingia* are associated with taxa which post-date the Idamean and its correlatives.

Scandinavia

The upper Cambrian faunal succession for Norway has been summarized by Henningsmoen (1958) and that for Sweden by Westergaard (1947). Biostratigraphic schemes for the two countries are very similar. Few genera are shared with Australia but the cosmopolitan species *G. reticulatus* makes its appearance at the base of the Scandinavian *Olenus* Zone and this horizon is correlative with the base of the Idamean. The association of *Olenus* with *G. reticulatus* in Australia supports this contention. *Proceratopyge* in Scandinavia ranges below *G. reticulatus* into the *Agnostus pisiformis* Zone considered by Öpik (1967) as correlative with the Mindyallan Stage.

The Scandinavian correlative of the upper Idamean is uncertain. *G. reticulatus* is restricted to the basal three of six Olenid subzones in Sweden and the upper limit of *Proceratopyge* is within the lower portion of the succeeding *Parabolina–Orusia* Zone. *Irvingella* is known from Sweden but its horizon is uncertain and tentatively placed at the base of the *Peltura–Sphaerophthalmus–Ctenopyge* Zone, three zones and fourteen subzones above the incoming of *G. reticulatus* and immediately below the first appearance of *Lotagnostus*. The inferred position of the Swedish *Irvingella* seems anomalously high and synchroneity between the *Peltura–Sphaerophthalmus–Ctenopyge* Zone and the upper Idamean unlikely. This contention is supported by the association of *Olenus delicatus* Öpik with *I. tropica* in western Queensland (Öpik 1963).

Siberia

Ivshin and Pokrovskaya (1968) proposed a twofold stage subdivision for the upper Cambrian in Siberia. The Tuorian Stage, the older of the two, is based on a succession on the Lena River in the Tuora-Sis area of the north-western Siberian Platform. Three zones are recognized in the Tuorian and the highest of these is a correlative of the lower Idamean. It is characterized by *G. reticulatus* and shares *Aphelaspis*, *Aspidagnostus*, and *Innitagnostus inexpectans* (Kobayashi) with Australia. The Australian species *Erixanium sentum* Öpik is restricted to the upper portion of the zone and apparently occurs with *G. reticulatus* suggesting that the Siberian teilzones for these species do not exactly match their Australian counterparts. The anomalous *Crepicephalus borealis* Lermontova also listed from the upper Tuorian has been reinterpreted by Palmer (1965*b*, p. 64) as representative of a new aphelaspid genus allied to *Eugonocare* Whitehouse and *Olenaspella* Wilson.

The Shidertinian Stage is based on a section from the Olenta River adjacent to Kujanda, Kazakhstan and is subdivided into four zones. The lowest of these contains *Irvingella* and is correlative with the upper Idamean. Early Shidertinian horizons in the Tuora-Sis area, succeeding the type Tuorian contain the Australian species *Agnostotes inconstans* Öpik and *Proceratopyge lata* Whitehouse in addition to *Irvingella*.

Upper Cambrian zonations and faunas throughout Siberia have recently been reviewed by Rosova (1968). Areas with Idamean correlatives show diverse faunas. Some, including those just discussed and faunas from the northern Anabarsk Rise adjacent to the Olyenyok River, the Chopko River district of the Norilsk Region, and the Altai Mountains have a cosmopolitan flavour with such taxa as *G. reticulatus*, *Irvingella*, *Olenus*, *Olenaspella*, *Proceratopyge*, and *Aphelaspis*. Others, however, such as the faunas of the Igarsk Region studied in considerable detail by Rosova, the Kureysk Region, north-western Salair, and Shoriya are almost exclusively endemic in their generic aspect.

Northern China and Korea

The Idamean Stage appears to be an approximate correlative of the Paishan 'Stage' which was first introduced by Endo as a formation for a thin interval of limestone in a substantial late Cambrian section at Paichiashan, Liaotung Peninsula, northern China. Fossils were described from the formation by Endo and Resser (1937). The name Paishan has subsequently been widely used by Kobayashi and others to denote a *de facto* stage division. It is regarded as partially correlative with the Changshan 'Stage' introduced by Sun as a lithostratigraphic unit of shales recognized in the east Hopei district, northern China. A small late Cambrian fauna was described from it by Sun (1924) and it too has been subsequently employed as a *de facto* stage division.

According to Kobayashi (1967, p. 389) the Changshan 'Stage' is equal to the Paishan 'Stage' and succeeding Daizan 'Stage' of the Paichiashan section.

Paishan faunas are widely distributed in northern China and Korea (Kobayashi 1966*a*, *b*) and differ markedly from those of the preceding Kushan 'Stage'. Kobayashi (1967, p. 410) records that none of the approximately forty genera of polymerid trilobites known from the Kushan survived the 'Stage'. Paishan elements shared with the Idamean Stage are *Prochuangia*, *Irvingella*, *Pseudagnostus*, and *Proceratopyge*. An association of *G. reticulatus* with *Olenus* is known from South Korea (Kobayashi 1962), but its position relative to the reference 'stage' divisions remains to be established.

Southern China

Literature relating to early upper Cambrian trilobites from the Yangtze Basin and adjacent areas is summarized in Kobayashi (1967). No comprehensive local biostratigraphic scheme is as yet available. The succession from the Hunan–Kueichow border area recorded by Jegorova *et al.* (see Kobayashi 1971, pp. 176–177) is in part an Idamean correlative. Collections from the three localities highest in the succession jointly contain *Aphelaspis*, *Prochuangia*, *Proceratopyge*, and *G. reticulatus*. They appear to represent the equivalent of the lower Idamean. The reported association of *G. reticulatus* with *G. stolidotus* at one stratigraphically lower locality and of *Yuepingia* with *Drepanura* and *Blackwelderia* at another conflict with range data for these taxa from other regions and needs confirmation.

A small fauna recorded from the highest Cambrian unit of the Yüping region of eastern Kueichow by Lu (1956*b*) contains *Pseudagnostus*, *Prochuangia*, *Yuepingia*, and probably *Stigmatoa*. It is an upper Idamean correlative.

Antarctica

A fauna of Idamean age is recorded from the Ellsworth Mountains, western Antarctica by Webers (1972). *Aphelaspis*, *Eugonocare*, *Pseudagnostus*, and a new, unnamed genus compared to *Onchopeltis* and possibly identical with *Prismenaspis* gen. nov. are elements affiliated with the Australian fauna reported here.

Trilobites from northern Victoria Land first reported by Laird *et al.* (1972) and described by Shergold *et al.* (1976) are also of Idamean age. They include *Prochuangia*, *Stigmatoa*, *Irvingella*, and probably *Aphelaspis*.

STATUS OF THE BIOMERE CONCEPT

The Biomere was introduced by Palmer (1965*a*) as a new type of biostratigraphic unit characterized by a space/time plexus of fossils with a common evolutionary fabric, discriminated from preceding and succeeding biomeres by a sharp faunal discontinuity. The type example is the Pterocephaliid Biomere, based on polymerid trilobite faunas from the U.S.A. which have been thoroughly described from the Great Basin region by Palmer (1962, 1965*b*) and which are fairly well known from several other regions. The feature which sets the biomere apart from other units employed in biostratigraphy is that its boundaries are diachronous. Palmer thus envisages biomeres as spatial entities separated by a geographic boundary which migrated with time. With evolution continuing unabated in each subjacent biomere, the actual record of the faunal discontinuities separating them will be represented by different taxa at different geographic locales as determined by the spatial movement of the discontinuities in time.

The Idamean Stage is clearly an Australian counterpart of the Pterocephaliid Biomere. It shows an internal evolutionary continuity and has a striking faunal break at its base as already noted by Öpik (1966). Of thirty-four genera of polymerid trilobites known from the preceding upper zone of the Mindyallan Stage, only *Blountia* continued into the Idamean. Agnostids fared slightly better; of five Idamean genera known, three are holdovers from the Mindyallan Stage. Post-Idamean faunas are yet to be documented from Australia and the nature of the upper Idamean boundary is therefore unknown.

Öpik's designation of the Idamean as a stage is supported here and it is thus pertinent to discuss the status of the biomere concept.

The essential biomere characteristic of diachronous boundaries has been argued by Palmer (1965*a*, *b*) for the faunal discontinuity between the Pterocephaliid Biomere and the preceding Crepicephalid Biomere. In the McGill section, Nevada and the Cedar Bluff Section, Alabama three taxa, *G. r. angelini* (Resser), *A. buttsi* (Kobayashi), and *Olenaspella separata* Palmer are represented at the base of the *Aphelaspis* Zone which is the basal zone of the Pterocephalid Biomere. In all other known sections, the earliest *Aphelaspis* Zone taxa can be matched with forms occurring a little higher in the McGill and Cedar Bluff sections. The data can be explained in one of three ways: the faunal discontinuity is synchronous in all sections and the species teilzones are diachronous; the discontinuity in all but the McGill and Cedar Bluff sections constitutes a paraconformity; or the species teilzones are synchronous and the discontinuity diachronous. A more substantial indication of the geographic distribution of sections of the McGill and Cedar Bluff type is required before a reliable choice can be made. Palmer cites the biostratigraphy of the McGill section as compared to that of the Snake Range section 50 miles to the south-east as confirmation of the diachronous nature of the faunal discontinuity. The upper two zones of the Crepicephalid Biomere are the *Cedaria* Zone (lower) and *Crepicephalus* Zone (upper). At McGill the discontinuity lies between the *Cedaria* Zone and the basal *angelini-buttsi-separata* faunule of the *Aphelaspis* Zone, while at Snake Range it lies between the *Crepicephalus* Zone and a higher faunule of the *Aphelaspis* Zone. These data are interpreted by Palmer as evidence of the faunal boundary migrating with a south-easterly component in time. However, such an explanation seems unlikely because the same faunal boundary which migrated 50 miles between these sections so as to allow the complete elimination of the *Crepicephalus* Zone from the McGill section moved much more rapidly over a substantial portion of the U.S.A. as demonstrated by widely scattered sections with the full succession of *Cedaria*, *Crepicephalis*, and *Aphelaspis* zones.

It can be argued, as has Palmer (1972), that faunal replacement of the Pterocephaliid and Idamean type cannot be synchronous as it is not evolutionary in nature. Thus the replacing elements must have existed elsewhere in prior time. But this is the situation for almost all traditional biostratigraphic units be they zones, stages, series, periods, or eras. The number of biostratigraphic boundaries recognized by a point in an evolutionary continuum are completely overshadowed by the number recognized on the basis of a sudden faunal change. Even for a boundary recognized in an evolutionary continuum, some measure of space/time ambiguity remains unless the populations concerned are panmictic. It must be concluded that the logical basis of the biomere concept is faulty, and there is little advantage in employing the term in preference to traditional names for biostratigraphic units.

SIGNIFICANCE OF THE BASAL IDAMEAN FAUNAL DISCONTINUITY

The basal Idamean faunal discontinuity is a striking local extinction event and is correlative with similar phases of extinction in China and the U.S.A. It is tempting to consider it as a world-wide event as did Öpik (1966), with an extraterrestrial cause. Siberian data, however, conflict with such a view as they show no evidence of a faunal discontinuity at that time; indeed Ivshin and Pokrovskaya (1968) note a faunal discontinuity at the division between their Tuorian and Shidertinian Stages, a horizon approximately correlative with the base of the *Irvingella tropica* Zone in Australia and the *Elvinia* Zone in the U.S.A. Much of the Siberian fauna remains to be described and the basal Idamean discontinuity may be still obscured for this reason. It is worth recalling that at the time of introduction of the Dresbachian and Franconian Stages in North America, the basal Pterocephaliid discontinuity was not recognized as a convenient position for a stage boundary.

In both Australia and the U.S.A. the faunal discontinuity lies between the teilzones of *G. stolidotus* Öpik and *G. reticulatus* (Angelin), both of which are apparently cosmopolitan taxa. Further, the bioseries of *G. r. angelini* (Resser) and *G. r. reticulatus* appears to be represented in Australia as well and may also prove to be cosmopolitan. The existence of this striking extinction event and a potential independent means of establishing its space/time distribution is deserving of attention among palaeontologists. It may provide a unique opportunity to examine the phenomenon of extinction which is the least well understood major feature in the history of life.

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ECOLOGICAL STUDIES ON TWO UNATTACHED CORALLINE ALGAE FROM WESTERN IRELAND

by DANIEL W. J. BOSENCE

ABSTRACT. Two free-living coralline algae occur sublittorally in Mannin Bay, Connemara, Eire. Locally they form 30-cm high autochthonous banks which cover areas up to 1 sq km and have a diverse associated fauna. The algae are restricted by light to depths between 1 m and 16 m. Within this depth range the development of the banks is controlled by wave-induced currents and the algae are broken down to form an algal gravel which supports a poor fauna.

There is variation in growth form within the species and a scheme is suggested for describing morphology in free-living corallines. Shapes vary from spheroidal, ellipsoidal, to discoidal. Within these shape classes branching density varies. Densely branched forms are found in the exposed areas and open-branched forms in the quiet areas of the bay. Wave-tank studies suggest that densely branched forms are most easily transported. Dense branching develops as a response to rolling on the substrate which damages the growing apex. Following abrasion, lateral branches form within the thallus.

The palaeontological implications of the work are discussed and comparisons made with other algal bank deposits.

UNATTACHED coralline algae (subfamily Melobesioideae) can be important producers of carbonate sediment in the sublittoral zone where they form both autochthonous banks and transported algal gravels. These algal sediments are known from both tropical (Turmel and Swanson 1972) and temperate environments (Foslie 1894; Cabioch 1966, 1970; Adey and MacIntyre 1973) where they are referred to as maerl (Lemoine 1910).

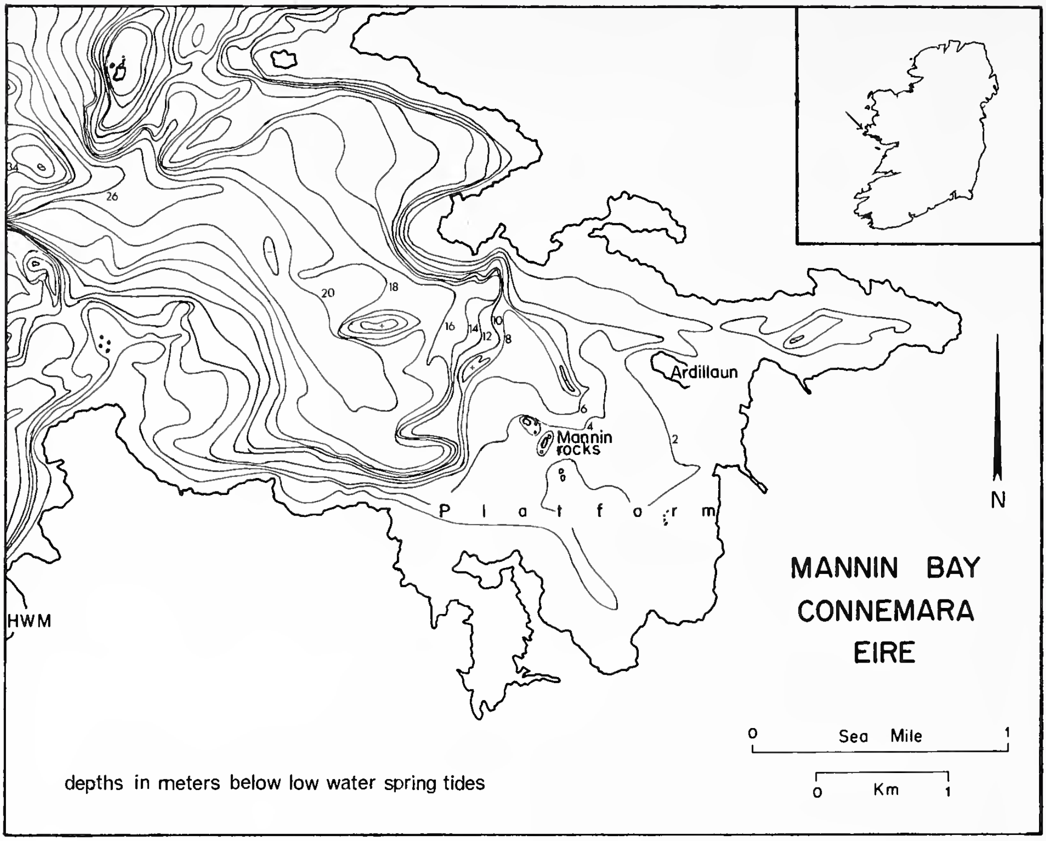
These unattached algae differ from the epilithic crustose corallines in their morphology, reproduction, and ecology. The unattached forms live in soft substrate areas. Their morphology varies from open branched thalli to densely branched algal nodules (rhodoliths). Reproduction is by vegetative means and by spores which settle on carbonate or clastic grains. The epilithic corallines of temperate waters have been studied in some detail by Cabioch 1972 and refs. and Adey and Adey 1973 and refs. Although the morphology and systematics of unattached corallines have been described by Cabioch 1966 and Adey and McKibbin 1970 there is little information on their ecology and sedimentology (Adey and McKibbin 1970; Adey and Adey 1973).

The object of this paper is to describe and interpret the distribution of autochthonous banks formed by two unattached corallines, analyse the ecological factors responsible for the variation in growth form, and to discuss the palaeontological implications arising therefrom.

ENVIRONMENTAL SETTING AND LITHOFACIES

The bathymetry and location of Mannin Bay are shown in text-fig. 1. A submarine valley leads into the bay and up to a slope levelling off at about 8 m to form a platform with occasional rocky outcrops. The shore is mainly rocky (Dalradian metasediments) but some sandy carbonate beaches and dunes are present. In the sheltered lagoons a muddy shore is found.

[Palaeontology, Vol. 19, Part 2, 1976, pp. 365–395, pls. 52–53.]



TEXT-FIG. 1. Location and bathymetry of Mannin Bay (after Buller 1969).

The sea-water is normal marine with seasonal water temperatures varying from a February mean minimum of 5 °C. to an August mean maximum of 15 °C. Salinity varies seasonally from 33·5 to 35‰ (Lees *et al.* 1969).

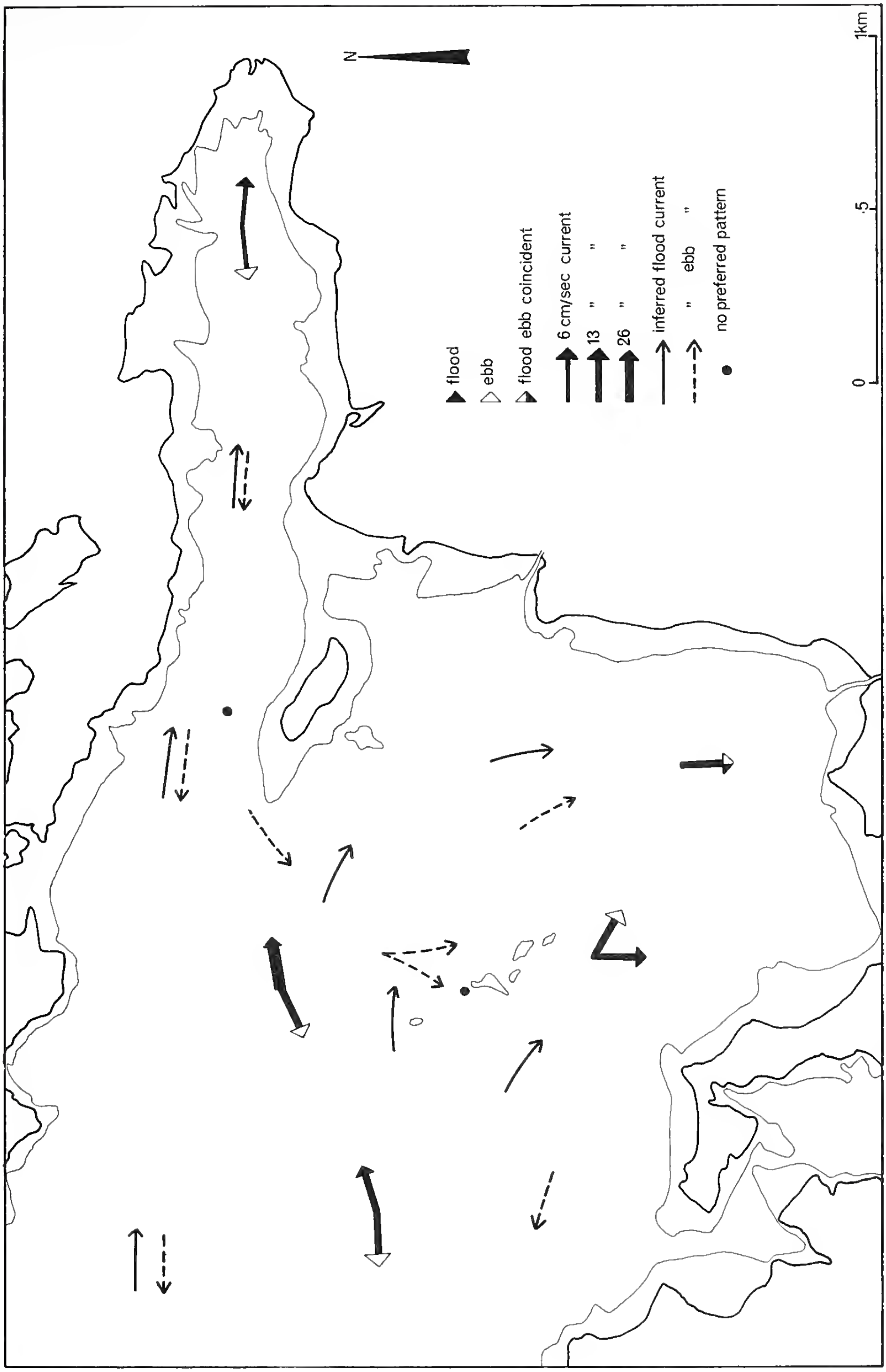
The normal marine environment is the result of mixing by tidal currents which show a simple ebb-flood pattern with a superimposed rotary pattern in South Mannin Bay (text-fig. 2). The currents measured are not strong enough to transport the algal clasts (Buller 1969). Study of the gravel bed forms shows that the main hydraulic forces are oscillatory currents produced by waves.

The strongest and most frequent winds are from the south-west (Lees *et al.* 1969).

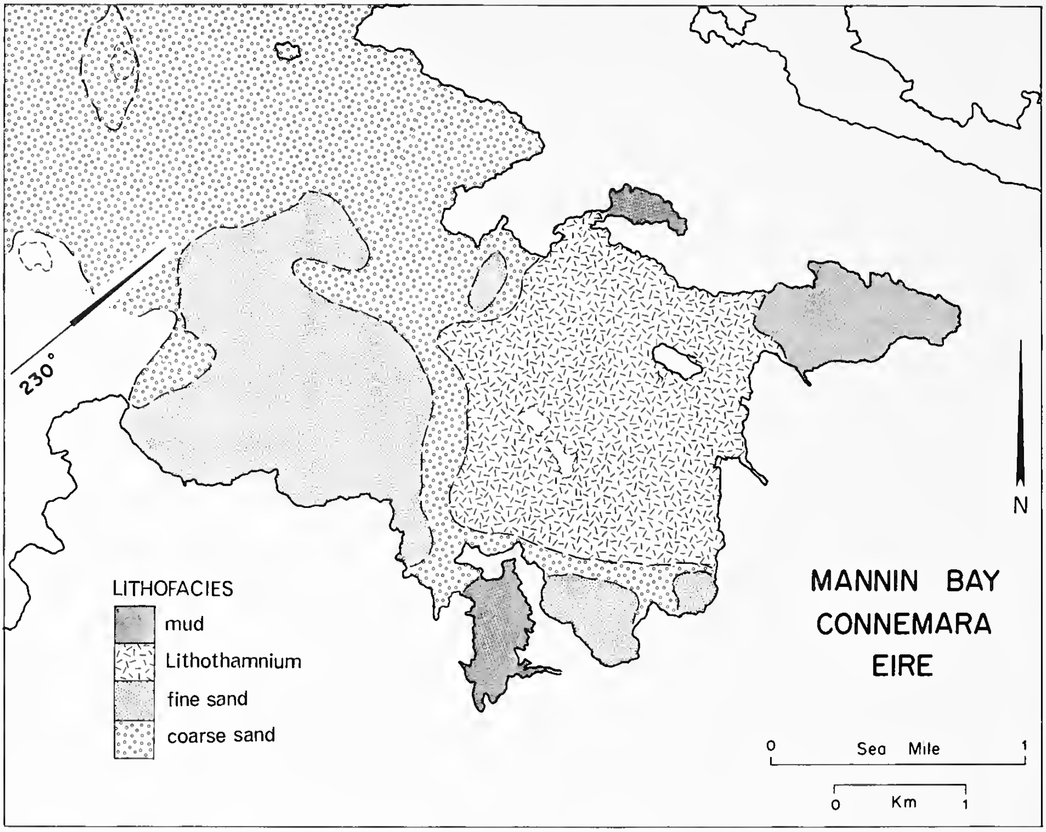
Lithofacies

The sediments of Mannin Bay are mainly carbonate as is the case with much of the littoral and sublittoral of the coast of western Eire (Keary 1969, 1970; Lees *et al.* 1969). The sediments of Mannin Bay can be divided into four major sedimentary facies (text-fig. 3) based on particle size, composition, and mineralogy of the carbonate grains (Buller 1969; Gunatilaka 1972).

Mud facies. Dark muds are found in the shallow and most sheltered parts of Mannin



TEXT-FIG. 2. Direction and strength of tidal currents, Mannin Bay (after Buller 1969).



TEXT-FIG. 3. Lithofacies and input of hydraulic energy, Mannin Bay (after Buller 1969; Gunatilaka 1972).

Bay where currents are weak. The carbonate content of the muds rarely exceeds 40% (Gunatilaka 1972). Epiphytic filamentous algae are common in these quiet areas and they trap mud as they grow, so forming oncolites (Pl. 52, fig. 1).

Lithothamnium *facies*. This facies, the principal concern of this paper, covers the platform area of Mannin Bay and is composed of both living and dead unattached coralline algae (Pl. 52, figs. 4–6).

EXPLANATION OF PLATE 52

Fig. 1. Underwater photograph of filamentous algae epiphytic on *Lithothamnium corallioides* forming oncolites, × 1/6.

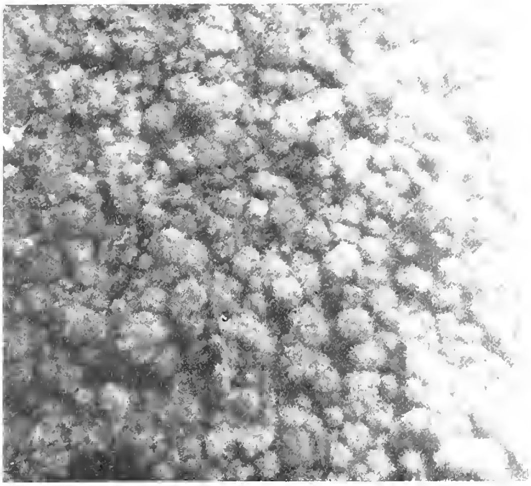
Fig. 2. Underwater photograph of fine-sand facies with bioturbated surface, × 1/20.

Fig. 3. Underwater photograph of coarse-sand facies with wave-formed ripples, × 1/20.

Fig. 4. Underwater photograph of wave-rippled algal gravel with dead infaunal bivalve shells in ripple troughs, × 1/20.

Fig. 5. Underwater photograph of surface of algal bank of *Phymatolithon calcareum* with *Asterias rubens*, × 1/4 (foreground).

Fig. 6. Core through algal bank. Note stacking of algal thalli and grain-supported sediment with micrite matrix at depth, × 0·5.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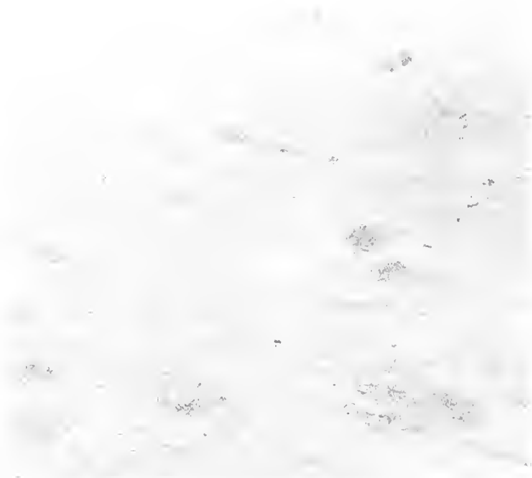
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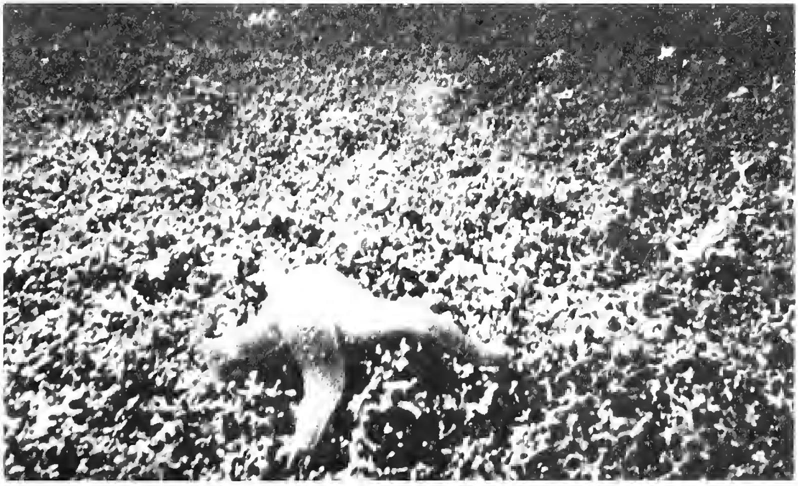
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BOSENCE, coralline algae

Fine sand facies. This facies accumulates in the sheltered parts of the bays and is composed mainly of foraminifera, echinoderm, bryozoan, and ostracod debris (Pl. 52, fig. 2).

Coarse sand facies. The more open parts of the bay contain a very coarse sand or gravel composed of large proportions of *Mytilus edulis* and barnacle grains suggesting derivation from the offshore islands and 'reefs' (Pl. 52, fig. 3).

The distribution of the sedimentary facies can, in the main, be explained in terms of the input of hydraulic energy into the bay. The tidal, wind, and longest fetch directions indicate that the maximum energy is derived from about 230° N. (text-fig. 3). The area most exposed to this direction is represented by the coarse-sand facies. Where slight protection is afforded fine sand accumulates and in the very sheltered bay heads mud is deposited (Buller 1969). The *Lithothamnium* facies does not fit this pattern as it is basically an autochthonous deposit and the grain size is related to the size of the thallus and its comparative rate of destruction.

THE MAERL SPECIES

General

The *Lithothamnium* facies of Buller (1969) is composed of the unattached calcareous algae *L. corallioides* Crouan and *Phymatolithon calcareum* (Pallas) Adey and McKibbin. The living algae cover up to 100% of the sea-floor and live in both quiet and exposed environments within the depth range of extreme low-water spring tides to 16 m (text-figs. 1, 6). Where growth is prolific an autochthonous three-dimensional growth structure is formed by the algal thalli which may be stacked to a height of 30 cm and covering areas measured in thousands of square metres, so forming a bank (Pl. 52, figs. 5–6; text-fig. 6). These banks are semi-rigid structures formed by branches of neighbouring algal thalli intergrowing. The strength of the bank is enhanced by the binding effect of epiphytic soft-tissued algae (see also Cabioch 1969). Cores through the bank (Pl. 52, fig. 6) show the three-dimensional structure of the living algae. Mud is trapped by the network of algal thalli and by the algal mucilage so that with depth a muddy matrix is formed. This matrix gradually buries and kills the algae. Excavation through the bank with an air-lift suction sampler shows a similar structure to a depth of 1 m.

The banks are broken down locally by physical and biological erosion to form a gravel-sized bioclastic sediment (Pl. 52, fig. 4). This is either transported into symmetrical ripples by wave-induced oscillatory currents with a small amount of living maerl in the ripple troughs, or it is a bioturbated bottom.

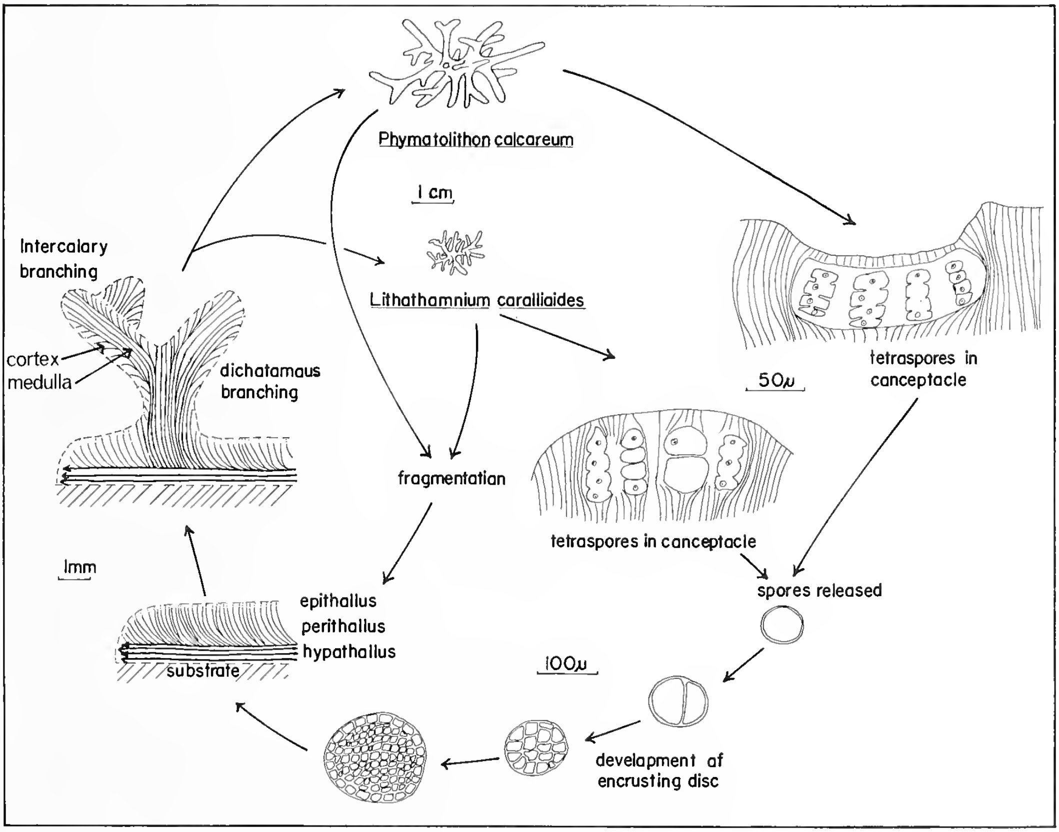
Biology

The banks can consist of one or both maerl species in varying proportions and they support a complex biota. The main ecological groups are: phytophagous gastropods (which utilize the organic debris trapped by algal mucilage); boring polychaetes, algae, and bivalves (which use the alga as a hard carbonate substrate); infaunal deposit and suspension feeders; nestling ophiuroids, crustacea, polychaetes, and bivalves; epifaunal attached bryozoa, serpulids, and sponges; vagile epifaunal vertebrates, echinoderms, decapods, and other crustacea; epiphytic algae, including filamentous red algae and red and brown macrophytes. The associated fauna has been studied by Cabioch (1968) in Brittany and Keagan (1973) in Kilkieran and Galway Bays, western Eire; the flora by Cabioch (1969) in Brittany.

The life cycles and morphogeneses of the maerl species have been recently described by both Cabioch (1972) and Adey and McKibbin (1970) and their results are summarized below and in text-fig. 4.

The main form of reproduction observed in Mannin Bay is vegetative. The thallus is broken by strong bottom currents and by organic reworking of the maerl. The plants only occasionally reproduce by the production of asexual spores. Sexual reproductive bodies have not been described, although Cabioch (1970) illustrates a sexual conceptacle of *P. calcareum*. The asexual spores are borne in conceptacles developed from the perithallial meristem in *L. corallioides* and within the perithallium in *P. calcareum*. Their development is shown in text-fig. 4.

The branches of the thallus are of multiaxial or 'fountain' construction with filaments of unlimited growth forming a central medulla (secondary hypothallus of



TEXT-FIG. 4. Life cycles and morphogeneses of *Phymatolithon calcareum* and *Lithothamnium corallioides* (after Cabioch 1972; Adey and McKibbin 1973).

Cabioch 1972). These axial filaments branch and grow laterally as filaments of limited growth forming a cortex with a width typical for the species.

Growth is periodic as illustrated by layers of different cell size. These growth layers cover the apex and some way down each branch (Pl. 53, fig. 1). The growth layers and filaments illustrate that growth may be patchy and occasionally abrasion and rehealing can be found (Pl. 53, figs. 15–16).

Branching occurs in two different ways. In dichotomous branching the axial filaments diverge to form two equal branches with a plane of symmetry between them (Pl. 53, fig. 1). Intercalary branching occurs through rejuvenation of the lateral filaments. This is recognized by the initiation of new medulla from pre-existing lateral filaments (cortex) (Pl. 53, fig. 2) resulting from rejuvenation of the intercalary meristem, and so contrasting with dichotomous branching, which involves divergence of two parts of the apical meristem.

When the original sedimentary grain is covered and the branches form and rebranch the characteristic free-living growth forms are produced from the original encrusting stage.

Both the cortex and the medulla can be regenerated after breakage. Similarly old conceptacles can be filled and overgrown by new perithallium.

The relative importance of the two methods of asexual reproduction over a long period of time is not known but observations in the Baie de Morlaix by Cabioch (1969) show that the formation of conceptacles is very infrequent (about every 4–6 years).

Distribution

Seventy-three stations were dived on during the months of May–August 1972. At each station notes were taken on a perspex sheet and the percentage cover of the living maerl was estimated using a 50-cm quadrat. Live specimens are easily identified by their red colour. When dead, the thallus turns to a white or creamy brown colour. Most stations were photographed in colour using a Nikonos camera. A sample 10 × 20 cm and 10 cm deep was taken with a shovel and placed directly into a polythene bag. At the surface it was transferred to 10% neutralized formalin. When the sample was sorted the live algal material was stored in formalcohol.

Text-fig. 6 shows the percentage cover of living maerl in Mannin Bay. The distribution is discontinuous and three main concentrations (banks) can be noted: a northern central area, a central eastern area, and a small southern area. This distribution is discussed below with respect to the physical and chemical parameters operating in the bay.

The living maerl species occur from extreme Low Water Spring tidal level to a maximum depth of about 16 m but dense growth is not recorded below 8 m or above 1 m below Low Water Spring tides. This depth is somewhat shallower than the 7- and 25-m depth range found in Brittany by Lemoine (1910) and Cabioch (1970). Many environmental factors may change with depth of water. I now discuss which of these may be important in determining the distribution of the maerl species in Mannin Bay.

The salinity of the sea-water in the bay is normal marine and does not vary at one point of time. This cannot therefore be of importance to the distribution of the maerl species. This agrees with the work of Cabioch (1969) in the Baie de Morlaix in Brittany.

Experimental work by Adey and McKibbin (1970) suggests that low salinity may reduce growth rates.

Nutrient distribution has not been studied but the analyses for salinity, Ca, Mg, and pH indicate a very well mixed open marine environment and in the absence of any large streams or rivers bringing in concentrated nutrients there are not likely to be any areas of nutrient enrichment.

The availability of O_2 and CO_2 reflected in the Eh is not limiting as this is constantly positive (Gunatilaka 1972).

Grazers on the algae are unimportant. Although abundant, gastropods only brush the surface mucous and debris. There is no grazing by echinoids.

Although within the *Laminaria* Zone, there is no competition between the maerl species and these brown algae. The laminarians are restricted to hard substrate areas and the maerl species to the soft substrate areas of the bay. However, epiphytic filamentous algae cover the living maerl in quiet waters. In addition to this the filamentous algae trap mud and eventually smother the coralline algae to form oncolites (Pl. 52, fig. 1) thereby limiting the growth of the corallines.

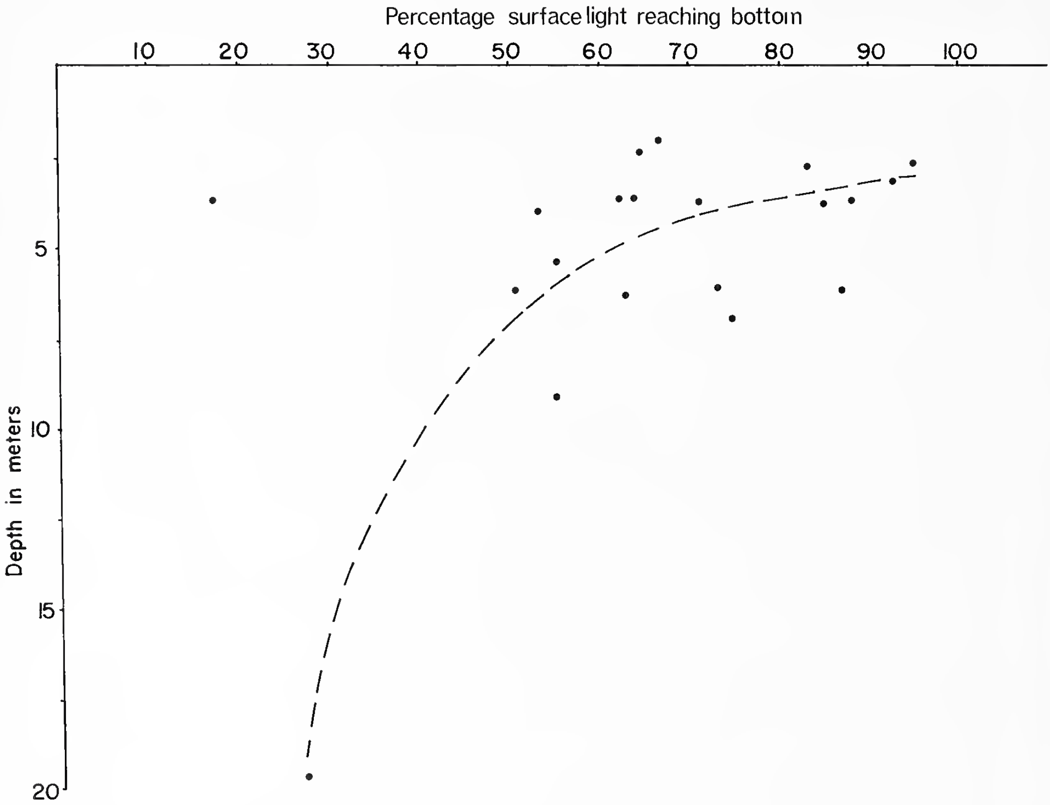
The combined effects of temperature and light on the distribution of boreal and sub-arctic corallines has been studied both in the field and experimentally by Adey 1966, 1970, Adey and McKibbin 1970, and Adey and Adey 1973. Adey (1970) concludes that temperature and light control on growth are the major factors determining both depth distribution and geographic distribution of crustose and unattached corallines. The distribution of many corallines can be mapped into well-defined depth and latitudinal zones. However, an important problem is establishing the separate effects of light and temperature which both decrease with depth and may vary together with respect to latitude. This problem was overcome by Adey (1966) by plotting abundance data as a function of both depth and temperature and through experimental work which supports the correlations found in the field (Adey 1970). Most species show a combined effect but some show a depth distribution controlled by light and others are controlled by temperature.

Experimental work by Adey and McKibbin (1970) indicates maximum growth rate at 12–13 °C. for *Phymatolithon calcareum* and 10–12 °C. for *Lithothamnium corallioides* and very little growth at 170 lux at these temperatures. The luminosity for maximum growth was not established. Field measurements showed a maximum growth in the summer months for both species. The maerl species are distributed from the Mediterranean to Norway and, therefore, are well within their latitudinal range in western Eire.

I now compare these results and observations with the distribution of the maerl species in Mannin Bay where the summer mean bottom temperature varies from 11·75 °C. at 22 m to 13·5 °C. at 1·8 m (Scott 1970). If temperature were the overriding factor living maerl should be abundant within this depth range as it is in the temperature zone for maximum growth and the substrate, lack of mud sedimentation, and water currents appear to be suitable.

However, within this depth range growth is only found from extreme low-water springs to about 16 m and dense growth between depths of 1 and 8 m. This suggests that temperature is not the primary factor limiting depth in Mannin Bay although it is probably important on a larger geographic scale (Adey and Adey 1973) and may be the cause of the lower depths recorded by Lemoine (1910) and Cabioch (1970) for Brittany.

The cut-off of surface irradiance in Mannin Bay by the sea was measured throughout the summer (1972) at various depths, conditions of turbidity, and surface roughness. This was measured just above the water surface and on the sea-bed with a calibrated light meter in a waterproof case. The effect water has on the different wavelengths was not measured as the absorption spectra of the maerl species is not known. Text-fig. 5 shows the measurements expressed as the percentage of surface luminosity (lux) reaching the bottom. The graph shows a rapidly decreasing penetration of light with depth and at the maximum depth at which the algae are found only about 30% of the surface light is reaching the sea-bed.



TEXT-FIG. 5. Graph illustrating cut-off of surface luminosity with depth, Mannin Bay.

The values of luminosity measured within the depth range of 1–8 m vary from 160 to 1760 lux depending on ambient surface light, surface roughness, and turbidity. Therefore even at these shallow depths the luminosity is occasionally reaching the lowest values for growth recorded by Adey and McKibbin (1970).

The parameter used for estimating the relative bottom-current velocities was the presence or absence of wave-ripple marks. This has been noted for about seventy stations during May–August 1972 and if present their orientation has been recorded with an underwater compass (text-fig. 7).

From wave theory (Barber 1965; Allen 1970) and experimental work (Bagnold 1947; Putnam and Johnson 1949) I interpret the distribution of wave ripples as follows. When deep-water waves enter the bay they only rarely have sufficient power to move sediment. I have occasionally found wave ripples (λ65 cm, H 5 cm) developed after storms on a normally bioturbated fine sand at stations 0·5 km to the west of Mannin Rocks. As the waves approach the platform they pass into shallower water. This results in an increase in velocity of the oscillating water currents and they frequently transport the gravel into wave ripples (λ100 cm, H 20 cm). A belt of rippled gravel is seen (text-fig. 7) on the edge of the platform.

When the waves pass over the platform their power to transport sediment is altered by two factors. Firstly, the sediment-transport potential of the waves, which are now shallow-water waves, is reduced by friction on the bottom. This is caused by primary porosity, bed forms, and grain size (Putnam and Johnson 1949). This I interpret as the cause of the loss of wave ripples as waves travel shorewards over the platform (text-fig. 7). The second factor to affect the power of the waves is caused by changes in topography of the bottom, leading to wave refraction. When wave orthogonals converge, at islands and submarine ridges, the wave energy increases. This I take to explain the wave ripples around Mannin Rocks, the shallow ridge extending shorewards from the rocks, and also the ripples to the south-west of Ardillaun (text-figs. 7 and 1). When wave orthogonals in embayments diverge, this results in a dissipation of energy and there are no wave ripples.

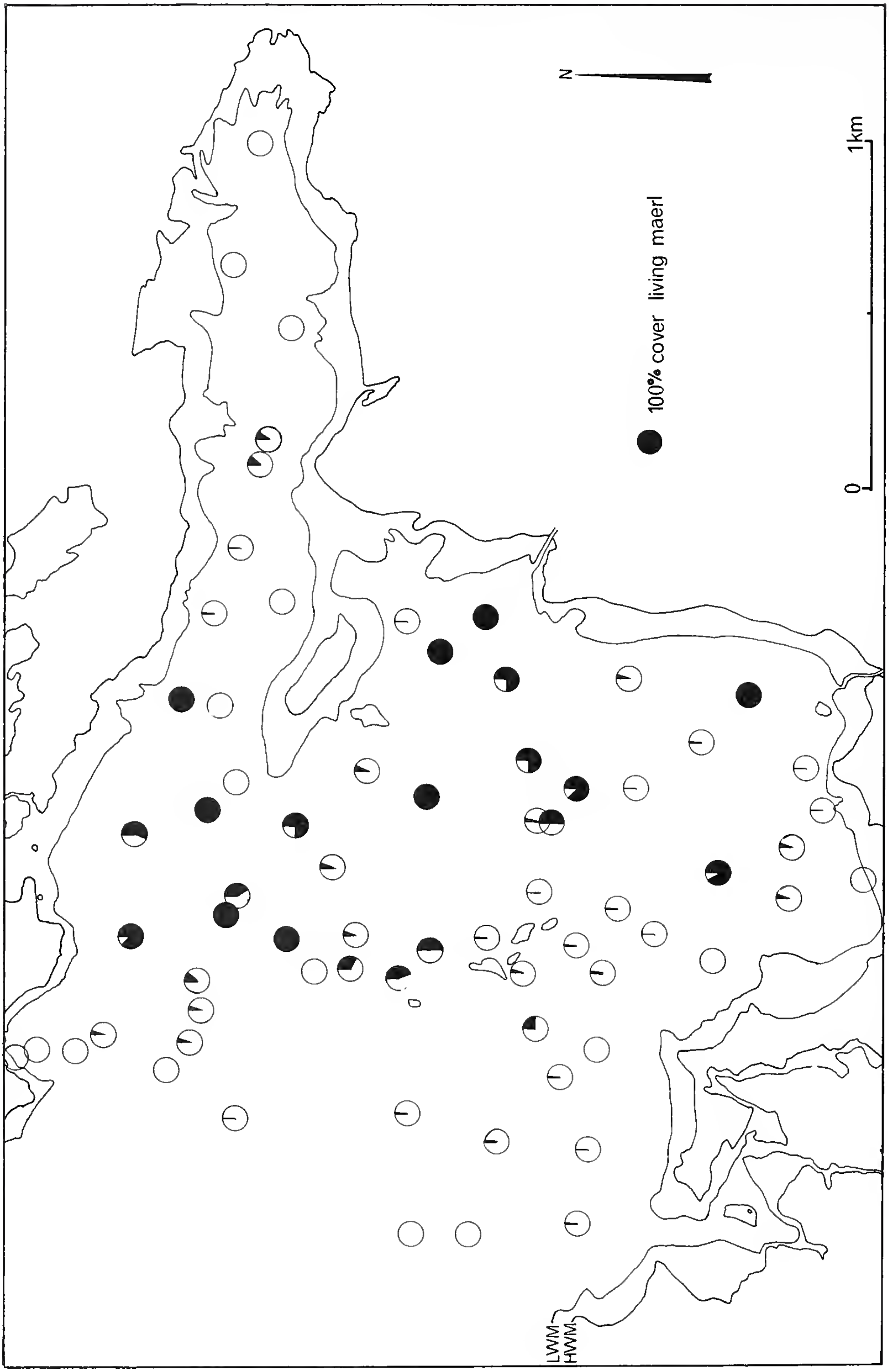
From the above, the Mannin platform can be divided into two hydraulic regions; one where waves are effective in moving bottom sediment and one where they are ineffective (text-fig. 7).

Text-figs. 6 and 7 show the presence and orientation of ripples and the distribution of the living maerl species. There is a marked negative correlation between these two parameters. Eighty-two per cent of those stations with more than 50% maerl do not have ripples. This suggests an inverse relationship between the oscillating bottom currents and the algal thallus and this is supported by observations made whilst diving that the growing apical tips are abraded when the algae are rolled on the seabed (Pl. 53, fig. 15). Thus the currents are possibly prohibiting growth.

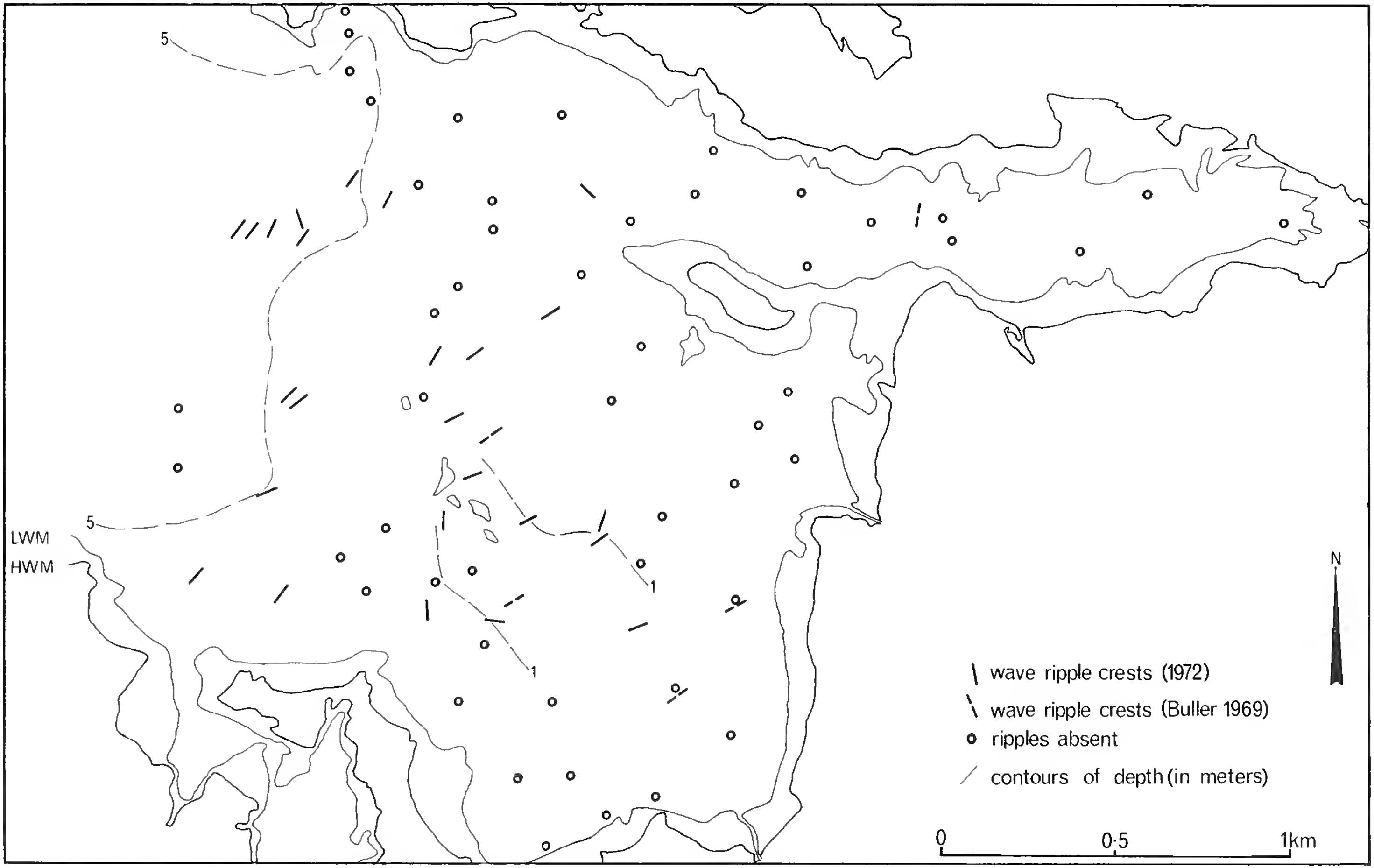
Conclusions

From the above discussion it can be seen that there is an over-all depth restriction on the algae. I believe this to be primarily due to the light penetration of the bay waters. The only two parameters which vary with depth are temperature and light. The variation in temperature is very small (2 °C. over 20 m) in the bay due to its well-circulated waters. The summer temperatures recorded within the whole of the bay correspond to those given for maximum growth rates by Adey and McKibbin (1970). Light is therefore the only parameter which varies significantly with depth and it is therefore considered to be primarily responsible for the depth distribution of the maerl species in Mannin Bay.

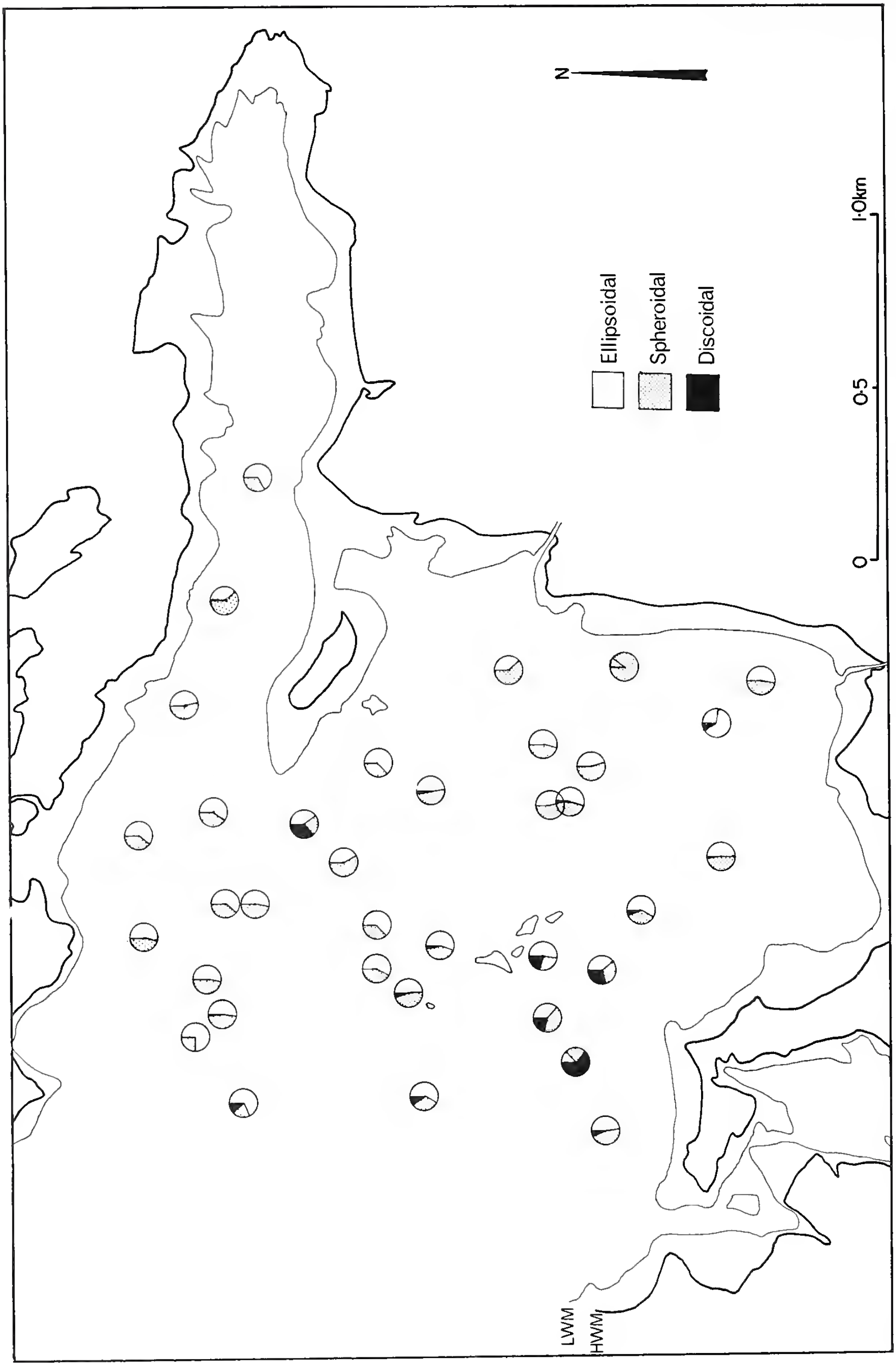
Within this depth range the distribution is limited in two ways. Firstly, in sheltered quiet creeks the algae are buried by mud which is stabilized by epiphytic filamentous



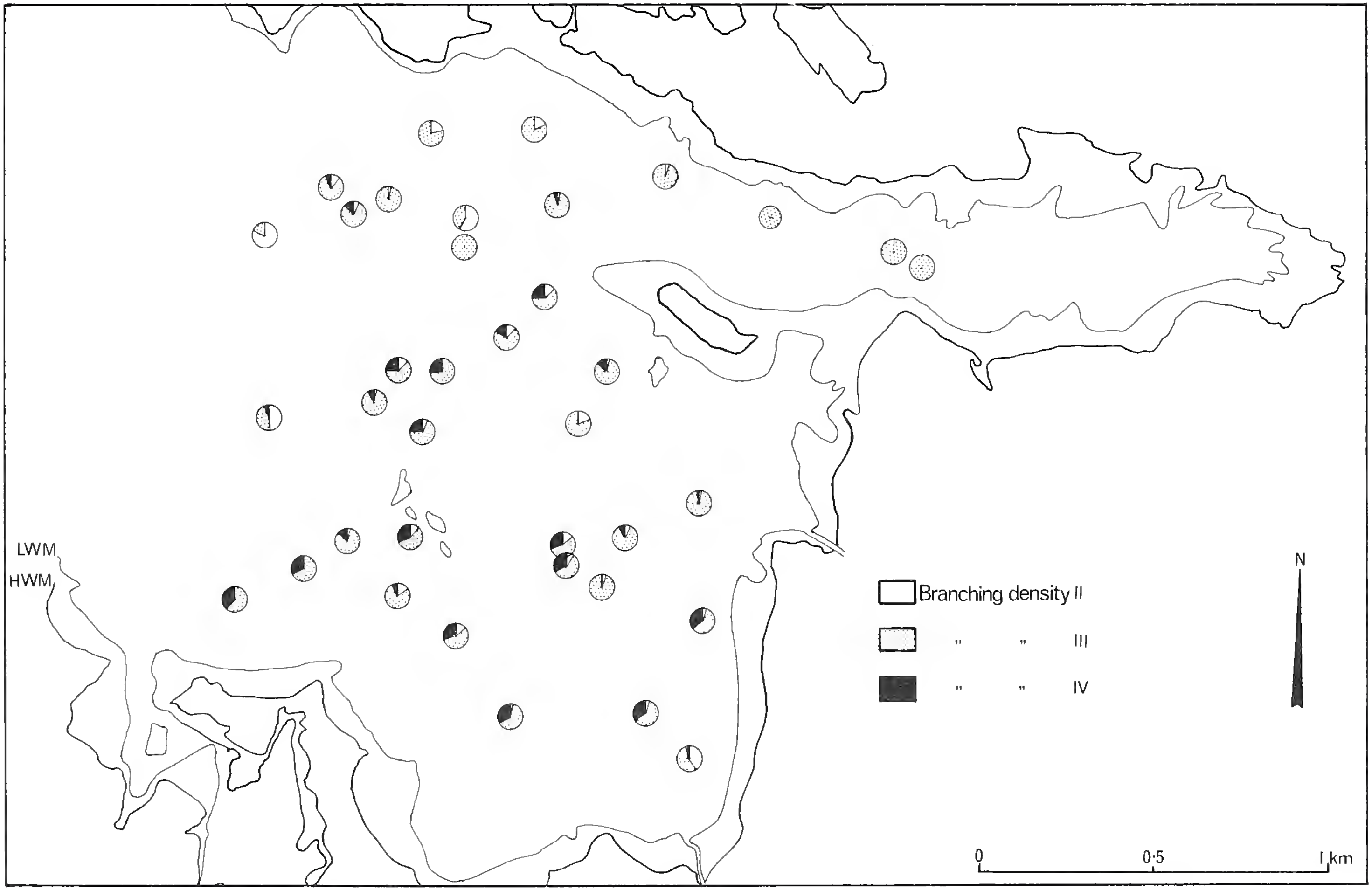
TEXT-FIG. 6. Distribution of living maerl as estimated from 50 × 50 cm quadrats.



TEXT-FIG. 7. Distribution and orientation of wave ripples in *Lithothamnium* facies, Mannin Bay.



TEXT-FIG. 8. Distribution of shape classes of thalli of *Lithothamnium corallioides*, Mannin Bay.



TEXT-FIG. 9. Distribution of branching density of classes of thalli of *Lithothamnium corallioides*, Mannin Bay.

algae. Secondly, growth is controlled by the action of wave currents. This agrees with the conclusions of Adey and Adey 1973.

In Mannin Bay, *L. corallioides* is the dominant free-living calcareous alga, *P. calcareum* occurs as a smaller percentage of the total cover and at fewer stations. The relative abundance of these two species appears to be controlled by bottom currents. Whereas *L. corallioides* is ubiquitous but with more luxuriant growth in quieter waters *P. calcareum* occurs only in those areas of the bay where there are no ripples.

ANALYSIS AND DISTRIBUTION OF GROWTH FORMS

Variation of growth form

Both the maerl species show a parallel series of growth forms (text-fig. 10). This variation was first noticed and recorded by Foslie in 1894 and later by other authors including a detailed study by Cabioch (1966 and refs.). The growth forms shown in Plate 53, figs. 3–14 and text-fig. 10 illustrate those described by Cabioch and they are a continually varying morphological sequence. The value of the morphological groups is that they allow a fairly rapid and reproducible description of the varieties found. The nature and variability of the branching preclude the use of a relatively quick and accurate numerical analysis (but see below). However, one of the drawbacks is the use of form names to describe the variation in different species. If the same complex variation is found in other free-living corallines, as is apparent from the work of Bosellini and Ginsburg (1971) and Wray (1972), the use of separate form names for each variant of each species will add a large amount of new nomenclature into a subject which already has numerous taxonomic problems (for example, see Cabioch 1966). In addition to this Cabioch's method does not fully describe the variation of the discoidal forms (*compressa* and *flabelligera*).

An alternative scheme is suggested for describing the variation found in the free-living corallines which incorporates the systems of Cabioch (1966) and Bosellini and Ginsburg (1971) by relating forms to shape and branching density classes. Three shape classes can be recognized: spheroidal, ellipsoidal, and discoidal. These may be quantified using the method of Sneed and Folk (1958) for describing pebble shape. The three shape classes (see below, p. 386) may be related to environmental

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EXPLANATION OF PLATE 53

Fig. 1. Longitudinal section of *Lithothamnium corallioides* illustrating growth layers and dichotomous branching (acetate peel), ×60.

Fig. 2. Longitudinal section of *Lithothamnium corallioides* illustrating intercalary branching (acetate peel), ×60.

Figs. 3–4. Stereopair *Lithothamnium corallioides* spheroidal II, ×2.

Figs. 5–6. Stereopair *Lithothamnium corallioides* spheroidal IV, ×2.

Figs. 7–8. Stereopair *Lithothamnium corallioides* ellipsoidal II, ×1·5.

Figs. 9–10. Stereopair *Lithothamnium corallioides* ellipsoidal IV, ×1·5

Figs. 11–12. Stereopair *Lithothamnium corallioides* discoidal II, ×2.

Figs. 13–14. Stereopair *Lithothamnium corallioides* discoidal IV, ×2.

Fig. 15. *Lithothamnium corallioides* showing healing over of previously dead apices, ×3.

Fig. 16. Longitudinal section of *Lithothamnium corallioides* illustrating regeneration of secondary hypothallus and perithallus over old abraded apex (SEM micrograph), ×114.


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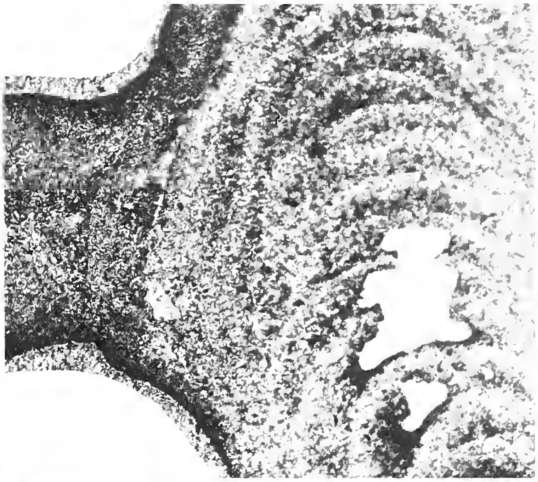
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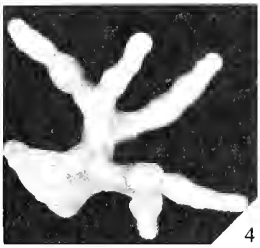
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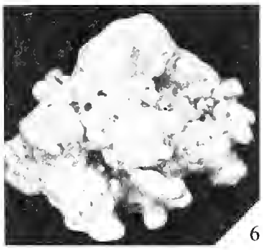
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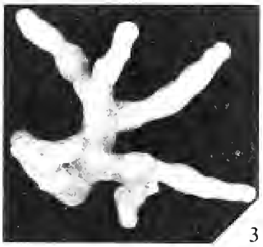
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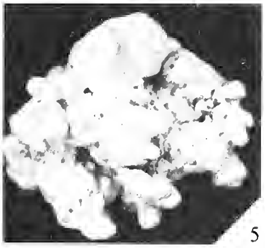
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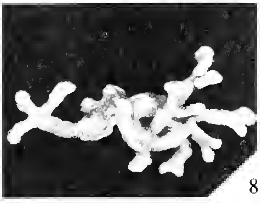
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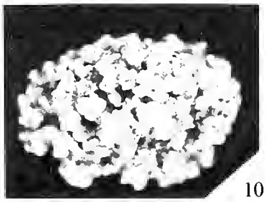
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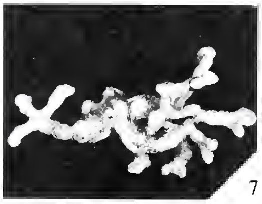
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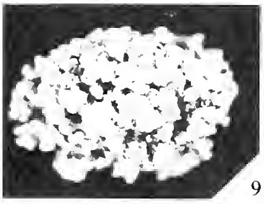
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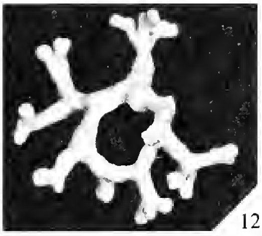
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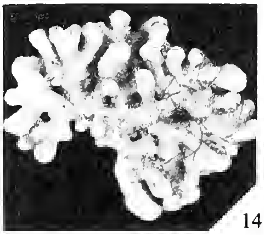
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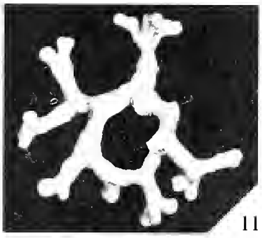
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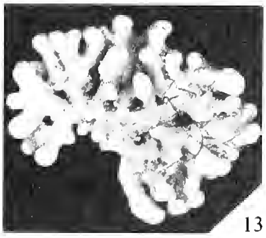
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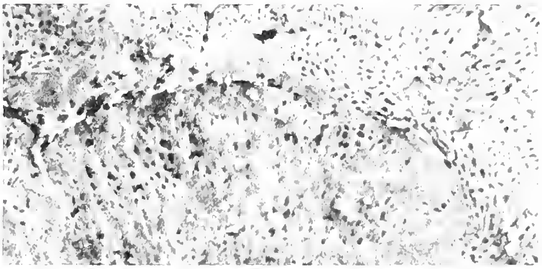
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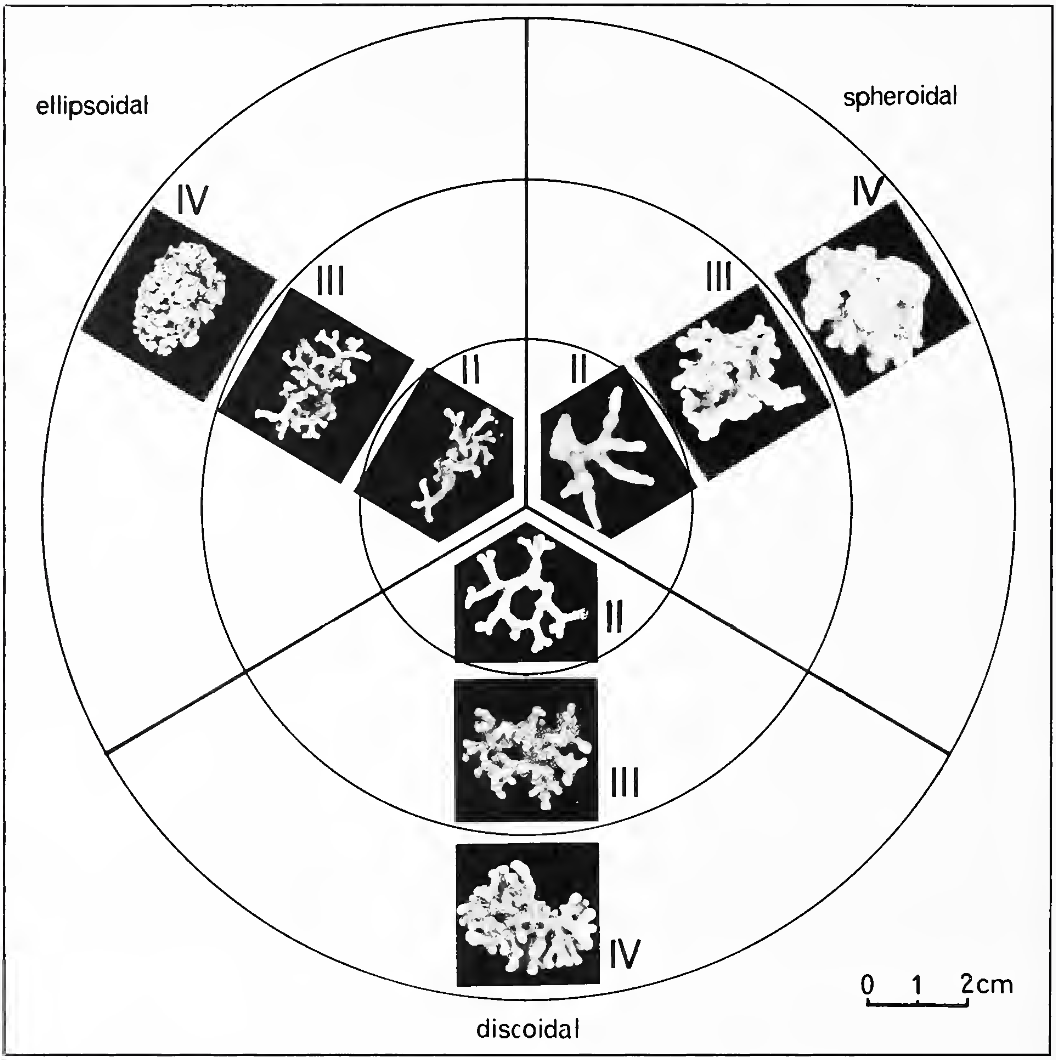
BOSENCE, coralline algae

parameters. Within these shape classes four groups of relative density of branching can be seen: (i) one single main branch, (ii) few branches, (iii) frequent branching, and (iv) dense and solid intergrown thallus (nodule or rhodolith). This may be quantified by dividing the volume (taking as the volume of an ellipsoid with the same long, intermediate, and short axes) into the dry weight.

For very simple and young thalli the designation of shape class may be difficult but the system allows all the growth forms to be expressed in a practical and simple way, e.g. *L. corallioides spheroidal II* (text-fig. 10). Stereopairs of the three shape classes and branching density classes are on Plate 53, figs. 3–14.



TEXT-FIG. 10. Diagram illustrating proposed classification of growth forms. Three shape classes are recognized: ellipsoidal, spheroidal, and discoidal. Within these shapes branching density varies from open branching (II) through frequent branching (III) to densely branched forms (IV).

The following list shows the relation between Cabioch's form names and the classification proposed here:

L. corallioides f. *subsimplex*	ellipsoidal I
L. corallioides f. *subvalida*	ellipsoidal II
L. corallioides f. *australis*	ellipsoidal III
L. corallioides f. *corallioides*	spheroidal III
L. corallioides f. *globosa*	spheroidal IV
L. corallioides f. *flabelligera*	discoidal III

An examination of the microstructure of the thallus was undertaken to investigate the nature of the branching. Cleaned specimens were embedded in a low-viscosity Araldite resin under vacuum and then longitudinal sections were ground through the branches and examined by taking acetate peels. An analysis of specimens of *L. corallioides* shows a close correlation between branching type and branching density:

	Branching type		
	Dichtomous	Intercalary	Uncertain
Branching density			
II and III (n = 28)	25 (90%)	none	3 (10%)
IV (n = 44)	17 (38·6%)	19 (43·2%)	8 (18·2%)

Therefore, whilst open branched forms (II and III) are characterized by dichotomous branching, densely branched forms are mainly formed by intercalary branching.

Distribution of growth forms

Lithothamnium corallioides. Text-figs. 8 and 9 show the distribution of thallus shape and branching density respectively. The commonest shapes for *L. corallioides* are spheroidal and ellipsoidal but these two growth forms show no obvious pattern of distribution. However, discoidal forms show a concentration in the southern part of the bay. The substrate in this area is a moderately well to poorly sorted fine to coarse sand (text-fig. 3) in contrast to the poorly sorted coarse algal substrate of the rest of the platform. The distribution of the branching density types illustrates a close correlation with exposure to wave-induced currents as shown by the presence of ripple marks (text-fig. 7). Seventy-two per cent of stations with more than 5% branching density IV are rippled. This is also noted from observations made whilst diving that the densely branched forms are found growing in the ripple troughs.

Phymatolithon calcareum. Ellipsoidal and spheroidal growth forms are again commonest as is branching density III but because of the limited distribution of the species no obvious patterns of distribution can be seen. The data has not, therefore, been presented.

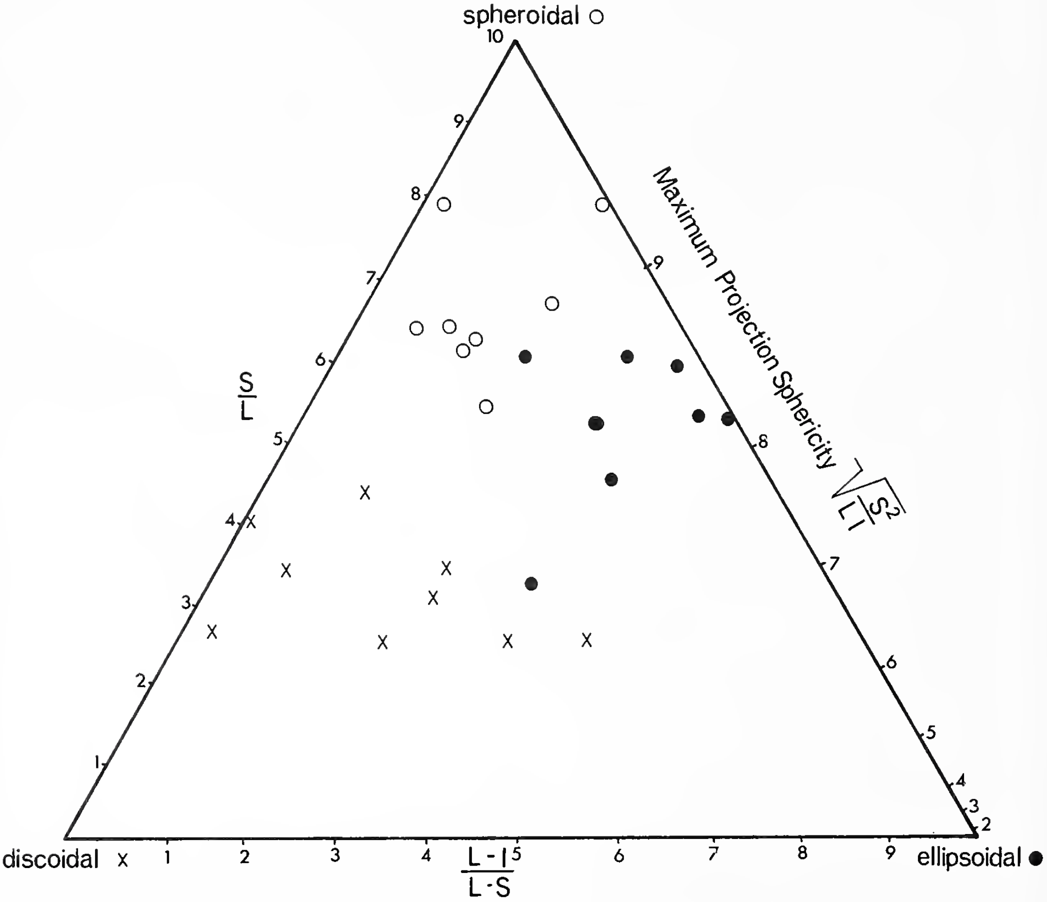
Conclusions

The variation in growth forms in Mannin Bay indicates that the branching of the thallus increases with increasing exposure. This complements the work of Bosellini and Ginsburg (1971) and possibly Wray (1972). A discussion of the possible relationship between growth form and exposure must include an investigation into the hydrodynamics of the thallus. In particular the effect branching density has on the velocity for transport of the plants as this appears to be related to exposure.

THE HYDRODYNAMICS OF *LITHOTHAMNIUM CORALLIOIDES*

Experiments were designed to investigate the effect of thallus shape and branching density on the velocity for transport by wave-induced oscillatory currents.

Cleaned specimens of *L. corallioides* were selected to represent the range of shapes and branching densities found in Mannin Bay (Table 1; text-fig. 11); each shape class having nine specimens chosen to be as close as possible the same size. This was measured as the volume of an ellipsoid enveloping the thallus with the same long, intermediate, and short axes (Table 1). Branching density was quantified (see above, p. 382), II having an average density of 0·21, III 0·37, and IV 0·97 gm/cc (Table 1).



TEXT-FIG. 11. Sphericity-form diagram (after Sneed and Folk 1958) with experimental specimens plotted as independent fields of spheroidal, ellipsoidal, and discoidal shape classes.

Methods

Because of the many variables involved in the entrainment of particles by bottom currents, shape and density included, it was necessary to eliminate as many irrelevant factors as possible. The same substrate was used for all of the experiments; a single layer of medium-grained sand stuck on to a metal plate which was then placed on the floor of the tank. This was designed to be rough enough to restrict sliding of the

TABLE 1. Measurements and results of wave-tank studies for *Lithothamnium corallioides*. (Nos. 1–9 spheroidal forms, 10–18 discoidal forms, and 19–27 ellipsoidal forms. A1–4 and B1–4 models.)

Specimen no.	Volume cc	Weight gm	Density gm/cc	Velocity for transport	
				Mean	Standard deviation
1	1·16	1·14	0·98	10·2	
2	1·00	0·37	0·37	12·4	3·6
3	0·46	0·08	0·17	11·4	1·3
4	0·84	0·61	0·73	9·8	
5	0·88	0·26	0·30	11·5	1·22
6	0·75	0·13	0·17	12·2	0·23
7	1·09	0·87	0·80	12·1	
8	1·53	0·38	0·25	11·5	1·02
9	1·30	0·14	0·11	12·0	2·13
10	0·71	0·63	0·88	12·6	
11	0·77	0·50	0·67	12·3	
12	0·76	0·26	0·34	18·9	
13	2·41	1·75	0·73	23·9	
14	1·41	0·59	0·42	16·2	3·1
15	1·32	0·21	0·16	11·0	
16	1·15	0·60	0·52	11·0	
17	1·65	0·83	0·51	26·4	
18	0·49	0·22	0·45	17·5	
19	2·07	1·72	0·83	9·1	0·29
20	1·56	0·50	0·32	8·3	0·73
21	2·30	0·54	0·23	8·3	0·73
22	2·45	2·37	0·97	8·2	
23	1·54	0·58	0·38	7·9	0·69
24	2·31	0·34	0·12	10·1	2·75
25	2·73	1·85	0·68	9·4	1·3
26	2·30	0·47	0·20	10·0	1·42
27	2·21	0·36	0·16	11·1	0·60
A1	14·1	1·06	0·07	19·2	0·64
A2	14·1	1·76	0·12	13·9	0·81
A3	14·1	2·30	0·16	12·4	0·72
A4	14·1	4·78	0·33	11·1	0·81
B1	14·1	1·16	0·08	15·1	1·69
B2	14·1	1·47	0·10	14·5	2·0
B3	14·1	2·26	0·16	11·4	1·15
B4	14·1	3·70	0·26	9·5	0·29

algae along the bottom (a mode of transport which has not been observed to occur in nature) but not rough enough to create turbulence which might interfere with the entrainment of the specimens. This was checked by observing the oscillation of fine particles in the water. Observations in Mannin Bay with dyes show that the waves produce currents around the thallus with an orbital motion with a slight shoreward drift. These conditions were obtained in the tank.

The wave tank used is at the Hydraulic Laboratory, Department of Civil Engineering, Imperial College, London. (Dimensions: 40 cm deep, 30 cm wide, and *c.* 6 m long.) Waves are generated by the vertical oscillation of a wedge-shaped piston against one end of the tank so that waves are only produced in one direction. The waves produced were varied in two ways: (*a*) by draining or filling the tank for variation of water depth, and (*b*) by varying the motor speed which drives the piston, this varies the wave height and celerity. The progressive waves so produced are absorbed by an artificial beach at the opposite end of the tank. For each of three runs of the experiments a specimen was placed on the substrate in varying positions and the motor speed increased until the specimen was transported by the oscillating currents. When transport occurred the amplitude and celerity of the waves was measured.

Because the values for transport are only relative and not comparable with those in nature (this is due to the density difference of the water and the algae not having their coating of uncalcified cells and mucilage) the true near-bed velocity was not required for these experiments. Therefore the relative velocities were obtained by measuring depth (d), celerity (c), and amplitude (A) of the waves and from wave theory for shallow-water waves the maximum velocity is obtained from $U_{max} = cA/d$.

There were two main stages to the experiments. Firstly, qualitative observations were required on how transport occurred in the varying growth forms and what the controlling factors were in terms of the shape of the algal thallus. These were recorded on 16-mm film. The second stage was quantitative and designed to establish the relative velocities for transport of the various shapes and branching densities of the thallus to compare with their known distribution in Mannin Bay.

Qualitative observations

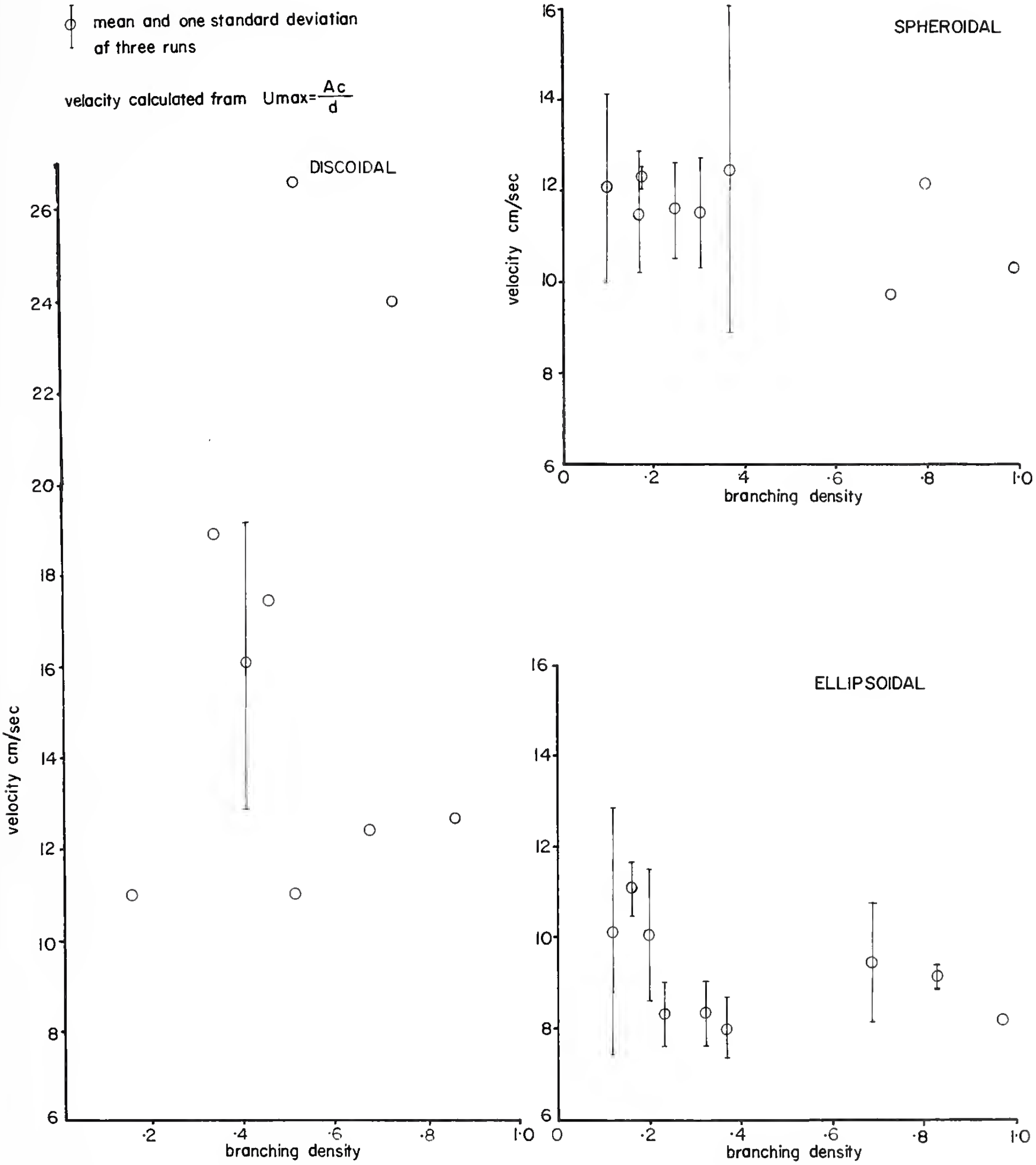
Spheroidal forms. The initial motion of the thallus with increasing current is determined by the support of the thallus on its branches which form a three- or four-point base. If these points are far apart (typical of open branched forms) a specimen will be more stable than one with the points closer together (typical of a densely branched form). This is because the centre of gravity of the thallus of the former will be lower and therefore the thallus will have to be pivoted higher to become unstable and brought into motion by the current. In addition, for a given volume the denser branched forms are perched higher than the open forms and this exposes them to the higher current values found away from the boundary layer. Associated with this is the observation that less densely branched forms appear to require greater velocities for transport than the more dense forms. This may be partly due to the increased surface area presented to the current and partly because the densely branched forms are less stable. The increased weight of these dense forms does not appear to be significant. The detail of the shape and pattern of branches on individual thalli can be seen to be very important in the initial rolling prior to transport.

Ellipsoidal forms. In addition to the points mentioned above which apply to all the growth forms, ellipsoidal forms appear to be transported at lower current velocities than spheroidal forms and at even lower velocities when placed with the long axis parallel to the wave crest than when placed normal to the wave crest. This would appear to be due to the increased surface area presented to the current.

Discoidal forms. These as would be expected from their shape, require greater velocities than both spheroidal and ellipsoidal forms for transport to occur. Those specimens which were slightly elongate orientate themselves with the long axis normal to the wave crest during motion.

Quantitative experiments

Each of the twenty-seven specimens (Table 1) was placed in three or sometimes two positions in the tank and the wave properties measured when the specimens were transported. This was defined as consistent turning induced by both forward- and backward-oscillating currents and a slight shoreward movement. The results are shown in text-fig. 12. They confirm that ellipsoidal forms are more easily transported than spheroidal forms and that discoidal forms are the most stable (cf. Sneed and Folk 1958). Also the graphs for spheroidal and ellipsoidal forms suggest a slight negative correlation (not statistically significant) between branching density and current speed for transport, indicating that the open branched forms may be the most stable.



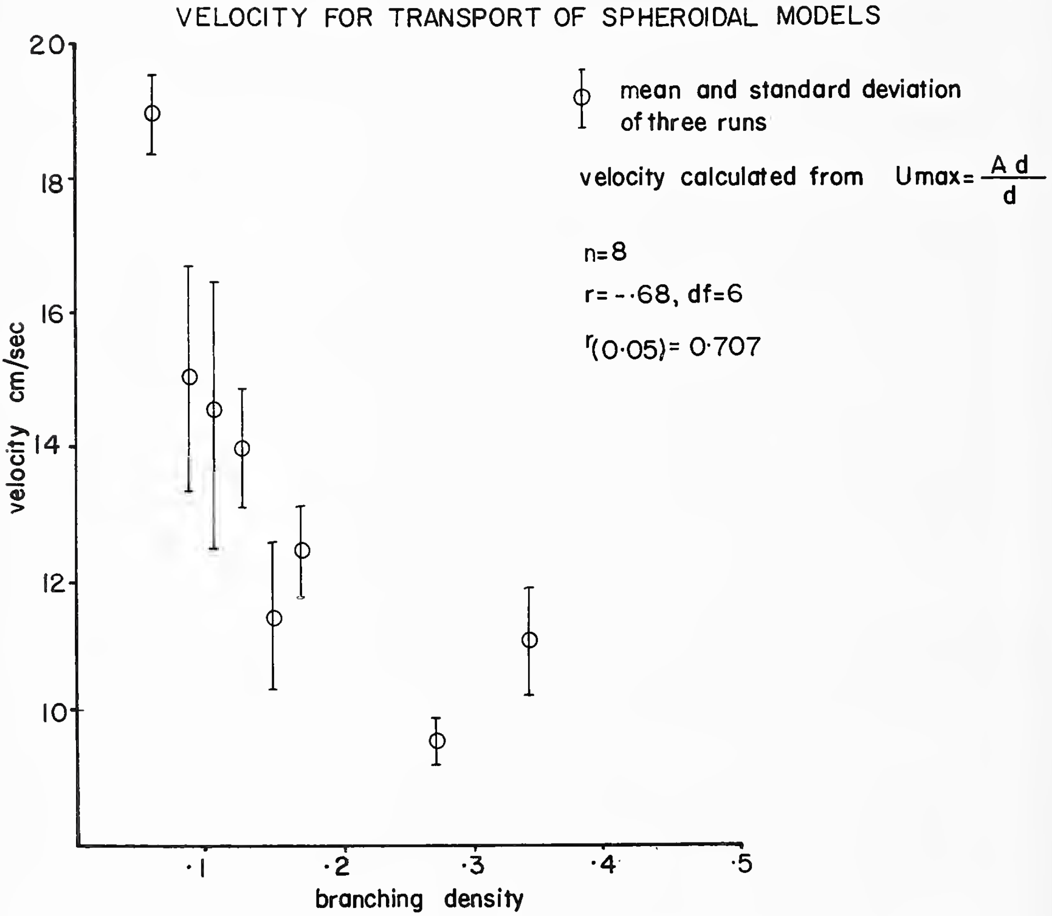
TEXT-FIG. 12. Graphs showing relationship between velocity for transport and branching density for *Lithothamnium corallioides*.

Discussion

The graphs illustrating the relationship between transport and branching density have plots which have a wider scatter. Close examination of individual specimens used indicates the unique shape of each specimen and a possible reason for its hydrodynamic behaviour. Small differences such as one slightly flattened surface are important in determining the velocity for transport. Therefore it is not always certain that one parameter of the thallus, such as branching density is always being compared, when other parameters such as size and shape are changing. There is a limitation in the material and exact replicates cannot be obtained (Table 1).

To ascertain whether branching density was more important than size and weight in limiting entrainment two series of models were constructed from plasticene which were the same size and shape (they were all spheres with the same diameter of 3 cm). The weights and branching densities of the models are shown in Table 1.

Text-fig. 13 shows the relationship between branching density and velocity of



TEXT-FIG. 13. Graph showing relation between velocity for transport and branching density for models of the maerl species.

transport and it indicates that an increase in branching density correlates with decreasing velocity for transport. The volume and shape of the models is the same but since the weight increases the branching density is the overriding factor. In conclusion, the densely branched forms are the most easily transported.

PREVIOUS WORK AND DISCUSSION

Previous work

It has been known for a long time that the Corallinaceae show great variation in growth form within one species (Johnson 1961, 1962; Cabioch 1966; Adey and Adey 1973) but this has only rarely been examined in the fossil record. This is partly due to the preoccupation with thallus microstructure and systematics by workers on ancient algae and, possibly, partly due to the fact that the studies made on specific variation in recent corallines have never been detailed and they lack any functional interpretation. To map or just record a correlation between growth form and an ecological factor does not prove that they are related but it leads to further detailed study and experiments.

Previous work on the distribution of growth forms of the free-living coralline algae is by Foslie (1894); Lemoine (1910); Jacquotte (1962); Cabioch (1966, 1969); Wray (1972); Bosellini and Ginsburg (1971); Adey and MacIntyre (1973); Adey and Adey (1973); Adey and McKibbin (1970).

Lemoine (1910) plotted the distribution of growth forms of *P. calcareum* form *squarrulosa* (= ellipsoidal III) and *crassa* (= spheroidal IV) for an area of southern Brittany. Form *squarrulosa* is found throughout the Isles de Brehat between depths of 4–18 m and in the outer regions of the Baie de Concarneau at depths of 10–15 m. This form is often found on muddy substrates where there is little current activity. She concludes that this ramifying form is adapted to life in a muddy environment. Form *crassa* is found in slightly shallower waters (3–15 m) to the north of the Isles de Brehat and south of the islands in the mouth of the Baie de Concarneau. She quotes from Foslie (1894) that the ball-like forms grow under the influence of strong currents.

Jacquotte (1962) working in the Mediterranean near Marseilles (Isles de Riou), studied the distribution of the two maerl species by diving, submersible, and drag sampling and found that *L. corallioides* was found on the upper part of a submarine slope on a clean gravel whereas *P. calcareum* was found at the deeper end of the slope on a muddy substrate. No variation of growth forms was noted.

Following Cabioch's (1966) systematic description of the growth forms of the maerl species she published (1969) a study on the beds of the Baie de Morlaix and concluded that the growth forms described were characteristic of different substrates (dredged samples). A coarse shell sand as found at Pighet, Terenez, and Primel contains all forms of *L. corallioides* var. *corallioides* (at Primel only *globosa* (spheroidal IV) is found), and with *P. calcareum* forms *calcarea* (ellipsoidal III), *squarrulosa* (spheroidal III), and *compressa* (discoidal III) are present. In contrast, a fine sand and mud substrate supports *L. corallioides* var. *minima* (not found in Mannin Bay). No information is given to explain the distribution of the growth forms or the two maerl species.

Bosellini and Ginsburg (1971) describe in detail the formation of rhodoliths from free-living coralline algae, e.g. *L. occidental* in Bermuda. The branching forms (spheroidal and ellipsoidal III and IV) grow in the relatively sheltered *Thallasia testudinum* beds and may be transported out of the beds into adjacent sand-floored channels where they are frequently turned. The apices of the branches grow laterally, in response to abrasion, and fuse with adjacent branches to form a laminar coating. Subsequent laminae of the same or different species of encrusting corallines produces a rhodolith.

Recently Wray (*in* Ginsburg *et al.* 1972) illustrated a hypothetical coralline alga showing an increase in branching density and thickness of branches from deep to shallow water. No evidence is given to support the illustration and the change is not explained in terms of the many physical and chemical factors which vary with depth.

The work of Adey and authors (op. cit.) contains general statements on the variation of growth form in the unattached corallines and emphasizes the need for further work in this field.

Distribution of the maerl species in Mannin Bay

Observations in Mannin Bay confirm the work of Jacquotte (1962) who showed that *P. calcareum* grows in hydrodynamically quieter areas than *L. corallioides*. This may be due to the fact that the thallus of *P. calcareum* being the larger of the two species would extend further away from the lower velocity boundary layer and into faster-flowing water which would make it easier to transport than the smaller thallus of *L. corallioides*. The work of Cabioch (1969), however, suggests another interpretation. Long-term observations (1897–1964) in the Baie de Morlaix show that the proportions of the two species has varied over time. Sometimes this change is related to a change in the sediment of the area but at other times the relative proportions of the two species has been interpreted to be due to the very infrequent reproduction by spores (up to 6 years) which is then followed by an increase for that species. Therefore, the relative abundance and distribution of these two species may be due to spore-bearing periods rather than a direct environmental factor. Adey (1973) has shown that spore production is related to low water temperatures in a crustose coralline.

Distribution of shape classes in Mannin Bay

The variation of thallus shape has not been explained by previous workers. In Mannin Bay the origin of the discoidal forms can be interpreted as a response to a moderately to poorly sorted sand substrate in a relatively strong current area. A thallus living on sand will be prevented from growing downwards into the sand by the lack of light and will therefore grow upwards and laterally. If the thallus is frequently turned only lateral growths will be possible. In the coarse maerl this will not apply as the thallus is well supported by its neighbours.

The spheroidal and ellipsoidal forms do not appear to be related to any regional environmental parameters and the development of either of these forms must involve the detail of its position with respect to the substrate and its nearest neighbours throughout its life. Shape will also be affected by breakage during transport and biological activity.

Distribution of branching density classes in Mannin Bay

Comparing the results from the wave-tank studies with the distribution of forms with different branching density in Mannin Bay (text-fig. 9) shows that the open branched forms are found in the quiet areas and the dense forms in the exposed areas. The most stable form is therefore found in the quiet areas whereas the most unstable form is found in the most exposed areas. This may be explained as follows: when the thallus is rolled the apical tips of the branches are observed (Pl. 53, fig. 15) to be abraded and perhaps broken, further growth is restricted from these apical meristems. If abrasion is not prolonged the apex may heal from lateral undamaged cells growing over the tip (Pl. 53, fig. 16). However, if abrasion continues, growth may occur by resumption of previously dormant cells to produce an intercalary meristem within the protection of the main branches. This process will lead to an increase in branching density and also to a stronger form, because the branches may join, which will resist breakage but will also be more easily entrained.

This ties in well with the relative proportions of the dichotomous branching and intercalary branching (above, p. 383) found in the different growth forms; the densely branched forms having intercalary branching and the open branched forms dichotomous branching. The frequency of intercalary branching in the dense forms would indicate that the dense forms are a passive response by the alga to wave motion.

To test this, experiments could be designed involving the removal of specimens from one environment to another and noting any possible change in growth form. However, the longevity of the plants (*c.* 10 years) precludes this approach.

PALAEONTOLOGICAL IMPLICATIONS AND COMPARISONS

Autochthonous carbonate facies are sometimes used as indicators of tropical or subtropical climates in ancient sediments. This paper describes a regional autochthonous carbonate facies from a cool temperate climatic belt. The banks occur in an area of regional biogenic carbonate deposition which is probably forming because of the lack of dilution by terrigenous clastics. The banks are restricted to depths of between 1 and 18 m and to relatively unexposed parts of the bay. Locally the banks are broken down to form an algal gravel.

The analysis of phenotypic variation in *L. corallioides* is based on mapping, thallus structure, and experimental work. Two sequences of variation are found which would enable palaeontologists to (*a*) make detailed interpretation of the palaeoenvironment, and (*b*) to beware of using these characters for taxonomic purposes. Shape is found to vary with substrate and possibly with exposure. Discoidal forms develop on an exposed medium-fine grained substrate whereas ellipsoidal forms grow on a coarse gravel substrate in quiet and exposed areas. Increase in branching density and lateral, as opposed to dichtomous, branching both increase with exposure to bottom currents.

The algal banks recorded in Mannin Bay are very similar in structure to the *Goniolithon* banks described by Turmel and Swanson (1972) and Ginsburg and James (1974) from Florida. Major differences are that these subtropical banks are zoned (e.g. Rodriguez Bank) and the free-living *Goniolithon* forms only one zone on the windward margin of the bank. The associated fauna and flora appears at first sight to be equally diverse in both temperate and subtropical banks but to confirm this detailed studies are still required from both areas. When deciding whether ancient banks are temperate or tropical the associated skeletal fauna and flora will be conclusive. The temperate banks lack corals (*Porites porites*) and the calcified Chlorophycean algae (*Halimeda*, *Penicillus*, *Rhipocephalus*). The distinction between the petrography and geochemistry of temperate and tropical carbonates is discussed by Buller (1969), Gunatilaka (1972), Lees and Buller (1972).

As far as I am aware no analogous pre-Pleistocene algal facies have been described. The most similar Palaeozoic examples are the Pennsylvanian algal limestones described by Wray 1964, 1972, and Frost 1975. These banks are constructed by species of *Archaeolithophyllum* which have a platey thallus. The banks are always associated with soft substrate areas and are occasionally intercalated with cross-bedded skeletal debris. The main difference between these limestones and the algal banks described in this paper is the shape of the algal thallus. However, the construction of the bank and the relationship of the bank to the skeletal debris facies is similar.

Algal limestones produced by closely related genera are common in the Tertiary sediments of the Mediterranean and Pacific regions (Elliott 1959 and refs., 1970; Lemoine 1939; Mastorelli 1967; Johnson 1961, 1962, 1963; Pedley 1974). However, most of the work is concerned with the systematics of the algae and very little information is given apart from the detailed internal morphology of the thallus. The preservation and limestone petrography is rarely explained.

An exception to this is Pedley's (1974) study from Malta where algal limestones are found in the Oligocene Lower Coralline Limestone Formation (*Lithothamnium* sp. and *Archaeolithothamnium* sp.) and Miocene Upper Coralline Limestone Formation (*Lithophyllum* cf. *destefonii* Samsonoff). The limestones are formed on a broad shelf with a 27 × 6 km bioherm facies stretching north–south through Malta and Gozo.

The bioherms which are up to 16 m thick are established on a sharp-topped horizon of the Blue Clay Formation. The algal thalli are roughly elliptical in shape with diameters varying from 50 to 100 mm. They are partially micritized and are preserved in a micrite matrix. Mud deposition was relatively rapid as the bioherm is built of alternating layers of micrite and algae. The mud is thought to have been stabilized by marine grass. Surrounding the bioherms are beds composed of transported algal debris. Associated with the bioherms is an abundant fauna with representatives of the same ecological groups as those found in Mannin Bay with the addition of infaunal echinoids in the micrite interbeds.

In many respects these bioherms and algal debris facies are analogous to the recent deposits of the platform in Mannin Bay. However, the coral and foraminifera species indicate that the limestones were formed in a tropical to subtropical climate and they may turn out to have more in common with the *Goniolithon* banks of Florida Bay.

CONCLUSIONS

Algal sediments are forming within an area of regional temperate carbonate deposition with associated biogenic carbonate facies. The sea-water is normal marine with water temperatures varying from 5 °C. in winter to 15 °C. in summer.

The unattached corallines are found at depths from extreme low-water spring tides to 16 m. However, prolific growth is only found between depths of 1 and 8 m.

The algal sediments are composed of autochthonous algal banks surrounded by an algal debris facies. The growing banks have a positive relief of up to 30 cm and cover areas measured in thousands of square metres. They support a diverse fauna in comparison with the surrounding algal debris facies.

The distribution of the maerl species is discussed with respect to the salinity, pH, Eh, calcium and magnesium ion concentration, temperature, light, and exposure of the bay waters. It is concluded that there is an over-all depth restriction controlled by light penetration and within this zone growth is restricted by exposure to wave currents. The algal banks are therefore found in the quieter areas of the bay.

The life cycles, morphology, and mode of branching of the two corallines is described. Branching can occur in two ways. Either through apical dichotomy or by resumption of previously dormant cells to form a lateral branch.

The two species show a parallel series of phenotypic morphological variation. A scheme is suggested for describing the variation found in the free-living corallines. Three shape classes are recognized: spheroidal, ellipsoidal, and discoidal. Within each shape class four groups of relative density of branching can be seen. These vary from open branched forms through frequently branched thalli to closely branched solid thalli or rhodoliths.

A study of the microstructure of the thallus shows that open branched forms are characterized by dichotomous branching and densely branched forms by intercalary branching.

The distribution of the shape and branching density classes is mapped. The commonest shapes are spheroidal and ellipsoidal forms which show no obvious pattern of distribution. Discoidal forms, however, are found on fine- to medium-grained substrates in the relatively exposed parts of the bay. The distribution of the densely branched forms is found to be closely correlated with exposure to bottom currents.

A study is made of the hydrodynamics of the thallus of *Lithothamnium corallioides* using a wave tank. The results show that ellipsoidal forms are more easily transported than spheroidal forms and that discoidal forms are the most stable. The open branched forms are more stable than the densely branched forms.

From the analysis of the distribution and hydrodynamics of the growth forms of the two species their occurrence in Mannin Bay is discussed. Discoidal forms develop as a response to frequent turning on a fine- to medium-grained substrate where downward growth is prohibited. Spheroidal and ellipsoidal forms do not appear to be related to any regional environmental parameters. Branching density is positively correlated with exposure. Therefore, the most easily transported forms are found in the most exposed areas and the stable forms in the quieter areas. This is explained through the analysis of branching of the thallus; following apical abrasion after transport it is suggested that the thallus undergoes lateral branching. If this continues a densely branched solid thallus or rhodolith is formed. With little or no transport in the quieter areas of the bay, the thallus undergoes dichotomous branching.

The palaeontological implications of the work are discussed and comparisons made with recent subtropical algal banks, Tertiary algal banks, and Pennsylvanian algal banks.

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FISH TRAILS FROM THE EARLY PERMIAN OF SOUTH AFRICA

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ABSTRACT. In the lower Karroo Dwyka and Ecca Series there are widespread trace fossils which can be attributed with reasonable confidence to fish. Each trail is composed of a bilaterally symmetrical set of up to nine distinct waves. The waves in a set share a common wavelength and direction of travel, but they vary in form and amplitude. The marginal pair of waves has the lowest amplitude; this pair was apparently left by the pectoral fins. Pelvic appendages appear to have been responsible for the remaining paired wave(s). The unpaired wave has the greatest amplitude and was probably produced by the caudal fin. A new ichnogenus is erected to contain these trails. It is divided into three ichnospecies on the basis of increasing complexity: *Undichna bina*, *U. simplicitas*, and *U. insolentia*.

THE early Permian in South Africa is represented by the lower Karroo Dwyka and Ecca Series (see Anderson, J. M. 1973, Chart 35). The Dwyka Series consists essentially of glacial diamictites; the succeeding Ecca Series is predominantly argillaceous (see Haughton 1969). These two litho-units are diachronous. The fish trails are preserved in isolated glacial lake deposits in the Dwyka Series and in various finely laminated sequences in the more extensive Ecca basin.

Haughton (1925) first reported the 'peculiar parallel sinuous lines' from the Ecca Series. He suggested then that they could be markings made by ventral spines of a fish armed after the fashion of *Acanthodes*. One of these trails was illustrated by Abel (1935, fig. 161). He held amphibians responsible. The Dwyka Series examples were introduced by Plumstead (1970, pl. XI) and discussed by Anderson (1970), who favoured the piscean interpretation.

SEVEN FISH-TRAIL LOCALITIES IN THE GREAT KARROO BASIN

The first two localities described are in Dwyka limnoglacial deposits at opposite ends of the Great Karroo basin. The other five localities are in the Ecca Series: two are from the southern 'turbidite' facies, two are from the quiet-water facies towards the centre of the basin (see Ryan 1967*b*), and the last, also from the centre of the basin, is in the transition zone between the Ecca Series and the overlying Beaufort Series, which is rich in tetrapod remains. Refer to text-fig. 1.

1. *Swart Umfolozi* (lat. 27° 57′ 6″ S., long. 31° 10′ 48″ E.)

Swart Umfolozi is the type locality of the arthropod trackway *Umfolozia sinuosa* Savage, 1971. It is also the only glacial deposit that has yielded well-preserved fish trails (text-fig. 2). Fish trails account for less than 5% of the trails at the locality. However, a good collection of them has been obtained as they could be selected from the vast amount of material made available by commercial quarrying operations.

The quarry, no longer worked, is on the southern bank of the Thongwane (Hloyan) River, in the north-eastern corner of the farm Rooipoort 565, about 45 km south-east of Vryheid.

The varves in which the fish trails are preserved are approximately 200 m from the top of the glacial sequence. They are underlain by a massive diamictite which includes some local fluvioglacial elements. The diamictite directly overlying the varves is shaly and bedded for about 6 m before becoming massive.

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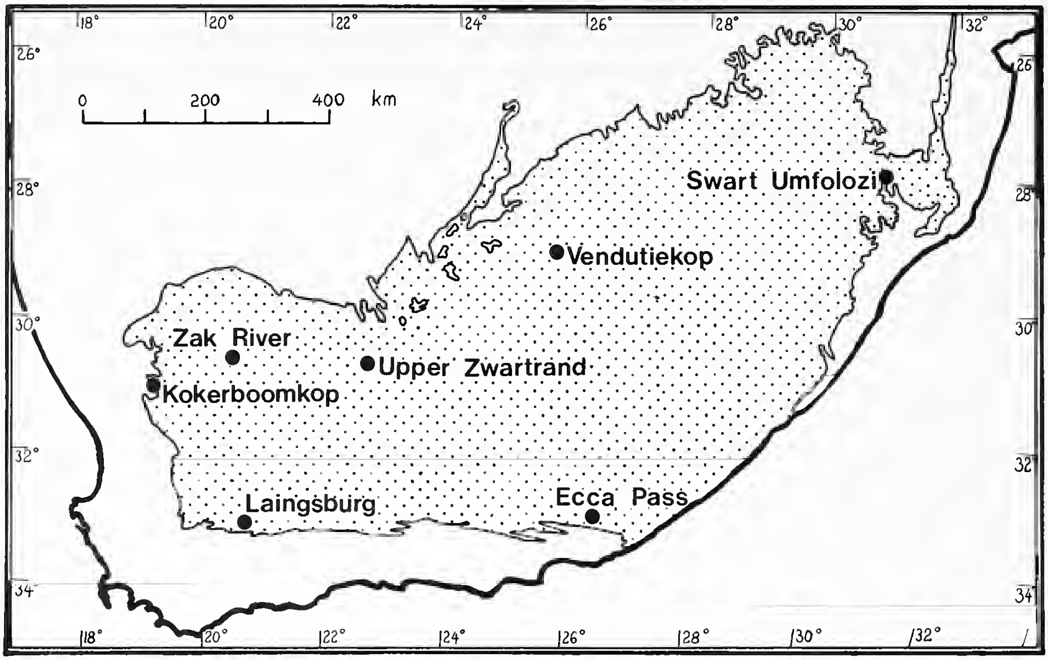


TEXT-FIG. 1. Sketch map of South Africa showing the present extent of the lower Karroo strata in the Great Karroo basin (stippled) and the general positions of the *Undichna* fish-trail localities described in this article.

Individual varves range between a few to 20 mm in thickness. The contact between the pale silty 'summer' portion of a varve and the dark carbonaceous fine-grained 'winter' portion is usually sharp. The fish trails and arthropod trackways are preserved in the carbonaceous partings, less than 1 mm thick. Dropped pebbles and grit are frequent in some units.

2. *Kokerboomkop* (lat. 31° 07′ S., long. 19° 16′ 30″ E.)

This locality is west of Kokerboomkop hill on the farm Potkley Clv. Q. 24-31, about 33 km north-north-east of Nieuwoudtville.

The single fish trail from Kokerboomkop is from a flagstone horizon which has also yielded arthropod trackways and turbidity-current scour structures (Anderson, in press). Individual flagstones are a few millimetres to 15 cm thick. They occupy approximately 1 m within a thick sequence of otherwise massive diamictite. The horizon is approximately 100 m below the advent of widespread lamination preceding the final disappearance of direct glacial deposition in the area.

3. *Laingsburg* (lat. 33° 11′ 30″ S., long. 20° 50′ E.)

Cuttings along the national road both east and west of Laingsburg transect the steeply dipping Karroo deposits almost perpendicular to strike, so bedding plane exposures are infrequent. The largest productive surface is north of the road, 2 km west of the Buffels River bridge on the outskirts of the town.

Theron (1967) logged in detail the lower Ecca Stages exposed in the cuttings. He recognized a vertical transition up the section from distal turbidity current deposits to proximal. Intrasediment horizontal burrows are common, but surfaces with arthropod trackways and associated fish and gastropod trails are rare.

4. *Ecca Pass* (lat. 33° 11′ S., long. 26° 37′ E.)

Ecca Pass, on the main road between Fort Beaufort and Grahamstown, is one of the Ecca Series localities mentioned by Haughton (1925) (Pl. 54, fig. 1). Fish trails and arthropod trackways still can be found *in situ* in the cuttings there but they are extremely scarce. Marginally more success is enjoyed further east along the national road between Grahamstown and King William's Town, 6 km south-west of the bridge over the Great Fish River.

Greywackes, shales, and flagstones are present. As at Laingsburg, this is a turbidite succession (Lock 1973). Intrasediment burrows are common. Fish trails are preserved occasionally on partings between flagstone layers. Arthropod trackways are not necessarily also represented.

5. *Upper Zwartrand* (lat. 30° 45′ S., long. 22° 31′ E.)

The farm Upper Zwartrand V.W. Q. 1-24 is about 45 km north-east of Carnarvon. Outcrops of central Ecca facies flagstones, intruded by dolerite, are fairly good along the Uintjiesleegte River.

The river bed is usually dry. It is littered with loose slabs of flagstone, often lavishly inscribed with pairs of parallel sinusoidal waves (Pl. 54, fig. 2). No trackways are preserved, and intrasediment burrows are rare.

6. *Zak River* (lat. 31° 01′ 24″ S., long. 20° 17′ E.)

The South African Museum, Cape Town, has a fine collection of fish trails, arthropod trackways, and other trace fossils from Zak River. Flagstone has been quarried commercially at the locality since the turn of the century.

The quarries are on the farm Brasse Fontein 371, Clv. Q. 13B-51, about 58 km south of Brandvlei. They exploit a 2-m thickness of yellow, somewhat silty, flagstones over a wide area. Individual units, frequently with subsidiary laminations, are usually less than 4 cm thick. A dolerite sill outcrops approximately 6 m stratigraphically above the flagstones.

7. *Vendutiekop* (lat. 29° 43′ 54″ S., long. 25° 37′ 24″ E.)

At Vendutiekop the fish trails (Pl. 54, figs. 3, 4) are not associated with *Umfolozia*-style arthropod trackways as is the case elsewhere, instead there are limulid trackways (Anderson, 1975). This distinction has both environmental and interpretational implications (see below).

The farm Vendutiekop 120 is about 19 km east of Jagersfontein. The flagstones bearing the trace fossils are being quarried in the bed of a tributary to the Kromellenboogspruit stream.

There are 2 m of light grey fine-grained flagstones. Beaufort Series type sandstone outcrops in the vicinity less than 30 m stratigraphically above the flagstones, but it could not be established whether similar sandstone occurs below as well. The 1:1 000 000 geological map (1970) indicates that the site falls within the Beaufort Series. However, as the map was based on reconnaissance mapping (Ryan 1967*a*) and as the two characteristic lithologies (Ecca shale/Beaufort sandstone) interfinger, the boundary must be regarded as somewhat arbitrarily defined at present (Haughton 1969, p. 358). The lithofacies of the trail-bearing horizon is of the Ecca type.

SYSTEMATIC PALAEONTOLOGY

Fish leave a variety of traces: see Richter 1930, Wachs 1930, Häntzschel 1935, Abel 1935, Linck 1938, Fiege 1951, van Dijk 1959, Fliri *et al.* 1970, 1971, Anderson 1970, Stanley 1971, Cook 1971, and Nicholson 1971.

Anything without a particular name is awkward to discuss and apt to be overlooked. This is a minor problem where there is only a single occurrence; the problem is greater where the occurrence is widespread. It is for this reason that the lower Karroo fish trails need to be systematically defined.

As the Zoological Code (1964) provides little specific guidance, a binomial nomenclature is employed in the sense of the Botanical 'form' nomenclature (1972, Articles 3, 59). It is a classification based on the morphologies of the trace fossils themselves (Sarjeant and Kennedy 1973). As such, the connotation of the 'ichno-genera' and '-species' is necessarily different from that of phylogenetic genera and species. None the less, because the Karroo fish trails do reveal something of the anatomy of the animals responsible, there is a phylogenetic element in their classification.

The following abbreviations for repositories are used herein:

Bernard Price Institute for Palaeontological Research, Johannesburg	B.P.I.P.R.
Geological Survey, Pretoria	G.S.P.
Natal University Geology Departments in Durban and Pietermaritzburg	N.U.
South African Museum, Cape Town	S.A.M.

Unless otherwise stated, museum specimen numbers refer to B.P.I.P.R. material.

In Anderson (1970) photographs 1–8 are of B.P.I.P.R. specimens S.U./K.D. 25, 23, 29, 33, 1, 5, 26, and 2 respectively.

Phylum CHORDATA
Subphylum VERTEBRATA
Class PISCES
Ichnogenus UNDICHNA nov.

Type species. Undichna simplicitas sp. nov.

Definition. The genus includes those trace fossils comprising a set of distinct, horizontal waves with a common wavelength and direction of travel. Most of the waves are paired, and a set is more or less bilaterally symmetrical. There may be as many as nine waves in a set. Frequently there are only two. Occasionally only one wave is preserved. The waves are impressions on epichnial surfaces (and mould ridges on hypichnial surfaces).

Derivation of name. Unda -ae f. (Latin) = wave + ichna.

Comparison. Where there is more than one wave present, certainly where there is more than two, there does not appear to be another ichnogenus with which *Undichna* readily may be confused (see Häntzschel 1962). If none but isolated waves are encountered at a locality, and especially where these are sinusoidal, identification as *Undichna* is unwarranted (cf. ichnogenus *Cochlichnus* Hitchcock, 1858).

Material examined in this study

(*a*) B.P.I.P.R. material selected at various localities: Kb./K.D. 1–3 (1 trail); S.U./K.D. 1–134 (at least 32 trails); B.R./K.E. 1–4 (several trails); Bb./K.E. 1–8 (5 trails, silicone rubber moulds); E.P./K.E. 1–10 (several poor trails); Lb./K.E. 1–45 (several trails); U.Z./K.E. 1–8 (several long trails); Vd./K.E. 1–16 (a few trails); Z.R./K.E. 1–29 (1 trail).

(*b*) N.U. material from Swart Umfolozi (several good trails) uncatalogued except for Savage's (1971) figured specimens.

(*c*) Dr. D. E. van Dijk, Zoology Department, Pietermaritzburg, private collection.

(*d*) S.A.M. specimens 11333–11335 from Ecca Pass (1 good trail); 3535–3551, 3584–3591, 11598–11617, 11680–11688, and nine other specimens from Zak River (about 10 good trails).

(*e*) G.S.P. specimens I 1–64 from a locality in the southern Ecca facies (1 poor trail).

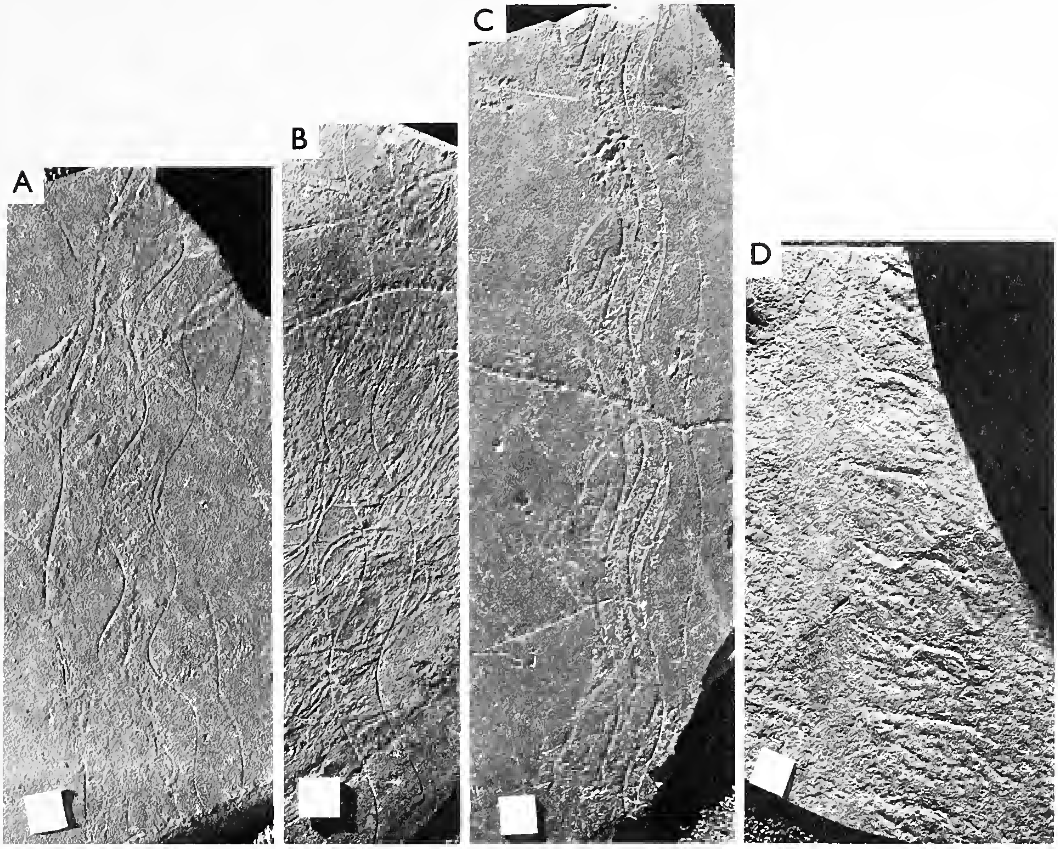
Undichna simplicitas nov.

Plate 54, figs. 3–4; text-fig. 2A, D

1970 undesignated fish trails, Anderson, pl. 1, figs. 2, 4.
1972 undesignated trails of eel-shaped animals, Warren, figs. 2–3.

Definition. In this species there are two sets of paired waves and one unpaired wave in a complete set.

The paired waves with members furthest apart have a lower amplitude than the



TEXT-FIG. 2. *Undichna* fish trails from the Swart Umfolozi fresh-water glacial locality (×0·5—the white scale is 1 cm^2). A, S.U./K.D. 4, holotype of *U. simplicitas* nov. showing the two marginal scolloped waves made by the pectoral fins, the two sinusoidal waves made by the pelvic fins, and the vague disturbance caused by the caudal fin. This disturbance partly obscured both the pectoral and pelvic wave on the left side. It is not possible to determine the direction of movement because the caudal wave is not cleanly incised (cf. Anderson 1970, pl. I) and there are no extensions on the scolloped waves. B, S.U./K.D. 8, *U. bina* nov. which consists of two sinusoidal waves in phase. C, S.U./K.D. 6, *U. insolentia* nov. paratype with three pairs of sinusoidal waves almost in phase: the wave-pair with members closest together has the highest amplitude and its phase position is slightly further towards the top of the photograph than the others, while the wave-pair with members the intermediate distance apart has the lowest amplitude and its phase position is slightly further towards the bottom of the photograph than the others. This indicates that the animal moved from the bottom to the top of the photograph as orientated. The scolloped wave on the right is complete, but that on the left is preserved only on the 'bottom' end of each scollop. The unpaired wave is represented by the asymmetrical sinusoidal area of disturbance obscuring parts of the paired sinusoidal waves on the left. D, S.U./K.D. 117, *U. simplicitas* nov. in which only the unpaired wave is recorded. Its form is unusual, consisting of a series of unconnected transverse sigmoids similar to those in the more complete trail illustrated in Anderson (1970, pl. II-7). In this case the fish probably was swimming at an angle with its head higher than its tail.

other waves in a set. These waves generally define the outer margins of the set, although the unpaired wave often does extend beyond. Each wave of this widest pair is usually scolloped with the convex side of the scollops directed outwards. The scollops often overlap, the major extensions off the general scolloped wave are consistently on the same ends of the scollops in both members. Sometimes these outer scolloped waves are composite, being composed of a number of concentric lines.

The other paired waves have a smaller distance between them than the scolloped pair, and usually are contained by them, but do tend to lie nearer to one of the limiting waves than to the other. Their form, ideally, is sinusoidal, but asymmetry increases with displacement from the central position. These waves rarely are broken. Their amplitude is always greater than that of the continuous scolloped waves (Anderson 1970, pl. I-4).

The unpaired wave has a median position when the sinusoidal waves are centrally placed and both scolloped waves are present; otherwise, it can extend well beyond the outer edge of one of the scolloped waves. It is seldom cleanly incised and its expression is very variable: it can take the form of a continuous sinusoidal wave (Pl. 54, fig. 3), a chain of linked (Anderson 1970, pl. I-3) or unconnected sigmoids (Pl. 54, fig. 4; text-fig. 2D), a series of aligned ladle-shaped scoops (1970, pl. I-2), or of opposing herring-bone-like flicks (1970, pl. I-1).

Any of the waves can be missing in one trail, but if the paired sinusoidal waves are represented at all, both members of the pair are usually present. At least one of the scolloped waves or the unpaired wave must be preserved to permit identification of this species.

Derivation of name. Simplicitas -atis f. (Latin) = straightforwardness.

Types. Type locality: Swart Umfolozi. Holotype: B.P.I.P.R. specimen S.U./K.D. 4 (text-fig. 2A). Paratypes: B.P.I.P.R. S.U./K.D. 10–12, 23, 25, 27, 29–34, 106, 118.

Museum specimens studied

B.P.I.P.R. material from Swart Umfolozi; Vd./K.E. 8, 11, 15.

Comparison

U. insolentia nov. has more than one pair of sinusoidal waves. *U. bina* nov. has only the pair of sinusoidal waves, no paired scolloped or unpaired waves.

Notes on the occurrence of the ichnospecies

In the South African early Permian glacial deposits, *U. simplicitas* has been observed only at Swart Umfolozi where a variety of forms are represented (text-fig. 2A; Anderson 1970, pl. I). It has been nominated type locality for the ichnospecies, but the possibility that the trails there may merely be incomplete *U. insolentia* cannot be refuted.

The presence of diatectic varves at Swart Umfolozi indicates that the water was fresh, because saline conditions would have inhibited their formation due to flocculation of the clay particles (cf. Flint 1971, p. 402; Pettijohn 1957, p. 163; Duff *et al.* 1967, p. 50). Conversely, the presence of limulid trackways at the only other *U. simplicitas* locality, Vendutiekop, suggests that conditions there were at least marginally marine (cf. Goldring and Seilacher 1971).

Two characteristic trails were collected from the upper Ecca Series at Vendutiekop. One of these (Pl. 54, fig. 3) is almost identical with a trail illustrated from the late Permian in Queensland, Australia (Warren 1972, fig. 2): each has a prominent high-amplitude sinusoidal wave flanked (on the left in both pictures) by a fainter sinusoidal wave with a lower amplitude. The two waves are attributed respectively to the caudal and one of the pectoral fins. The other fish trail from Vendutiekop (Pl. 54, fig. 4) is closely comparable with a rare form at Swart Umfolozi (text-fig. 2D).

Undichna bina nov.

Plate 54, fig. 2; text-fig. 2B

Definition. This trail consists of one pair of clear-cut lines a constant distance apart. These usually follow a sinusoidal or slightly asymmetrical sinusoidal course, but at times they may undulate in an irregular way; they are never altogether straight.

Derivation of name. Binus -a -um f. (Latin) = two.

Types. Type locality: Upper Zwartrand. Holotype: B.P.I.P.R. specimen U.Z./K.E. 8 (Pl. 54, fig. 2). Paratypes: B.P.I.P.R. U.Z./K.E. 1, 2, 4, 6, 7.

Museum specimens studied

B.P.I.P.R. material from Upper Zwartrand; S.U./K.D. 8, 13; B.R./K.E. 1–4; Bb./K.E. 8 (silicone rubber mould); E.P./K.E. 3–6, 8; Lb./K.E. 1, 5, 7, 8, 10–14, 18, 30, 32, 39, 43, 44B.

Comparison

U. simplicitas nov. has the pair of sinusoidal waves accompanied by at least one other wave.

Notes on the occurrence of the ichnospecies

U. bina is present in the early Permian of South Africa at one glacial locality (Swart Umfolozi) and it is common in the southern and central Ecca facies. At the type locality, Upper Zwartrand, the trails of various widths occur *en masse* (Pl. 54, fig. 2), accompanied occasionally by a *U. insolentia* wave set. Where there are also trackways, the *U. bina* trails are less frequent. At Laingsburg they may be unusually irregular in form.

Undichna insolentia nov.

Plate 54, fig. 1; text-fig. 2C

1935 ? amphibian swimming trail, Abel, fig. 161.
1970 undesignated fish trail, Plumstead, pl. XI.
1970 undesignated fish trails, Anderson, pl. II, fig. 5.

Definition. Like *U. simplicitas*, this species is more or less bilaterally symmetrical with a pair of low-amplitude scolloped waves at the outer limits and a very variable, high-amplitude, unpaired wave that may project beyond the scolloped margin. Instead of having only one pair of unbroken, generally sinusoidal waves as in *U. simplicitas* and *U. bina*, this species has two or three such pairs.

The distance between the members of each pair of sinusoidal waves is distinctive, as is the amplitude. The wave-pair with the lowest amplitude is the pair the intermediate distance apart; the wave-pair with the intermediate amplitude is the pair the greatest distance apart; the wave-pair with the greatest amplitude is the pair the closest together. The phase-positions of the waves are staggered according to amplitude: the phase of the pair an intermediate distance apart approaches that of the scolloped waves more nearly than does that of the other two pairs, while the phase of the closest pair is more like that of the unpaired wave, with the pair of greatest width in the intermediate position. The direction of declining amplitude of the three pairs of sinusoidal waves, which are only slightly out of phase, is the same as the major overlap extensions off the scolloped waves and also the longer arm of the asymmetrical markings in the unpaired wave.

The two or three pairs of sinusoidal waves are not necessarily accompanied by any of the other waves.

Derivation of name. Insolentia -ae f. (Latin) = unusual character, excess, extravagance.

Types. Type locality: Swart Umfolozi. Holotype: B.P.I.P.R. specimen S.U./K.D. 5 (Anderson 1970, pl. II-6; Plumstead 1970, pl. XI). Paratypes: B.P.I.P.R. S.U./K.D. 1–4, 24, 26, 130.

Museum specimens studied

(*a*) B.P.I.P.R. material from Swart Umfolozi; E.P./K.E. 9–10; Kb./K.D. 3; Bb./K.E. 1–3 (silicone rubber moulds); Lb./K.E. 41; Z.R./K.E. 29.

(*b*) S.A.M. 11334 from Ecca Pass; 3541, 11598, 11606, 11610–11612, 11616 from Zak River.

Comparison

U. simplicitas nov. has only one pair of sinusoidal waves with its pair of scolloped waves and variable unpaired wave; *U. insolentia* has three pairs of sinusoidal waves. *U. bina* nov. consists of only the one pair of sinusoidal waves.

Notes on the occurrence of the ichnospecies

Complete *U. insolentia* wave sets have been found only at Swart Umfolozi, the type locality (text-fig. 2C). Elsewhere in South African early Permian the ichnospecies is represented by only the three pairs of sinusoidal waves (Pl. 54, fig. 1) although there

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EXPLANATION OF PLATE 54

Undichna fish trails from non-glacial localities (the white scale is 1 cm^2).

Fig. 1. *Undichna insolentia* nov. S.A.M. 11334 Ecca Pass, ×0·5, in which only the three pairs of sinusoidal waves are preserved. As in text-fig. 2C the wave-pair with members closest together has the highest amplitude and its phase position is slightly further towards the top of the photograph than the others, while the wave-pair with members the intermediate distance apart has the lowest amplitude and its phase position is slightly further towards the bottom of the photograph than the others.

Fig. 2. *Undichna bina* nov. Holotype U.Z./K.E. 8 Upper Zwartrand, ×0·25, with numerous paired sinusoidal waves travelling in various directions. Each pair has a constant distance between its members and a generally constant wavelength and amplitude.

Figs. 3–5. Examples from the marginally marine Vendutiekop locality. 3, *Undichna simplicitas* nov. Vd./K.E. 15, ×0·25, in which the dominant wave (on the right) was made by the caudal fin, while the other fainter sinusoidal wave (on the left) was made by one of the pectoral fins. Compare Warren 1972, fig. 2. 4, *Undichna simplicitas* nov. Vd./K.E. 8, ×0·5, in which only the unpaired wave is recorded. Its form is similar to that of the glacial, non-marine example shown in text-fig. 2D. 5, ? *Undichna* sp. Vd./K.E. 9, ×0·5, in which two parallel sinusoidal waves with the same wavelength and different amplitudes are superimposed, crossing one another. This trail might have been left by a pair of mating limulid arthropods (see King 1975).

1

2

3

4

5

ANDERSON, Permian fish trails

is no such example from the type locality. There is a second glacial locality (Kokerboomkop), and these incomplete trails are common in the post-glacial Ecca deposits in the southern and central facies, where they usually occur with *U. bina* (Pl. 54, fig. 2).

The more widespread occurrence of the three pairs of sinusoidal waves unattended by the scolloped and unpaired members is a preservational feature. Goldring and Seilacher (1971) showed that for arthropod trackways the best-preserved tracks are likely to be those made slightly below the free sediment surface by the walking appendages penetrating the substrate and intersecting buried laminar interfaces. The same principle applies to the *Undichna* fish trails. In this case the propulsive thrust is not made against the sediment itself but against the water. It follows that the traces made by the active swimming organs are least likely to be preserved as undertracks. It has been demonstrated that the three pairs of spines responsible for the sinusoidal waves were rigid extensions not actively employed in propulsion (Anderson 1970, p. 641). However, in the complete trails it is the sinusoidal waves that are the most sharply incised, penetrating further into the sediment. Hence, these waves had the best preservation potential.

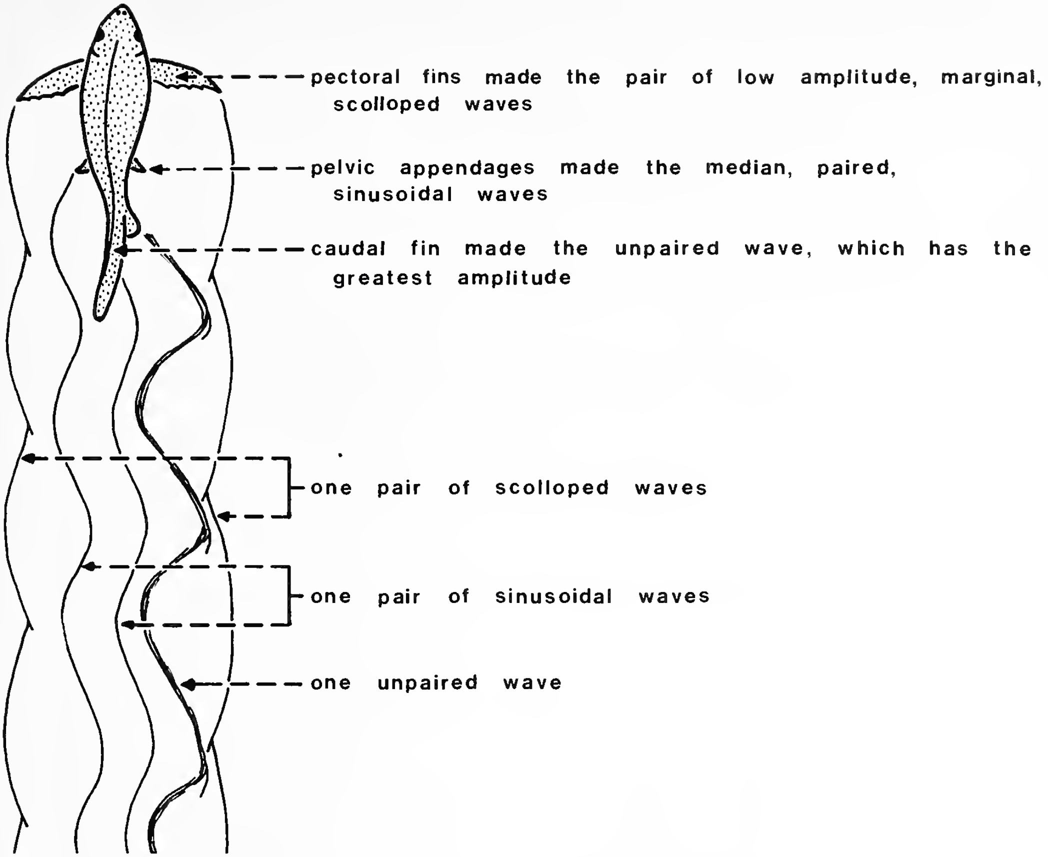
Although *U. bina* has been separated from *U. simplicitas* there is hardly justification for the creation of another ichnospecies similarly related to *U. insolentia*: the three pairs of sinusoidal waves certainly have a more exclusive explanation than the single pair.

COMMENTS ON THE IDENTITY OF THE CREATURES RESPONSIBLE FOR THE *UNDICHNA* TRAILS

The trace fossils have been attributed both to fish (Haughton 1925; Anderson 1970) and amphibians (Abel 1935; Warren 1972). Swimming animals of both classes could leave similar trails because the locomotion of a typical amphibian, even on land, and a typical fish are essentially similar: propulsion is chiefly by lateral undulation of the body. However, the piscean interpretation is favoured because of the absence of footprints or distinct points of pivot indicating that the creature was not attempting to walk in spite of maintaining contact with the substrate.

According to this reconstruction, the outermost paired scolloped waves with the lowest amplitude were left by the pectoral fins, the paired sinusoidal waves between them by the pelvic appendages, and the median unpaired markings with the largest amplitude by the caudal fin (text-fig. 3 and Anderson 1970, fig. 2). *U. simplicitas*, then, would have been made by classical Actinopterygiian fish, but the fish responsible for *U. insolentia* apparently has *three* pairs of pelvic appendages (1970, fig. 3), the nature of which is obscure. The direction of movement can be determined from the phase positioning of these three pairs of sinusoidal pelvic waves, which have slightly unequal characteristic amplitudes: the outer tips of the asymmetrical caudal flicks and the extensions on the scolloped pectoral waves point in the direction from which the animal moved (1970, p. 639).

The producers of the wave sets with fewer waves are less certain. *U. insolentia* examples may consist of only the three pairs of pelvic sinusoidal waves due to the ‘undertrack fallout’ effect described by Goldring and Seilacher (1971) (see above). By extension, *U. bina*, at least where the wave form is regular, can be regarded as the



TEXT-FIG. 3. Idealized sketch of a slightly asymmetrical *Undichna simplicitas* trail showing the proposed correlation between the component waves of the trail and fish fins (dorsal view).

trace of the pelvic fins of classical fish. Other interpretations doubtless can be applied (cf. Stanley 1971, fig. 7), but too little information generally is available to allow much extrapolation.

More problematic are those unnamed trails in which the two sinusoidal waves are not parallel, but out of phase and superimposed. Some such wave sets have been attributed to fish (Fliri *et al.* 1970, fig. 9; 1971, fig. 8), but King (1965) provided an ingenious explanation for other such which occur with limulid trackways. He reconstructed a Xiphosurid nuptial scene (1965, fig. 1): the sinusoidal wave with the lower amplitude apparently was left by the tail of the female, and the other wave by that of her mate. The same explanation could well apply to certain of the trails occurring with limulid trackways at Vendutiekop (Pl. 54, fig. 5), although they lack the lower amplitude discontinuous waves on either side of the crossed sinusoidal waves described by King (1965).

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SHORT COMMUNICATIONS

CRUSTACEAN ASSEMBLAGE FROM THE PENNSYLVANIAN LINTON VERTEBRATE BEDS OF OHIO

by FREDERICK R. SCHRAM

ABSTRACT. A pygocephalomorph and syncarids are recorded from the Upper Pennsylvanian fresh-water vertebrate beds near Linton, Ohio. This assemblage, characteristic of the Coal Measures, is known from several other localities throughout the Carboniferous.

THE Linton beds of Ohio represent a fresh-water, low coastal-plain deposit. They have long been noted for their well-preserved fauna of fish, amphibians, and reptiles (e.g. Baird 1964; Romer 1930, 1963; Steen 1931). The fossils occur in a highly pyritic, black shale and are Upper Pennsylvanian in age (Westphalian D). In over one hundred years of collecting, no invertebrates have previously been identified from these beds.

Dr. Richard Lund, Adelphi University, New York, referred some material to me for examination of poorly preserved eumalacostracan crustaceans, now deposited in the Field Museum of Natural History, Chicago. Specimen P 32075 is a pygocephalomorph displaying the ventral thoracic and abdominal sternites, along with some traces of thoracic appendages. Since the tail fan and carapace are absent, it is impossible to establish the genus of this specimen. Several other specimens (P 32076–P 32081) are highly pyritized compressions of syncarids. These also are too poorly preserved to identify, although vague outlines of body segments, appendages, and tail fan are visible. This is by no means the first discovery of an association between pygocephalomorph peracarids and syncarids in such beds. Such an assemblage has been found in the Middle Pennsylvanian (Westphalian C) Braidwood fauna of Illinois (Richardson and Johnson 1970); there the pygocephalomorph, *Anthracaris gracilis*, is associated with the palaeocaridacean syncarids, *Palaeocaris typus* and *Acanthotelson stimpsoni*. All through the British Westphalian Coal Measures there is a pygocephalomorph, *Pygocephalus cooperi*, associated with the syncarids *Palaeocaris retractata*, *Pleurocaris annulata*, and occasionally *Praeanaspides praecursor*. In addition to these Upper Carboniferous localities, the Viséan Pumpherston Shell bed (Caruthers 1927) has the pygocephalomorph, *Tealliocaris woodwardi*, associated with a new syncarid (to be described elsewhere).

The pygocephalomorph–syncarid assemblage has thus been found in several different areas and from beds of several ages, but its specific membership is different in each case. It appears to be a characteristic, indigenous element of the Coal Measure faunas, which we should expect to find in fresh- to brackish-water faunas of that age.

[Palaeontology, Vol. 19, Part 2, 1976, pp. 411–412.]

This low coastal-plain assemblage seems to be a rather specialized aberrant fauna of low diversity, having only a scavenger/low-level carnivore (the pygocephalomorphs) and an array of detritus/algal feeders (the palaeocaridaceans). Both these groups became extinct in the Permian, leaving no direct descendants. The assemblage may have evolved from a near-shore marine fauna containing a greater diversity of feeding types. In this, the scavenger and detritus/algal feeders were present and were important, but filter feeders and rapacious carnivores were also present. This marine fauna was relatively stable through a long period of time with little gross species changes, and is exemplified in part by the Scottish Viséan Glencartholm Volcanic bed crustaceans (Peach and Horne 1903), the Montana Namurian Bear Gulch fauna (Melton 1970), and the Illinois Westphalian D Mazon Creek Essex fauna (Richardson and Johnson 1970).

It is unfortunate that the Linton material is not preserved well enough to determine whether its exact taxonomic affinities be with the British or Illinois Coal Measure assemblages.

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COMMENTS ON 'THE LOOP-DEVELOPMENT AND THE CLASSIFICATION OF TEREBRATELLACEAN BRACHIOPODS'

by GRAHAM F. ELLIOTT

DR. Joyce Richardson's (1975) study of patterns of loop-development in terebratellacean brachiopods is most welcome. Her review deals essentially with Caenozoic and Recent forms, chiefly from Australasia, but it has considerable implications for the Mesozoic faunas of Europe. In particular her new nomenclature for the phases of loop-development refers essentially to morphology and structure, and not to comparisons with adult loops as previously. Also very different significance and importance is assigned to certain elements of the loops than hitherto, and she evaluates this in detail. She indicates the occurrence of lacunae in some immature terebratellid loops, though they are still, in my experience, much more characteristic of laqueinid development.

Richardson rightly points out the close similarity in loop-development of the three families reviewed (Dallinidae, Laqueidae, and Terebratellidae) as compared with the very different loop-development seen in other families of the Terebratellacea, e.g. Kraussinidae, whatever the relationship of these other families to each other. Her text-fig. 3 indicates that some genera of the Laqueidae may even pass through the same series of phases as Terebratellidae (though the duration and importance of particular phases differs in the two). Even without adequately large studies on variation in loop-development within a single species, it does seem that the different forms of loop-development outlined are closer than previously regarded, and perhaps of less value for detailed taxonomy than previously supposed.

Of Mesozoic forms affected by this classification, Zeilleriidae as now constituted are in loop-development a composite group. Those studied whose loops are known to develop in connection with a septal pillar, e.g. the Jurassic *Zeilleria leckenbyi* (Davidson) (Baker 1972) appear to be probably early Laqueidae as now defined. Those where development, with ring and descending branches not dissimilar, takes place *without* a pillar, free of the dorsal valve floor, e.g. the Triassic *Z. bukowski* (Bittner) and a similar Liassic species (Dagis 1968) have similarity to this 'non-septal pillar' type of development, found in certain Palaeozoic genera (cf. the Carboniferous *Cryptacanthia*: Cooper 1957). Which of these two groups in the Mesozoic retains the name Zeilleriidae depends on the evaluation of the loop-development of the Liassic type species *Z. cornuta* (J. de C. Sowerby), if this character continues to be decisive in classification. The peculiar loop-development of the Jurassic *Hamptonina* is relevant to this. The study of Moore (1860), which antedated the pioneer studies on Recent genera (Friele 1875, 1877), showed a developmental series in *Hamptonina* involving different growth stages both free of the valve floor, and attached to a septal

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pillar. My restudy (Elliott 1950) was carried out both on Moore's original specimens and on fresh material from his original locality. It showed that *Hamptonina* had a laqueinid development ('dallinid' as then termed), with normal early axial and annular phases, but with a minority of abnormal individuals. From their shell-characters these were members of the same species, *H. buckmani* (Moore), but with delayed loop-development relative to shell size, and without a septal pillar, i.e. they showed the 'Palaeozoic' type of loop-development. I ascribed this to possible retarded development of the lophophore relative to size increase, and to appearance of the calcareous descending branches first, instead of the early septal pillar. Whatever the reason, the presence in one species of two such different modes of development, even, with one as an abnormality, is significant and reinforces Richardson's assimilation of the far closer patterns within the 'septal pillar' type of development. It is probable that the rapid achievement of a plectolophe, so providing the maximum length of ciliated cirrated lophophore margin which can be accommodated, has been essential in development, both individual and phyletic. This may be due, as suggested (Elliott 1948, 1953) to intraspecific competition, since the replacement through geological time of brachiopods by bivalve mollusca is a fact, irrespective of brachiopod intra-regressive evolution. The elaborate and conspicuous loops and loop-developments are a consequence of the different calcification in the genera concerned superimposed on lophophore development, and the different patterns are not in themselves directly significant. The case of *Terebratulina* (Jurassic–Recent), as mentioned by Baker (1972, p. 468) is a pointer to this. In this the short posterior annular loop with heavy anterior spiculation of the lophophore seems as functional as any long loop, and it is a most successful brachiopod, so far as this term can be applied within this declining group after the Palaeozoic.

The tendency in biological classification has been for ever-increasing exploration of detail to be reflected in progressively more elaborate taxonomy, followed by a secondary simplification reflecting detailed understanding of underlying principles and their relative importance. Dr. Richardson's paper indicates perhaps a turning-point for our knowledge of long-looped brachiopods.

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A REPLACEMENT NAME FOR *PAROTOSAURUS* JAEKEL (AMPHIBIA: LABYRINTHODONTIA)

by R. L. PATON

IN 1889 Fraas recognized two different genera of capitosaurid labyrinthodont amphibian. Those in which the otic notch was 'closed' (i.e. lay within the skull roof and was therefore completely surrounded by bone) he placed in a new genus *Cyclotosaurus*; these specimens were largely confined to Upper Triassic deposits. Those in which the otic notch was 'open' (i.e. lay on the edge of the skull roof and was therefore incomplete posteriorly), Fraas left in the genus *Capitosaurus*; these were all from the Lower or Middle Trias.

This simple picture became complicated when Jaekel (1922) pointed out that the holotype and only specimen of the type species of *Capitosaurus*, *C. arenaceus* Münster, 1836, was from the Upper Trias (of Benk, near Bayreuth) and also lacked the crucial, diagnostic, otic notch region. It is therefore what would today be called a *nomen vanum* (Simpson 1945). To this taxonomic problem, Jaekel suggested a solution which has since been universally accepted: the genus *Capitosaurus* was to be regarded as indeterminate, and this name was to be used only for the single species *C. arenaceus*, while all other species formerly included in the genus *Capitosaurus* were to be placed in a new genus, for which Jaekel suggested the name *Parotosaurus*. Jaekel (1922) designated *P. nasutus* (Meyer) as the type species of this genus, and Welles and Cosgriff (1965) chose as the lectotype of the species the first skull described and figured by Meyer (1858, p. 222, pl. 24). The horizon of the lectotype is Middle Bunter (Lower Trias) and it comes from a quarry in the Hauptbuntsandstein near Bernburg.

Unfortunately, it now appears that *Parotosaurus* had already been used by Boulenger in 1914 as the name of a scincid lizard. Though *Parotosaurus* Boulenger 1914 may be a junior synonym for another genus of lizard (Mittleman 1952; Romer 1956), it nevertheless retains precedence over *Parotosaurus* Jaekel 1922 (see Article 17 (1) of the International Code of Zoological Nomenclature, Stoll 1964), and a new name must be found for the genus of capitosaur.

It was felt that a suitable replacement name would be formed by retaining the ending *-otosaurus* and merely changing the prefix to indicate the relatively primitive condition of the otic notch. The name *Archotosaurus* has therefore been chosen to replace the now invalid *Parotosaurus*, the type species of the genus being *A. nasutus* (Meyer).

According to Article 40 of the International Code of Zoological Nomenclature, a family name is to be retained even if the nominal type genus is rejected as a junior synonym. As pointed out by Welles and Cosgriff (1965), an extension of this would

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lead to the retention of a family name even though the nominal type genus were a *nomen vanum*. The family containing the genera *Archotosaurus* and *Cyclotosaurus* can therefore retain the name Capitosauridae.

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